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

Guoyu Lan (✉ langyri@163.com)

Rubber Research Institute <https://orcid.org/0000-0003-4019-4252>

Zhixiang Wu

Rubber Research Institute CATAS

Chuan Yang

Rubber Research Institute, CATAS

Rui Sun

Rubber Research Institute CATAS

Bangqian Chen

Rubber Research Institute CATAS

Xicai Zhang

Rubber Research Institute CATAS

Research

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

Posted Date: May 5th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-429143/v1>

License: This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at SOIL on March 2nd, 2022. See the published version at <https://doi.org/10.5194/soil-8-149-2022>.

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 such as when tropical rainforest are replaced with rubber plantations. In this study, we used Illumina sequencing and metagenome shotgun sequencing to analyze bacterial and fungal community network structure in a large number of soil samples from tropical rainforest and rubber plantation sites in Hainan Island, China. Our results showed only a few shared network edges were observed in both bacterial and fungal communities, which indicates that forest conversion altered soil microbial network structure. We found a greater degree of network structure and a larger number of network edges among bacterial networks in samples from tropical rainforest compared to samples from rubber plantations. The difference was especially pronounced during the rainy season and indicates that rainforest bacterial networks were more complex than rubber plantation bacterial networks. However, rubber plantations soil fungal networks showed more higher links and higher network degree, suggesting that forest conversion does not reduce fungal network complexity. We found that some groups of Acidobacteria were keystone taxa in our tropical rainforest soils, while Actinobacteria were keystone taxa in rubber plantation soils. In addition, seasonal change had a strong effect on network degree, the complexity of soil bacterial and fungal network structure. In conclusion, forest conversion changed soil pH and other soil properties, such as available potassium (AK) and total nitrogen (TN), which resulted in changes in bacterial and fungal composition and network structure.

Introduction

Tropical rainforest have the highest biodiversity of any ecosystem and harbor more than 60% of all known plant and animal species [1]. However, over the past several decades, logging, mining, slash and burn agriculture have caused widespread deforestation and forest degradation. Of these, the conversion of forest to agriculture has caused the most forest loss [2].

Hainan is home to a large area of tropical rainforest rich in biodiversity. It is a part of the Indian-Malay rainforest system and 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 [3].

The soil microbiome is highly diverse and comprises up to one quarter of Earth's diversity [4]. Soil microbes play a critical role in the maintenance of soil quality and function, and they represent the majority of biodiversity in terrestrial ecosystems [5]. A number of studies have investigated the impact of the conversion of tropical forests to rubber plantations on soil microbial composition and diversity [3, 6–12]. Studies conducted in Indonesia [6], Malaysia [7] and South China [8–10] 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 [7–8, 13–14]. However, there are few studies on the effects of forest conversion on soil microbial network structure.

Network analysis is an increasingly popular tool for investigating microbial community structure, as it integrates multiple types of information and may represent systems-level behavior [15]. The soil microbial network is viewed as a critical indicator of soil health and quality [16]. Network analysis of taxon co-occurrence patterns provides new insight into the structure of complex microbial communities, insight that complements and expands on the information provided by the more standard suite of analytical approaches [17]. Previous work has shown that agricultural intensification can reduce microbial network complexity [18]. Logging alters soil fungal network in tropical rainforests, i.e., a better-organized fungal community in the select cut stands when compared with the primary stands [19]. Soil bacterial networks are less stable under drought than fungal networks [20]. Soil networks become more connected as ecological restoration progresses [21]. So far, very few studies have assessed the impact of forest conversion on soil microbial networks and it is still unclear whether forest conversion as well as seasonal change influences the structure and complexity of microbial networks. Here we explored bacterial and fungal community network structure using Illumina sequencing based on samples collected from tropical rainforest and rubber plantations in Hainan Island, China. We aimed to test the hypothesis that (1) forest conversion alters microbial networks by altering microbial community composition [3] and that soil microbial activity is strongly influenced by plant species [22]. (2) Soil microbial network structure in rainforest sites is more complex and stable than in rubber plantations because natural systems were more connected than artificial systems [21]. By evaluating these hypotheses, we want to clarify the drivers and mechanisms 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.

