Network complexity of rubber plantations is lower than tropical forests for soil bacteria but not fungi

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Abstract:

Soil microbial communities play a crucial role in ecosystem functioning. Past research has examined the effects of forest conversion on soil microbial composition and diversity, but it remains unknown how networks within these communities respond to forest conversion, including when tropical rainforests are replaced with rubber plantations. Microbial networks are viewed as critical indicators of soil health and quality. They consist of two parts: nodes and edges. In this study, we used data from Illumina sequencing and metagenome shotgun sequencing to analyze bacterial and fungal community network structure in a large number of soil samples from tropical rainforests and rubber plantation sites in Hainan Island, China. Our results showed only 5-10% shared network edges (i.e., links between species A and B existing in both rubber plantations and rainforests) were observed in both bacterial and fungal communities, which indicates that forest conversion altered soil microbial network structure. The identity of keystone OTUs differed entirely between rubber plantation and rainforest sites, further underscoring the altered network structure. More edges and more negative correlations within the soil bacterial-fungal networks were observed in rubber plantation sites (dry season: 4,284 total edges, 844 negative; rainy season: 7,257 total, 1,744 negative) than in rainforest sites (dry season: 3,650 total, 149 negative; rainy season: 6,018 total, 489 negative), demonstrating that soil bacterial-fungal network structure was more complex and stable in rubber plantations than in rainforests. For bacteria, a larger number of network edges were observed among bacterial networks in samples from tropical rainforest than in samples from rubber plantations, indicating that rainforest bacterial networks were more complex than those from rubber plantations. However, soil fungal networks from rubber plantations showed more links, suggesting that forest conversion increased fungal network complexity. More edges of network and more links between species and functions were observed in the rainy season than in the dry season indicating that seasonal changes had a strong effect on network structure and function. Further analysis shows soil pH, potassium (AK), and total nitrogen (TN) had more links with species of some phyla. In conclusion, forest conversion results in an increase in soil pH, and a decrease in AK and TN, and these changes as well as seasonal variations had a great impact on soil microbial composition, network structure and function.

Keyword: Tropical rainforest, Rubber plantations, Networks, Soil microbial community, Forest conversion

1. Introduction

‘Soil microbiome’ refers to the enormous variety of microorganisms inhabiting the complex soil environment. It is highly diverse and comprises up to one quarter of Earth’s species (Wagg et al., 2019). Soil microbes play a critical role in the maintenance of soil quality and function, and they represent more than half of the biodiversity of terrestrial ecosystems (Philippot et al., 2013). A number of studies have investigated how the conversion of tropical forests to rubber plantations impacts soil microbial composition and diversity (Schneider et al., 2015; Kerfahi et al., 2016, Lan et al., 2017a; 2017b; 2017c; Lan et al., 2020a; 2020b; 2020c). Studies conducted in Indonesia (Schneider et al. 2015), Malaysia (Kerfahi et al. 2016) and South China (Lan et al. 2017a; Lan et al. 2017b; Lan et al. 2017c) have found significant differences between rubber plantations and tropical forests, specifically that the diversity of soil bacteria was higher in rubber plantations than in rainforest. Compared to primary forests, agricultural systems tend to have higher bacterial richness but lower fungal richness (Lan et al., 2017a; Cai et al., 2018; Tripathi et al., 2012; Kerfahi et al., 2016). Compared to Eucalyptus plantations, rubber plantations have been found to possess higher diversity of both bacteria and fungi (Ma et al., 2019). Song et al. (2019) reported that tropical forest conversion to rubber plantation results in reduced fungal microbial community network complexity. However, there are few studies on the impact of forest conversion on soil bacterial community network structure, nor on the drivers leading to changes in network structure.

The soil microbial network is viewed as a critical indicator of soil health and quality (Kuperman et al., 2014). Microbial networks consist of two parts: nodes and edges. Nodes indicate microbe types, generally OTUs or species, but can also indicate environmental variables of interest, such as soil pH. Edges (or links) indicate significant correlations between nodes. The number of links connected to a node is known as the node’s degree (Röttjers and Faust, 2018). Usually, the more links a network has, the more complex the community is. Similarly, the higher the degree of a node (OTU or species), the more important the species is to the network structure (Berry and Widder, 2014). In recent years, microbial network analysis has been used to identify keystone taxa (Banerjee et al., 2018) and provide comprehensive insight into the microbial community structure and assembly (Fuhrman, 2019). The complexity of network structure is understood by calculating the number of edges, while keystone species of the community are found by estimating the degree of each species. The stability of the microbial community is determined by calculating the ratio of positive and negative correlation of the network because a large proportion of positive correlations in a microbial community are thought to be unstable (Coyte et al., 2015).

Previous work has shown that agricultural intensification can reduce microbial network complexity (Banerjee et al., 2019). Logging alters soil fungal network in tropical rainforests, i.e., a better-organized fungal community in cut stands when compared with primary stands (Chen et al., 2019). Soil bacterial networks are less stable under drought than fungal networks (De Vries et al., 2018). While the exact drivers of microbial network structure still remain unknown. Previous work has shown that soil nutrients, such as soil phosphorus content, and soil pH, are the main drivers for the network structure for microbial communities (Banerjee et al., 2019). Seasonal variation also affects the network structure by changing the identity of keystone species in the community, given that a keystone species might be present only in a specific season or time period (Banerjee et al., 2018).

Hainan Island is home to a large area of tropical rainforest rich in biodiversity. It is a part of the Indian-Malay rainforest system at the northern edge of the world's rainforest distribution. However, rubber plantations now account for almost a quarter of the total extent of vegetated areas on Hainan Island (Lan et al., 2020a). Previous work on the island has shown that forest conversion from rainforest to rubber plantations can result in shifts in bacterial composition from the Proteobacteria to Chloroflexi, and fungal composition from Basidiomycota to Ascomycota (Lan et al., 2020a). Other research has shown microbial (including bacteria and fungi) diversity was higher in rainforest soils than in rubber plantation (Lan et al., 2020a). Therefore, we hypothesize the following: (1) the conversion of rainforest to rubber plantations results in changes in the dominant phyla of soil microbes, with concomitant changes in network structure and identity of keystone species. (2) Soil bacterial-fungal network structure is less complex but more stable in rubber plantation than in rainforest because high species diversity leads to complex network structure and unstable microbiome communities (Coyte et al., 2015). (3) Soil bacterial networks in rubber plantations are less complex than in rainforests because intensive cropping reduces the complexity of bacterial network, even as richness increases (Karimi et al., 2019). (4) Soil fungal network structure in rubber plantation sites is more complex than in the rainforest because organic farming showed a much more complex fungal network than conventional or no-tillage farm systems resulting from organic fertilizer and the return of litter to the field (Banerjee et al., 2019). By testing these hypotheses, we want to clarify the drivers and mechanisms of microbial community assembly that link forest conversion to differences in soil microbial network structure. This study will provide critical information for understanding and managing microbial communities in tropical forests of China and elsewhere.

2. Methods

2.1 Study site

This study was conducted on Hainan Island (18°10′–20°10′N and 108°37′–111°03′E), south China. The total area of Hainan Island is about 34,000 km^2 (Lopez et al., 2009). Hainan Island is the largest island within the Indo-Burma Biodiversity Hotspot of tropical Asia (Francisco-Ortega et al., 2010) and has a tropical monsoon climate. Hainan Island has a warm and humid climate all year round, with an average annual temperature of 22-26℃. Rainfall is abundant, ranging from 1,000 mm to 2,600 mm yearly, with an average annual precipitation of 1,639 mm. The rainy season occurs from May to October, with a total precipitation of about 1500 mm, accounting for

70-90% of the total annual precipitation. Only 10-30% of the total annual precipitation falls within the dry season, from November to April. The central part of Hainan Island is mountainous and contains old-growth tropical rainforests and monsoon forests. Rubber plantations are found on the plateaus surrounding the central mountainous zone.

2.2 Soil sampling

The tropical rainforests of Hainan are mainly distributed in Bangwangling, Diaoloshan, Wuzhishan, Yinggeling and Jianfengling. Therefore, we selected a tropical rainforest in each of these sites for our study objectives. There are about 530,000 hectares of rubber plantations on Hainan Island. Five rubber plantations were selected, one each in Wanning, Ledong, Danzhou, Haikou, Qiongzhong. These five rubber plantations are located in the east, south, west, north and middle of Hainan, respectively. (Figure S1). We selected 25-30 years old rubber trees (i.e., mature rubber plantations) for our study objectives. Latex harvest and fertilizer application are common management practices in rubber plantations. Usually, compound fertilizer (1-1.5 kg per tree) and organic fertilizers (20-25 kg per tree) were applied once or twice a year. More information on the study sites is provided in Table S1. Before soil sampling, we sterilized the soil drill with 75% alcohol. After the removal of the litter layer using a 5-cm diameter steel drill, top soil (0 to 20 cm) was collected, then homogenized and passed through a 2-mm mesh sieve. For each site, thirteen soil samples were collected, thus there were a total of 130 samples collected between the rubber plantation and tropical rainforest sites. Soil sampling was performed twice in 2018, once in January (dry season) and once in July (rainy season). There were thus a total of 260 soil samples (130 per forest type). Soil samples were divided into two parts. One was used to analyze soil water content, soil pH, total nitrogen, total phosphorus (TP), total potassium (TK), nitrate nitrogen (NN), ammonium nitrogen (AN), available phosphorus (AP), potassium (AK). Soil water content (%) was measured gravimetrically. Soil pH was measured in a soil/water suspension (1: 2.5, w/w) using a pH meter. TN was determined using a micro-Kjeldahl digestion followed by steam distillation. TP and TK were measured following digestion with NaOH. NN and AN were determined by steam distillation and indophenol-blue colorimetry, respectively. Soil samples were extracted with NaHCO3 and the extract was then used to measure available soil phosphorus AP via molybdate-blue colorimetry. To measure soil AK, soil was extracted with ammoniumacetate and then the extract was loaded onto an atomic absorption spectrometer with ascorbic acid as a reductant (Chen et al., 2019). Soil properties of the rubber plantation and rainforest sites are shown in Table S2. The other part of each soil sample was stored in ultra-low temperature (- 80 ℃) refrigerator for later DNA extraction.

2.3 DNA extraction and PCR amplification

Microbial DNA was extracted from 0.5 g of soil using E.Z.N.A.® Soil DNA Kits (Omega Bio-tek, Norcross, GA, U.S.) following the manufacturer’s protocol. The fungal ITS1 hypervariable region was amplified using the PCR primers ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3') (Adams et al., 2013). For bacteria and archaea, the V4 hypervariable region of the bacterial 16S rRNA gene was amplified using the PCR primers 515FmodF (5'-GTGYCAGCMGCCGCGGTAA-3') and 806RmodR (5'-GGACTACNVGGGTWTCTAAT-3') (Walters et al., 2016; Sampson et al., 2016). The PCR reactions were conducted using the following approach: an initial 3 min denaturation at 95°C, followed by 27 cycles of 30s at 95°C, 30s of annealing at 55°C, and 45s of elongation at 72°C, and a 10 min final extension at 72°C.

2.4 Illumina MiSeq sequencing

Amplicons were extracted from 2% agarose gels, purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, U.S.) and quantified using a QuantiFluor™ -ST Fluorometer (Promega, U.S.). Purified amplicons were pooled in an equimolar solution and then sequenced (paired-end, 2 × 250 bp) on an Illumina MiSeq platform according to standard protocols.

Metagenomic shotgun sequencing libraries were prepared and then sequenced by Majorbio, Inc. (Shanghai, China) using the Illumina HiSeq 2000 platform. The NR gene catalog was aligned against the Kyoto Encyclopedia of Genes and Genomes (KEGG) database using BLAST (Version 2.2.28+) and then functionally annotated using KOBAAS 2.0 according to previously described methods (Qin et al., 2010)

2.5 Bioinformatics and data analysis

Raw fastq files were demultiplexed and quality-filtered using QIIME (Caporaso et al., 2010) (version 1.17). Operational Taxonomic Units (OTUs) were clustered with a 97% similarity cut-off using UPARSE (Edgar, 2013), and chimeric sequences were identified and removed using UCHIME. Using the RDP Classifier, the phylogenetic affiliation of each 16S rRNA gene and ITS gene sequence was determined using a confidence threshold of 70% with the SILVA 16S rRNA database and UNITE database, respectively (Amato et al., 2013). For each site, the relative abundance of different taxa (Good, 1953) and the Shannon diversity index were calculated based on re-sampled sequence data using MOTHUR (Schloss et al., 2009). The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: SRP108394, SRP278296, SRP278319).

2.6 Statistical analysis

To make the co-occurrence network analyses simple, we only used the top 300 most abundant bacterial and fungal OTUs to analyze the network structure of the two forest types. These OTUs are roughly match the OTUs with a relative abundance greater than 0.05% (Jiao et al., 2016). Four networks, representing each habitat during each sampling period (rainforest and rubber plantations in the dry and rainy seasons), were constructed with 65 samples each. We also performed the bacterial-fungal community network analysis to investigate soil microbial network complexity of each of the four.

Interactions consisted of Spearman's rank correlations. Co-occurrence networks were constructed using only significant correlations of $\rho > 0.6$ ($P < 0.01$) (Barberan et al. 2012), because this cutoff includes a range of interactions strengths (De Vries et al., 2018). The networks were then visualized in R using the *igraph* package. To reveal the distribution pattern of correlation coefficients, the frequency of the coefficients of $\rho > 0.3$ ($P < 0.01$) were plotted. The Network Analyzer tool in Cytoscape (version 3.4.0) was used to calculate network topology parameters including number of nodes, edges, degree, betweenness, closeness. The number of shared edges and unique edges as well as keystone OTUs were calculated to evaluate whether the network structure changed. We defined a shared network edge as the link (edge) between species A and species B not only existing in rubber plantation network, but also in rainforest network. Similarly, a unique edge was a link that only existing in either rubber plantations or rainforests. The number of shared edges and unique edges were calculated using *igraph* and visualized using Venn diagrams. Keystone OTUs are known to be important for ecosystem structure and function and were selected on the basis of high network degree, high closeness centrality, and low betweenness centrality as defined by Berry and Widder (2014). To evaluate the proportional influence of each phylum on bacterial and fungal network structure, node degrees of each phylum were calculated and bar plots were created. Correlation coefficients between species and functions were calculated based on metagenomics data. Here we used the top 50 most abundant species and top 50 KEGG functions (pathway level 3). Then the species and function correlation network was constructed on the Major bio cloud platform (https://cloud.majorbio.com/). To reveal the relationship between microbial taxa and environment variables, two-way correlation networks were also constructed on the Major bio cloud platform. The topological role of each node in a network was assessed by the Z_i and P_i values, where Z_i represents the connectivity ofnode *i* within a module, and P_i measures the degree of node *i* 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 ($Z_i < 2.5$

and $P_i < 0.62$), connectors ($P_i > 0.62$), module hubs ($Z_i > 2.5$) and network hubs ($Z_i > 2.5$ and $P_i > 0.62$). The Z_i and P_i values were calculated using GIANT package of Cytoscape. The Z_i-P_i plot was created with *ggplot2* in R.