Methods

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 km² [23]. Hainan Island is the largest island within the Indo-Burma Biodiversity Hotspot in tropical Asia [24] 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°C. 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. Rainfall is abundant, ranging from 1,000 mm to 2,600 mm yearly, with an average annual precipitation of 1,639 mm. 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.

Soil sampling

We selected five rainforests as our study sites: Bangwang mountain, Diaoluo mountain, Wuzhi mountain, Yinge mountain and Jianfeng mountain. Five rubber plantations were selected in Haikou, Danzhou, Qiongzong, Wanning and Ledong (Figure S1). More information on the study sites is provided in Table S1. For each site, thirteen soil samples were collected, thus there were a total of 130 samples collected between the rubber plantations and tropical rainforest per sampling interval. Soil sampling was performed in the rainy season (July) and dry season (January). Thus, there were a total of 260 soil samples (130 per forest type). Soil samples were divided into two parts: one was used to analyze soil water contents, soil pH, total nitrogen, total phosphorus (TP), total potassium (TK), nitrate nitrogen (NN), ammonium nitrogen (AN), available phosphorus (AP), potassium (AK). The other was used for DNA extraction. Soil properties were analyzed following the methods described in by Lan et al. [11]. Soil properties of the rubber plantation and rainforest sites are shown in Table S2.

DNA extraction and PCR amplification

Microbial DNA was extracted from 0.5 g of soil using the E.Z.N.A.® Soil DNA Kit (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') [25]. 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') [26-27]. 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.

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 KOBAS 2.0 according to previously described methods [28]

Bioinformatics and data analysis

Raw fastq files were demultiplexed and quality-filtered using QIIME [29] (version 1.17). Operational Taxonomic Units (OTUs) were clustered with a 97% similarity cut-off using UPARSE [30], 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 [31]. The relative abundance was determined for each taxon [32] using MOTHUR [33].

Statistical analysis

For the co-occurrence network analyses, we only focus on the top 300 most abundant OTUs of the two forest types. The networks of each habitat during each sampling period (tropical rainforest and rubber plantations in dry season and rainy season) were constructed with 65 samples each. Interactions consisted of Spearman's rank correlations and co-occurrence networks were constructed using only significant correlations of $\rho > 0.6$ ($P < 0.01$) [17], because this cutoff includes a range of interactions strengths [20]. 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. In order to evaluate the network differences between tropical rain forest and rubber forest sites, Venn diagrams were plotted to reveal the number of shared edges and unique edges which were calculated using *igraph*. Keystone OTUs were selected on the basis of high network degree, high closeness centrality, and low betweenness centrality as defined by Berry and Widder [34]. 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 taxon 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 nodes connectivity within a module, and P_i measures the degree of a node connected with other modules [35]. All species can be divided into four groups according to the simplified criteria [36], 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.

Results

Bacterial and fungal networks

Our results showed most nodes of bacterial networks (Figure 1) and fungal networks (Figure 2) varied with forest type in both the dry season and rainy season. For bacterial networks, there were 2559 and 2501 edges in tropical rainforest and rubber plantation in dry season respectively, but these two networks only shared 262 edges, accounting only about 10% the total edges (Figure 3A-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 dry season and rainy season, respectively (Figure 3C-D).

The number of edges of bacterial and fungal networks were almost equivalent during the dry season. However, in rainy season, there were more edges in the bacterial network in tropical rainforest than in the rubber plantation (Table 1 & Figure 3B). For the network structure of the fungal community, more edges were observed in rubber plantations in rainy season (Table 1 & Figure 3D). Similarly, there were no significant differences in both bacterial and fungal network degree between tropical rainforest sites and rubber plantations in the dry season (Figure 4A, C). In the rainy season, rainforest sites had higher bacterial network degree, while rubber plantations showed higher fungal network degree (Figure 4B, 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) of rainforest were observed 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 rubber plantation fungal network structure was more complex than tropical rainforest during the rainy season, but that the reverse was true for bacteria.

When considering the ratio of positive to negative correlation coefficients, more correlations (greater than 0.3, $P < 0.05$) were calculated, and the results showed that the negative correlations between bacterial and fungal OTUs of rubber plantations were consistently stronger than for tropical rainforest in both dry season and rainy season (Figure 5).