3. Results

3.1 Bacterial and fungal networks

Our results showed that the bacterial-fungal community network were more complex in rubber plantations (4,284 edges in the dry season, 7,257 in the rainy season) than in primary forests (3,650 in the dry season, 6,507 in the rainy season), and more complex during the rainy season than the dry season (Figure 1). Most nodes of bacterial networks (Figure 2) and fungal networks (Figure 3) varied with forest type in both the dry and rainy seasons. For bacterial networks, there were 2,559 and 2,501 edges in the forests and rubber plantations, resepectively, in the dry season, but these two networks only shared 262 edges, accounting for only about 10% the total edges (Figure 4A-B). Similarly, these networks only shared 519 edges during the rainy season. For fungal networks, there were only 4 and 5 shared edges (i.e., no more than 5% of the total edges) in the dry and rainy seasons, respectively (Figure 4C-D).

The number of edges of bacterial and fungal networks were almost equivalent during the dry season. However, in the rainy season, there were more edges in the rainforest bacterial network than in the rubber plantation network (Table 1 & Figure 4B). For the network structure of the fungal community, more edges were observed in rubber plantations in the rainy season (Table 1 & Figure 4D). Similarly, there were no significant differences in either the degree of the bacterial and fungal networks between the tropical rainforest sites and rubber plantations in the dry season (Figure 5A, C). In the rainy season, rainforest sites had a higher bacterial network degree, while rubber plantations showed higher fungal network degree (Figure 5B, D). For bacterial networks, more nodes (OTUs) with high degree (rubber plantation had 2 nodes with degree greater than 75, rainforest had 8 such nodes) were observed in the rainforest during the rainy season (Figure S2B). For fungal networks, 15 nodes of higher degree (degree greater than 25) were observed in rubber plantations, however, only 7 such nodes existed for rainforest sites (Figure S2D). These results indicate that the fungal network structure in the rubber plantations was more complex than for tropical rainforests during the rainy season, but that the reverse was true for bacteria.

When considering the ratio of positive to negative correlation coefficients, the bacterial-fungal community network revealed that rubber plantations (844 edges in dry season, 1744 edges in rainy season) have more negative links than rainforest (149 edges in dry season, 489 edges in rainy season) indicating that the network of rubber plantation was more stable than that of the rainforests (Figure 1). More correlations (greater than 0.3, $P < 0.01$) were also calculated to investigate the ratio of positive to negative correlation and the results showed that negative correlations between bacterial and fungal OTUs in the rubber plantations were consistently stronger than in the tropical rainforests in both dry season and rainy season (Figure 6).

3.2 Keystone taxa

Module hubs and network hubs have been commonly identified as keystone taxa in networks. However, for both the bacterial and fungal communities, neither tropical rainforest nor rubber plantation networks possessed module hubs and network hubs (Figure S3-S4). The keystone taxa of bacteria were very different between rubber plantations and tropical rainforest sites in both the dry and rainy seasons. For bacteria, there were more keystone taxa in tropical rainforest sites than in the rubber plantations in both the dry and rainy seasons, indicating that the tropical rainforest networks had higher complexity. We found that some groups of Acidobacteria are keystone taxa in tropical rainforest sites but disappeared after forest conversion. There were more Actinobacteria in rubber plantations than in tropical rainforest sites (Table S3).

For fungi, more keystone taxa were observed in rubber plantations than in tropical rainforest sites during both the dry and rainy seasons, indicating that the rubber plantation networks were more complex. Most keystone taxa belong to Ascomycota, suggesting that member of this group are very important for network structure. In addition to forest conversion, seasonal changes also affect the keystone taxa of the fungal community network. There were more Basidiomycota OTUs in the dry season, but more Ascomycota in rainy season (Table S4).

3.3 Drivers of microbial composition and network structure

Two-way correlation network analysis of the 300 most abundant OTUs and environmental variables revealed elevation (106 degree), AK (104), and soil pH (86) were the main drivers of bacterial community composition (Figure S5A). For fungi, elevation had the highest degree (61), followed by AK (51) (Figure S5B). The relationship between OTU abundance and soil pH revealed that the soil pH negatively correlated with some species of Acidobacteria, but positively correlated with some species of Chloroflexi and some species of Ascomycota (Figure S6). AK positively correlated with species of Planctomycetes, Verrucomicrobia and Basidiomycota, but negatively correlated with Chloroflexi and Ascomycota. In words, AK and soil pH were important driver for microbial composition.

The total degree of each phylum were used to reveal the influence of each phylum on network structure (Figure 7). For bacteria, Proteobacteria, Actinobacteria and Acidobacteria had a large influence on network structure. Acidobacteria and Planctomycetes contributed more to rainforest networks than rubber plantation networks. However, Actinobacteria and Chloroflexi showed the opposite pattern. For fungi, Ascomycota and Basidiomycota had large influences on network structure. Both Ascomycota and Basidiomycota had stronger influences on rainforest networks than rubber plantation networks. The influence of Ascomycota was stronger during the rainy season than in the dry season, indicating seasonal change also had impact on fungal community networks. The degree of each phylum of bacterial and fungal network also revealed seasonality had effects on network degree (Figure S7).

3.4 Interaction between species and functions

Two-way network analysis of the 50 most abundant species (all belonging to bacteria groups based on metagenomic data) and the 50 most abundant KEGG functions revealed the interaction between microbial composition and functions. The results showed that soil network structure at rainforests sites (460 edges in the dry season, 1,750 in the rainy season) was more complex than that of rubber plantations (223 in the dry season, 451 in the rainy season) (Figure 8), indicating that more links between microbial species and functions were observed in soils of rainforest sites. Both rubber plantation and rainforest networks were more complex in the rainy season than in the dry season. We also found that metabolism was the most important function in soil microbial networks. Surprisingly, species of Actinobacteria negatively correlated with function in rubber plantations.

4. Discussion

4.1 Forest conversion reduces soil bacterial network complexity

Land-use changes increasingly threaten biodiversity, particularly in tropical forests (Gibson et al., 2011). However, we still have little understanding of how soil networks respond to forest conversion, such when rainforests are converted to rubber plantations. Our results showed that forest conversion had large effects on both soil bacterial and fungal networks. Tropical rainforest bacterial networks had more edges (Table 1) and a higher degree (Figure 4) than did rubber plantation networks, especially during the rainy season, indicating that the rainforest bacterial network was more complex than the rubber plantation network. This finding is consistent with previous observations that soil bacterial networks were more complex in natural systems than in crop soil (Karimi et al., 2019). Further study showed that soil networks become more connected through the process of ecological restoration (Morriën et al., 2017). The observed decrease in network complexity and cohesion supports the hypothesis that cropping may enhance the isolation of bacterial taxa

(Karimi et al., 2019), which results in lower numbers of connections in the network. In addition, at the microscale, the structure of tilled soils is more homogeneous, and the soil pores are less connected than in soils that are not tilled (Pagliai et al., 2004), such as rainforest soil. In nature, soil ecosystems are highly heterogeneous since hot spots of soil microbial biodiversity can form spatial and temporally within soil aggregates (Bach et al., 2018). This spatial heterogeneity likely plays an important role for the interactions among microbes and the mechanisms by which more complex and diverse communities drive various nutrient cycling processes on small spatial scales (Wagg et al., 2018).

A large number of studies employing microbial network analysis have enriched our understanding of microbial co-occurrence patterns in various soil ecosystems. However, very little is known of whether differences in the structure of microbial networks have consequences for microbiome functioning (Wagg et al., 2018). Our results demonstrated that more species correlated with metabolism in natural system than in the agricultural system, especially during the rainy season. This is in line with a previous study conducted in Sumatra, Indonesia, which found that the transformation of forest to rubber results in a 10-16% decrease in community metabolism (Barnes et al., 2014). Fewer interactions between microbial species (most of them are bacteria) and functions in rubber plantations demonstrated that forest conversion reduced soil bacterial network complexity.

4.2 Forest conversion increased soil fungal network complexity

Surprisingly, rainforest bacterial networks were characterized by fewer edges (Table 1) and a lower degree (Figure 4) than the rainforest bacterial networks, meaning that rubber plantation bacterial networks were more complex than those of native forests. Our results were not consistent with a study conducted in Xishuangbanna (Song et al., 2019) which showed that tropical forest conversion reduced fungal network complex, but is consistent with previous observations which found that fungal community networks were better organized in disturbed forest compared to primary forest (Chen et al., 2019). Banerjee et al. (2019)'s observation showed that organic agricultural fields harbored much more complex fungal networks with many more keystone taxa than conventionally managed fields. Forest conversion resulted in shifts in fungal composition from Basidiomycota to Ascomycota (Figure S8), as seen in previous investigations (Lan et al., 2020a; Lan et al., 2020b). Previous work showed that Basidiomycota species show higher drought sensitivity than Ascomycota species (Taniguchi et al., 2018), this would result in a shift in richness and abundance of Basidiomycota species (Figure S8). Many Basidiomycota species are capable of long-distance dispersal (Egidi et al. 2019, Geml et al., 2012), which may result in a decrease in fungal network complexity. This possibly explained why Ascomycota OTUs contribute more to the network structure than Basidiomycota (Figure 6). Overall, reductions in the abundance and richness of Basidiomycota species led to an increase in fungal links in rubber plantations.

4.3 Forest conversion enhanced the stability of soil network

The ability of a microbial community to resist and recover from disturbances is defined as the stability of the community (De Vries and Ashley, 2013). The ratio of positive to negative network links constitutes the balance between facilitative and inhibitive relationships within a network (Karimi et al., 2017). Theoretical studies, for example, predict that ecological networks that consist of weak interactions are more stable than those with strong interactions (Neutel et al., 2002, Coyte et al., 2015), and that compartmentalization and presence of negative interactions increase the stability of networks under disturbances (Coyte et al., 2015, Rooney et al., 2006, Stouffer & Bascompte 2011). In our study, more negative correlations were detected in rubber plantation, indicating the network structure of rubber plantation soils was more stable than that of rainforest soils（De Vries et al., 2018）. Forest conversion from rainforest to rubber plantations resulted in shifts in bacterial composition from Proteobacteria to Chloroflexi, and fungal composition from Basidiomycota to Ascomycota (Lan et al., 2020a). Proteobacteria and Basidiomycota are copiotrophic microorganisms, while

Chloroflexi and Ascomycota are oligotrophic (Yang et al., 2019; Lan et al., 2020a). This indicated forest conversion resulted in shifts in soil microbial composition from more *k*-strategists to more *r*-strategists (De Vries et al., 2013). R-strategists are quick-growing and less resistant but more resilient to disturbances. However, growth is not the only mechanism that could maintain community stability because the response of microorganisms to disturbance are very complex.

4.4 Main drivers for soil microbial composition and network structure

Forest conversion results in the loss of plant diversity, plant biomass and an increase in soil pH (Lan et al., 2017a, 2017b). Rubber plantations had a significantly higher pH, which explains the relative decrease in the abundance of Acidobacteria (Lan et al., 2017a). Our results demonstrate that forest conversion drives a shift in which soil microbes act as keystone species (Table 1). We found that many OTUs of Acidobacteria fit our criteria as keystone species for rainforest sites, which is consistent with previous findings (Banerjee et al., 2018). Unexpectedly, OTU11388 and OTU11373, both Acidobacteria, were observed in rainforest soils in both the dry and rainy seasons, indicating Acidobacteria were very important for rainforest soil bacterial networks (Figure 6 and table S3). Higher AK concentrations resulted in a higher abundance and more taxa of Actinobacteria (Figure 9), which suggests that Actinobacteria contributed more in rubber plantation than in rainforest (Figure 6). Indeed, forest conversion reduced the abundance of Actinobacteria OTUs (Figure S9). Due to the human disturbance in rubber plantations, the soil will inevitably be slightly polluted with herbicides and domestic garbage. Previous study showed member of Actinobacteria were observed in contaminated soil (Jiao et al., 2016).

Forest conversion also increases land use intensity (Brinkmann et al., 2019), including the application of fertilizer and herbicide. The application of herbicides has also been linked to significant decreases in root colonization and spore biomass of arbuscular mycorrhizal fungi in tropical agriculture (Zaller et al., 2014). Soil nutrient concentrations show a decline around the roots of rubber plantations compared to those from rainforests (Sahner et al., 2015). Our study was no exception. For instance, AK and TN concentration were significant lower in rubber plantations than in samples from rainforest sites (Table S2). Higher concentrations of AK reasonably explained the higher contribution of Basidiomycota to the network structure (Figure 8B) due to the positive association of AK with Basidiomycota.

Spatiotemporal heterogeneity can be a major driver of the abundance and distribution of keystone taxa in soil, which is a highly heterogeneous and multifaceted environment (Mills et al., 1993, Power et al., 1996; Mouquet et al., 2013). Seasonal variability determines the structural and compositional properties of microbiomes in an environment, and as such, a keystone species might be present only in a specific season or time period (Banerjee et al., 2018). It was interesting that more bacterial OTUs were identified as connectors during the rainy season than the dry season. Connectors have been characterized as generalists (Olesen et al., 2007), and generalists drive covariation among communities in a network (Chen et al., 2019). Previous observations have demonstrated that some keystone taxa that were found in the dry season disappeared during the rainy season (Lan et al., 2018). Seasonal changes possibly explain why some keystone taxa were observed in the rainy season but not in the dry season.