For both the bacterial and fungal communities, neither tropical rainforest nor rubber plantation networks possessed module hubs and network hubs (Figure S3-S4). For bacterial network, the majority of nodes in both the rubber plantation and tropical rainforest networks were connectors (Figure S3). However, for fungal networks, the majority of the nodes in both rubber plantation and tropical rainforest networks were peripherals and connectors (Figure S4). The ratio of peripherals and connectors of these two forest types was not different indicating the network structures of rainforest and rubber plantation were very similar as visualized in Figure 1 and Figure 2. However, the bacterial networks had more connectors than fungal networks, which suggests bacterial networks may contain more generalists than fungal networks do. This indicated bacterial network were more complex than fungal network, which can further confirmed by visualization of the network (Figure 1 and Figure 2).

For bacterial groups, members of the phyla Acidobacteria, Planctomycetes and Verrucomicrobia showed higher degree in the tropical rainforest sites than in rubber plantations, suggesting that these taxa are strongly associated with the other members of the community in tropical rainforest (Figure S5A). Members of the phyla Actinobacteria showed higher degree in rubber plantations. Seasonal change also had effects on network degree for soil bacterial networks. For instance, Chloroflex had higher degree in rubber plantation in the dry season, but the opposite is true in the rainy season. For fungal networks, members of Basidiomycota showed higher degree in tropical rainforest sites during in the dry season, however, Ascomycota showed higher degree in rubber plantations (Figure S5C-D) during the rainy season.

We used total degree of each phylum to reveal the influence of each phylum on network structure (Figure 6). For bacteria, Proteobacteria, Actinobacteria and Acidobacteria had a large influence on network structure (Figure 6). Acidobacteria and Planctomycetes contributed more to rainforest networks than rubber plantation networks. However, Actinobacteria and Chloroflex showed the opposite. For fungi, Ascomycota and Basidiomycota had large influence of network structure. Both Ascomycota and Basidiomycota had stronger influence 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.

Keystone taxa

Keystone OTUs of the bacterial and fungal communities were selected on the basis of high degree, high closeness centrality, and low betweenness centrality. The results showed that forest conversion altered the keystone taxa of bacteria and fungi. The keystone taxa of bacteria were very different between rubber plantations and tropical rainforest sites in both the dry season and rainy season. For bacteria, there were more keystone taxa in tropical rainforest sites than in rubber plantations in both the dry season and rainy season 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 bacteria 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 season and rainy season, indicating the rubber plantation networks were more complex. Most keystone taxa belong to Ascomycota suggesting 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).

Two-ways correlation networks

Two-way network analysis of the 50 most abundant species (metagenomic data, the 50 most abundant species all belong to bacteria groups) and the 50 most abundant KEGG functions revealed that soil microbial community structure in at rainforests sites was more complex than rubber plantations (Figure 7). Both rubber plantations and rainforest networks were more complex in the rainy season than in dry season. We also found that metabolism was the most important function in soil microbial network. Surprisingly, species of Actinobacteria negatively correlated with other species and function in rubber plantations (Figure 7).

Two-ways correlation network analysis revealed the interaction between microbial composition and environmental variables. This analysis includes different environmental factors as nodes in the network, and the number of connections these nodes have indicates the number of OTUs that are impacted by that environmental factor (Figure 8). For bacteria, elevation had the highest network degree at 106, and was

followed by AK (104), soil pH (86) and TK (9). In other words, elevations, AK, soil pH are all drivers of bacterial community composition. Soil pH negatively correlated with most bacterial Acidobacteria OTUs. For fungi, elevation had the highest network degree (61), followed by AK (51), longitude (15), and NN (11). AK positively correlated with most OTUs of Basidiomycota. Relationship between OTU abundance and soil pH revealed the soil pH negatively correlated with members of Acidobacteria, but positively correlated with members of Chloroflexi and members of Ascomycota (Figure 9). AK positively correlated with members of Planctomycetes Verrucomicrobia and Basidiomycota, however negatively correlated with Chloroflexi and Ascomycota.