4.5 Possible impact of forest conversion on microbial community function

Forest conversion results in a decrease in the abundance of Proteobacteria and an increase of Actinobacteria. Most species of Proteobacteria were positively correlated with metabolic function, while most of Actinobacteria were negatively associated with metabolic function (Figure 8). Therefore, the changes in the abundance of these two phyla results in a reduction of microbial community function after forest conversion. Because the metabolic function of a specific species is often affected by environmental conditions (Louca et al., 2018), some species are not correlated with any function in the dry season, but correlated with metabolic function in the rainy season, indicating there some microorganisms do not participate in the metabolic process during the dry season, especially for the rubber plantations. In conclusion, forest conversion as well as seasonal variation had a great impact on soil microbial community functions.

5. Summary

Our knowledge about land-use impacts on soil ecosystems is mostly limited to biodiversity and ecosystem functions, leaving uncertainty about how soil networks change after forest conversion. This study is the most comprehensive report on changes in network structure that occur when tropical rainforests are converted into rubber plantations. Our study showed that forest conversion altered both bacterial and fungal soil networks, reduced bacterial network complexity and enhanced fungal network complexity, especially during the rainy season. One possible reason maybe that forest conversion altered soil pH and other soil properties, which altered bacterial composition, subsequent network structure as well as certain soil ecosystem functions. Our study demonstrates the impact of forest conversion on soil network structure, which has important implications for ecosystem functioning, such as metabolic activity, and health of soil ecosystems in tropical regions.

Code availability

Not applicable

Authors' contributions

Guoyu Lan: Conceptualization, Methodology, Writing, Reviewing and Editing; Chuan Yang, Rui Sun, Bangqian Chen, Xicai Zhang and Zhixiang Wu: Investigation

Competing interests

The authors declared that they have no conflicts of interest to this study.

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Figure legend

Figure 1 The soil bacterial-fungal community network of rubber plantations and rainforests in the dry and rainy seasons. Red solid circles indicate fungi, and green solid circles indicate bacteria. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient $\rho > 0.6$, $P < 0.01$

Figure 2 Soil bacterial network structure of rubber plantations and tropical rainforests in dry and rainy seasons. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient $\rho > 0.6$, $P < 0.01$

Figure 3 Soil fungal network structure of rubber plantations and tropical rainforests in the dry and rainy seasons. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient $\rho > 0.6$, $P < 0.01$

Figure 4 Number of shared and unique edges of soil bacterial and fungal networks in rubber plantations and tropical rainforests in the dry and rainy seasons. The number where the two circles cross is number of shared edges. Numbers in the red circle presents the unique edges in rainforests, while in blue circle present the unique edges in rubber plantations.

Figure 5 Network degree of soil bacterial and fungal communities of rubber plantations (blue) and tropical rainforests (red) in the dry and rainy seasons.

Figure 6 Frequency distributions of correlation strength in bacterial (a: dry season, b: rainy season) and fungal (c: dry season, d: rainy season) networks of rubber plantations and tropical rainforests in the dry and rainy seasons. (absolute correlation coefficient greater than 0.3, $P < 0.01$) Correlations in rainforest networks are red, correlations in rubber plantation networks are blue.

Figure 7 Proportional influence of different phyla on bacterial and fungal network structure in both dry and rainy seasons. The influence was the number of degrees of nodes belonging to a particular phylum. (a: bacteria in dry season, b: bacteria in rainy season, c: fungal in dry season, d: fungal in rainy season).

Figure 8 Network of the top 50 most abundant species (based on metagenomics data) and top 50 most frequent KEGG functions (pathway level 3) of rubber plantations and tropical rainforest sites in the dry and rainy seasons. (A: rubber in dry season; B: rainforest in dry season; C: rubber in rainy season; D: rainforest in rainy season) The size of the node indicates the species/function abundance. A red line indicates positive correlation between species/functions, and green indicates negative correlation. Absolute value of correlation coefficient > 0.6, $P < 0.01$

Table 1 Topological properties of soil microbial (bacterial and fungi) network structure in rubber plantation and tropical rain forest in dry and rainy seasons

	Bacteria				**Fungi**			
	Rubber Dry	**Rainforest Dry**	**Rubber Rainy**	**Rainforest Rainy**	**Rubber Dry**	**Rainforest Dry**	**Rubber Rainy**	**Rainforest Rainy**
No. of nodes	291	287	296	296	220	235	243	244
No. of edges	2448	2559	4248	5019	791	769	1250	905
No. of positive edges	2052	2508.00	3385	4901	760	764	1195	897
No. of negative edges	396	51	863	118.00	31	5	55	8
Connectance	0.06	0.06	0.09	0.11	0.02	0.02	0.03	0.02
Average degree	16.82	17.83	16.67	33.91	16.67	6.54	10.28	7.41
Average betweenness	100.61	93.52	31.23	42.57	208.90	185.03	170.99	266.31
Average of shortest path length	2.92	2.92	2.56	2.45	4.00	3.626	3.81	5.27
Diameter	6.00	7.00	7.00	6.00	10.00	12.00	9.00	15.00
Cluster of coefficient	0.46	0.451	0.51	0.54	0.59	0.457	0.49	0.51
No of clusters	11.00	14.00	5.00	5.00	94.00	75.00	62.00	67.00
Degree centralization	0.12	0.11	0.17	0.18	0.08	0.08	0.10	0.10
Betweenness centralization.	0.0066	0.0067	0.0053	0.0049	0.02	0.03	0.121	0.04
Closeness centralization.	0.35	0.35	0.40	0.41	0.31	0.351	0.291	0.26
Neighborhood Connectivity	21.12	21.79	34.69	40.68	10.45	9.28	13.78	9.44
Topological coefficient	0.26	0.26	0.26	0.27	0.33	0.36	0.37	0.50

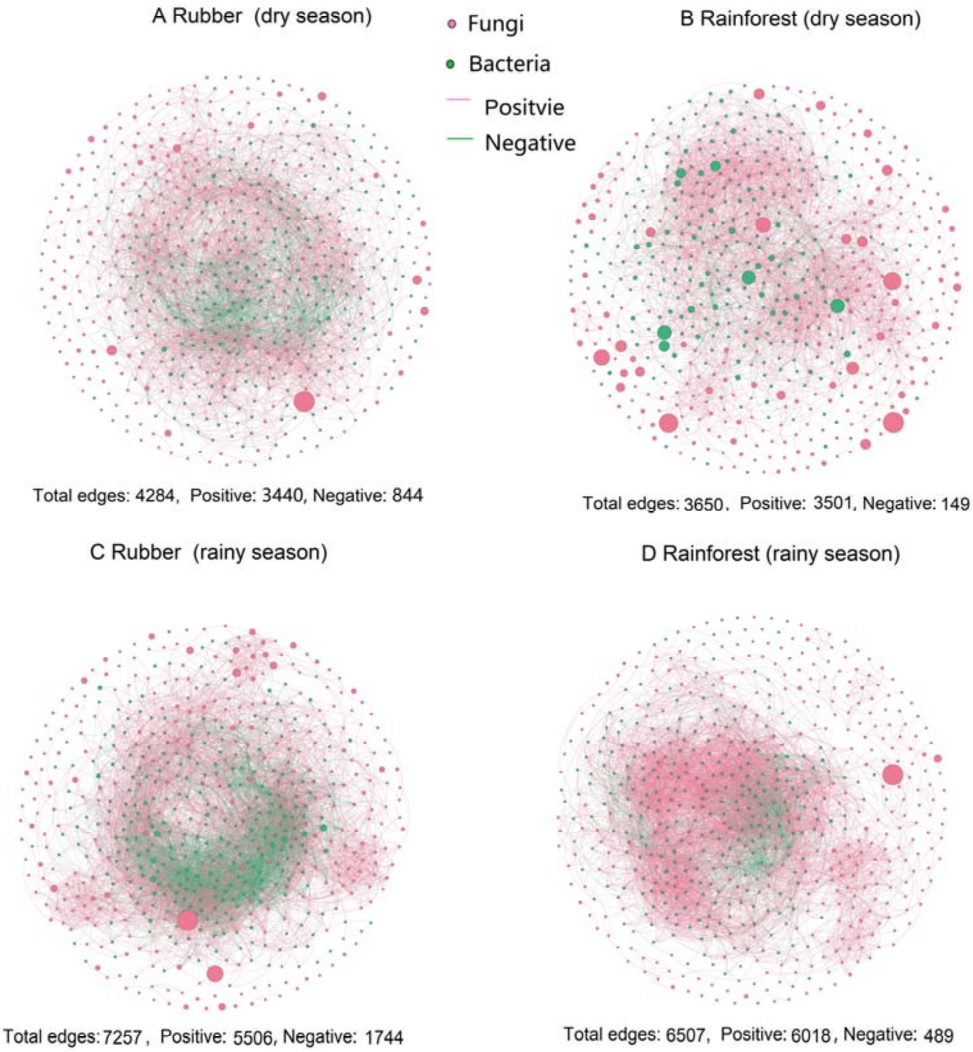


Figure 1 The soil bacterial-fungal community network of rubber plantations and rainforests in the dry and rainy seasons. Red solid circles indicate fungi, and green solid circles indicate bacteria. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient $\rho > 0.6$, $P < 0.01$.

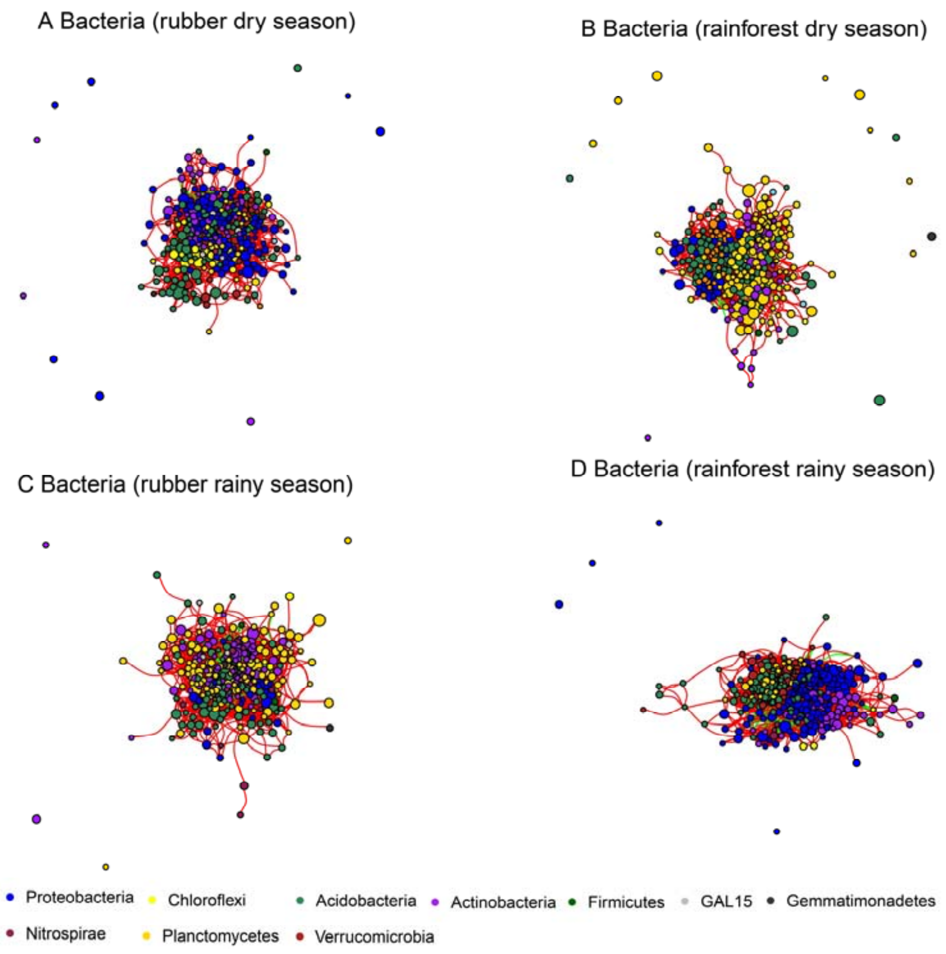
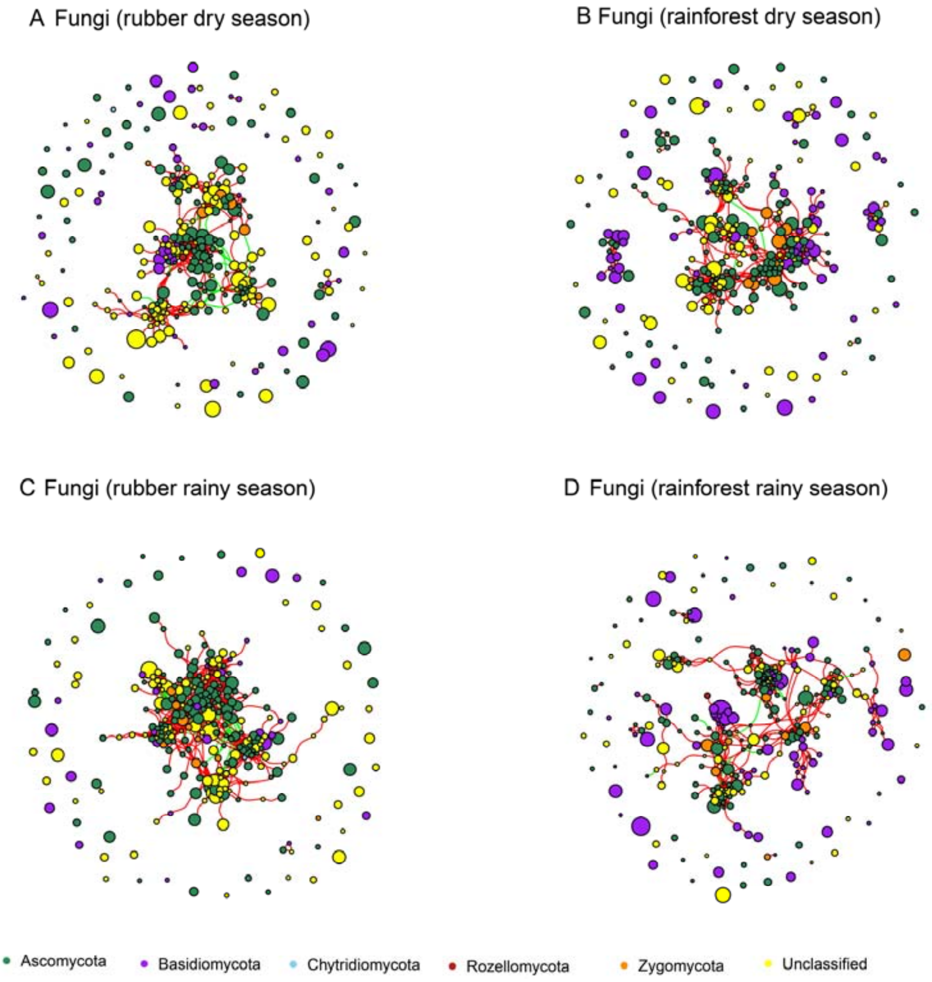