Discussion

Forest conversion reduces soil bacterial network complex

Land-use changes increasingly threaten biodiversity, particularly in tropical forests [37]. 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. More edges (Table 1) and higher degree (Figure 4) of tropical rainforest bacterial networks were observed, especially during the rainy season, which indicates that the rainforest bacterial network was more complex than the rubber plantation network. This consistent with previous observations that soil bacterial networks were more complex in natural systems than in crop soil [38]. Further study showed that soil networks become more connected as nature restoration progresses [21]. The observed decrease in network complexity and cohesion supports the hypothesis that cropping may enhance the isolation of bacterial taxa [38], which results in lower connection of 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 under without tillage [39], such as rainforest soil. In nature, soil ecosystems are highly heterogeneous since soil microbial biodiversity hot spots can form spatial and temporally within soil aggregates [40]. 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 [4].

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 [4]. Our results demonstrated that more species related with metabolism in natural system than in the agricultural system, especially in 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 [41]. Fewer interactions between microbial species (most of them are bacteria) and functions in rubber plantations demonstrated that forest conversion reduced soil bacterial network complex.

Forest conversion does not reduce soil fungal network complexity

Surprisingly, rainforest bacterial networks were characterized by fewer edges (Table 1) and lower degree (Figure 4), which means that rubber plantation bacterial networks were more complex than the native forest. Although, our results were consistent with previous observations which found that fungal community networks were better organized disturbed forest compared to primary forest [19]. Banerjee et al. [18]'s observation showed that organic agricultural fields harbored much more complex fungal networks with many more keystone taxa than conventional managed fields. Forest conversion resulted in shifts in fungal composition from Basidiomycota to Ascomycota (Figure S7), as seen in previous investigations [3, 11]. Previous work showed that Basidiomycota species show higher drought sensitivity than Ascomycota species [42], this would result in a shift in richness and abundance of Basidiomycota species (Figure S6). Many Basidiomycota species are capable of long-distance dispersal [43-44], which may result in a decrease in fungal network. This possibly explained why Ascomycota OTUs contribute more to the network structure than Basidiomycota (Figure 6). Overall, reduction in abundance and richness of Basidiomycota species led to an increase in fungal links in rubber plantations.

Forest conversion enhanced the stability of soil network

The positive to negative ratio of network links indicates the balance between facilitative and inhibitive relationships within a network [45]. Theoretical studies, for example, predict that ecological networks that consist of weak interactions are more stable than those with strong interactions [46-47], and that compartmentalization and presence of negative interactions increase the stability of networks under disturbances [47-49]. In our study, more negative correlations were detected in rubber plantation, indicating the network structure of rubber plantation soils was more stable than rainforest soils [20].

Driver of the network structure

Forest conversion results in the loss of plant diversity, plant biomass and increasing soil pH [8-9]. Rubber plantations had a significantly higher pH, which explains the relative decrease in the abundance of Acidobacteria [8]. Our results demonstrate that keystone taxa of soil microbes change after forest conversion (Table 1). We found that many OTUs of Acidobacteria fit our criteria as keystone species for rainforest sites, which is consistent with previous findings [50]. 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 concentration 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 S7) 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 [51].

Forest conversion also increases land use intensity [52], including the application of fertilizer and herbicide. Herbicide application also caused significant decreases in root colonization and spore biomass of arbuscular mycorrhizal fungi in tropical agriculture [53]. Soil nutrient concentration shows a decline around the roots of rubber plantations compared to those from rainforests [54]. Our observation is no

exception, for instance, AK and TN concentration was significant lower in rubber plantation than in samples from rainforest sites (Table 2). Higher concentration of AK reasonably explained the higher contribution of Basidiomycota on the network structure (Figure 8B) due to AK positive association 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 [55-57]. 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 [50]. It was interesting that more bacterial OTUs were identified as connectors during the rainy season than in the dry season. Connectors have been characterized as generalists [36], and generalists drive covariation among communities in a network [19]. Previous observation demonstrated that some keystone taxa that were found in the dry season disappeared during the rainy season [58]. Seasonal changes possibly explained the keystone taxa was observed in rainy season but not in dry season.

Conclusion

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 forest. 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 changed soil pH and other soil properties, which altered bacterial composition and subsequent network structure. Our study demonstrates the impact of forest conversion for soil network structure, which has important implications for ecosystem functions and health of soil ecosystems in tropical regions.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: SRP108394, SRP278296, SRP278319).

Competing interests

The authors have no conflicts of interest to declare.