Figure 2 Soil bacterial network structure of rubber plantations and tropical rainforest in the dry and rainy seasons. Red line indicates positive correlation between OTUs, and green indicates negative correlation. Absolute value of correlation coefficient $\rho > 0.6$, $P < 0.01$



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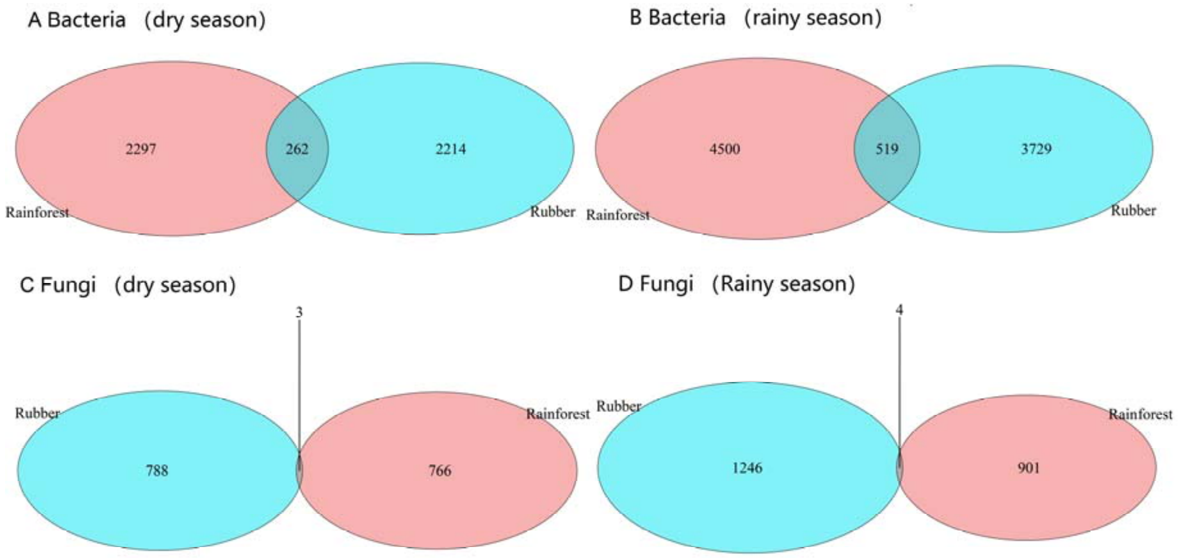

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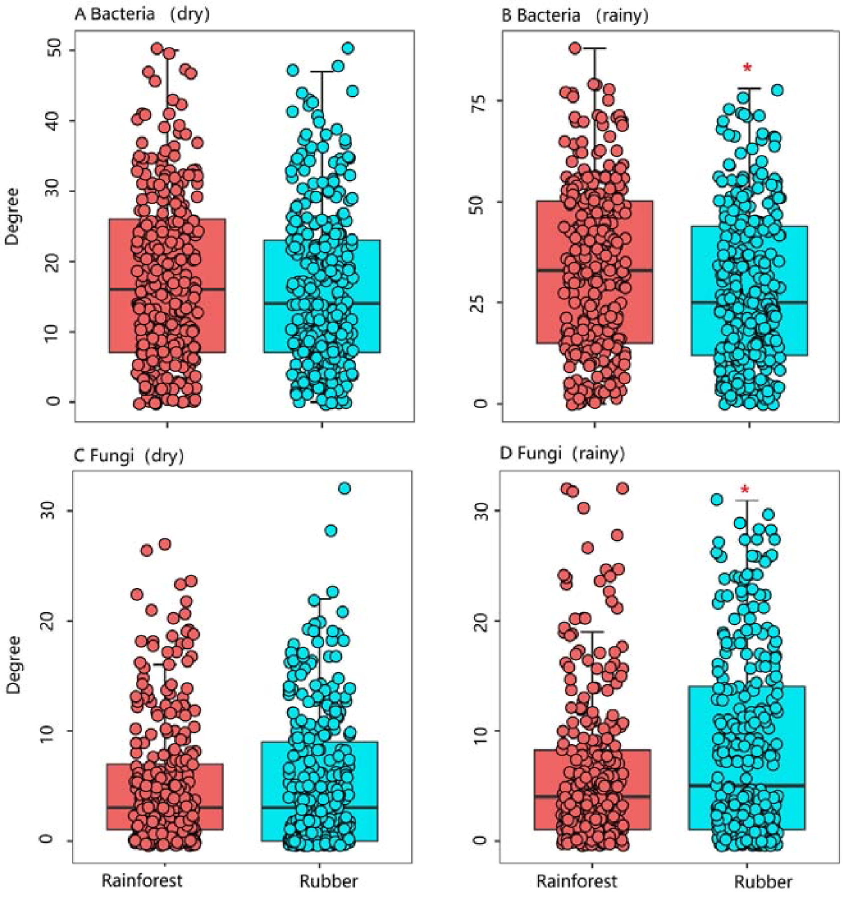

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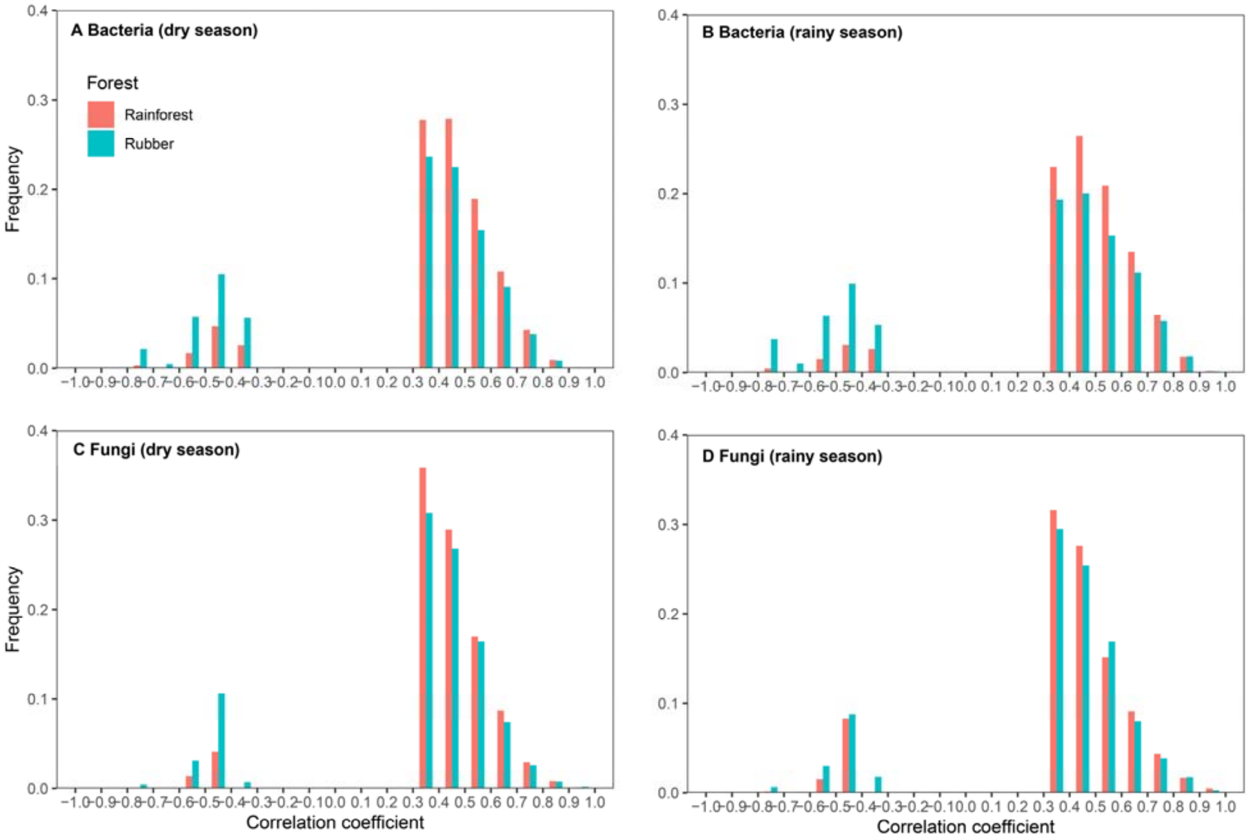

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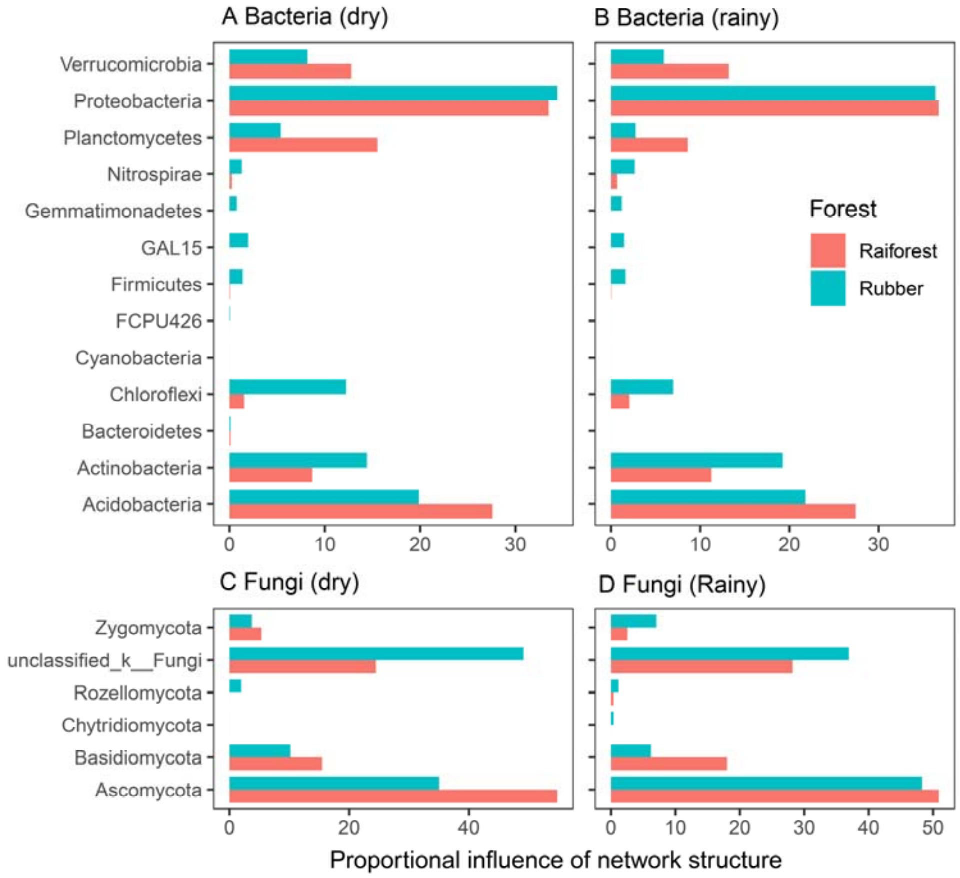

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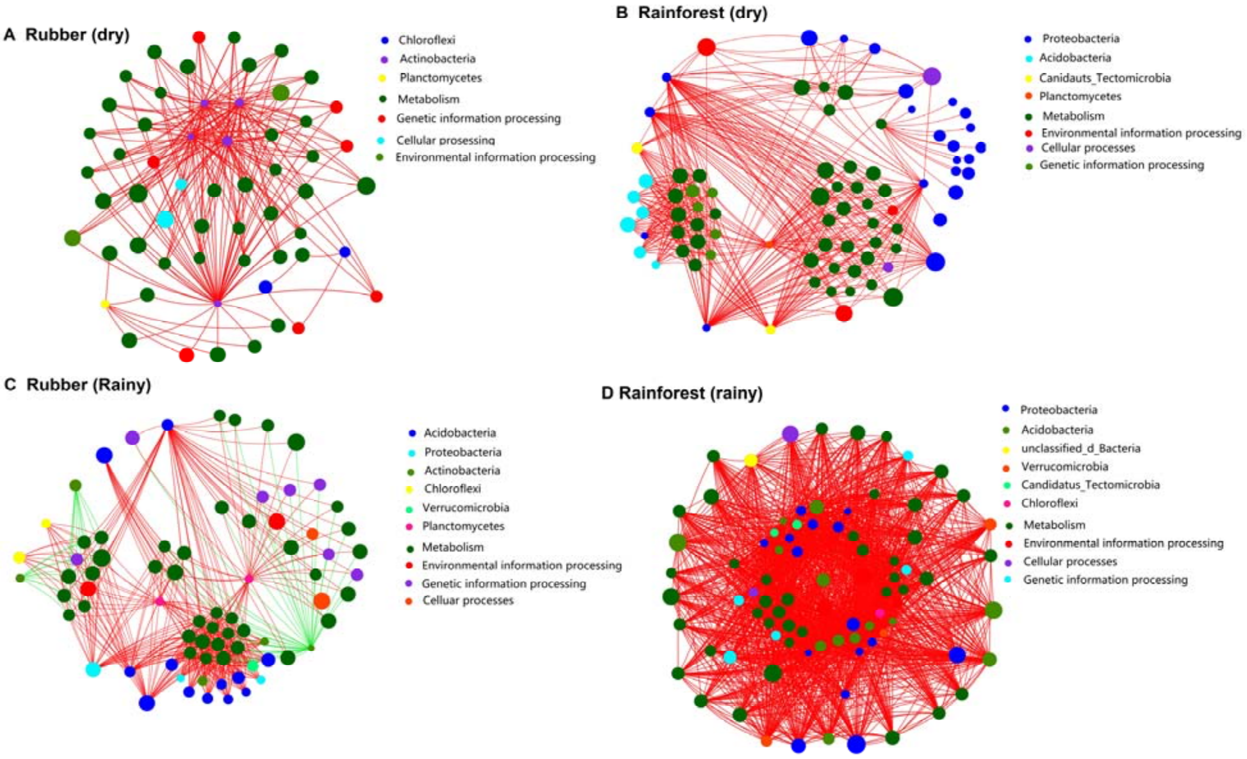

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