Funding

This work was supported by Finance Science and Technology Project of Hainan Province (ZDYF2019145); National Natural Science Foundation of China (31770661); High level Talents Project of Hainan Natural Science Foundation (320RC733); the Earmarked Fund for China Agriculture Research System (CARS-33-ZP3)

Authors' contributions

LGY, and WZX conceived of and designed the study; YC and SR conducted the sampling; CBQ, and ZXC performed analyses; LGY performed statistical analyses and wrote the manuscript, all authors edited the manuscript.

Acknowledgements

Not applicable.

References

1. Dirzo R, Raven PH. Global state of biodiversity and loss. *Annu Rev Environ Resour.* 2003;28:137–67.
2. Li. HM, Aide T, Ma YX, Liu WJ, Cao M. Demand for rubber is causing the loss of high diversity rain forest in SW China. *Biodivers Conserv.* 2007;16(6):1731–45.
3. Lan GY, Wu ZX, Sun R, Yang C, Chen BQ, Zhang XC Forest conversion changed the structure and functional process of tropical forest soil microbiome. *Land Degrad Dev.* 2020a. DOI: 10.1002/ldr.3757.
4. Wagg C, Schlaeppi K, Banerjee S, Kuramae EE, van der Heijden MG. A. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nat Commun.* 2019;10:4841.
5. Philippot L, Spor A, He´nault C, Bru D, Bizouard F, Jones CM, Sarr A, Maron PA. Loss in microbial diversity affects nitrogen cycling in soil Laurent. *ISME J.* 2013;7:1609–19.
6. Schneider D, Engelhaupt M, Allen K, Kurniawan S, Krashevskaya V, Heinemann M, Scheu S. Impact of lowland rainforest transformation on diversity and composition of soil prokaryotic communities in Sumatra Indonesia. *Front Microbiol.* 2015;6:296.
7. Kerfahi D, Tripathi BM, Dong K, Go R, Adams JM. Rainforest conversion to rubber plantation may not result in lower soil diversity of bacteria fungi and nematodes. *Microb Ecol.* 2016;72:359–71.
8. Lan GY, Li YW, Wu ZX, Xie GS. Soil bacterial diversity impacted by conversion of secondary forest to rubber or eucalyptus plantations—a case study of Hainan Island, south China. *For Sci.* 2017a;63:87–93.
9. Lan GY, Li Y, Wu ZX, Xie GS. Impact of tropical forest conversion on soil bacterial diversity in tropical region of China. *Eur J Soil Biol.* 2017c;83:91–7.

10. Lan GY, Li YW, Jatoi MT, Tan ZH, Wu ZX, Xie GS. Change in Soil Microbial Community Compositions and Diversity Following the Conversion of Tropical Forest to Rubber Plantations in Xishuangbanna Southwest China. *Trop Conserv Sci.* 2017b;10:1–14.
11. Lan GY, Wu ZX, Sun R, Yang C, Chen BQ, Zhang X. Tropical rainforest conversion into rubber plantations results in changes in soil fungal composition, but underlying mechanisms of community assembly remain unchanged. *Geoderma.* 2020b;375:114505.
12. Lan GY, Wu ZX, Li YW, Chen BQ. The drivers of soil bacterial communities in rubber plantation at local and geographic scales. *Arch Agron Soil Sci.* 2020c;66(3):358–69.
13. Cai ZQ, Zhang YH, Yang C, Wang S. Land-use type strongly shapes community composition, but not always diversity of soil microbes in tropical China. *Catena.* 2018;165:369–80.
14. Tripathi BM, Kim M, Singh D, Lee-Cruz L, Lai-Hoe A, Ainuddin AN, Adams JM. Tropical soil bacterial communities in Malaysia: pH dominates in the equatorial tropics too. *Microb Ecol.* 2012;64:474–84.
15. Röttgers L, Faust K. From hairballs to hypotheses—biological insights from microbial networks. *FEMS Microbiol Rev.* 2018;10:1093.
16. Kuperman RG, Siciliano SD, Römcke J, Oorts K. Deriving site-specific soil clean-up values for metals and metalloids: rationale for including protection of soil microbial processes. *Integr Environ Assess Manage.* 2014;10(3):388–400.
17. Barberan A, Bates ST, Casamayor EO, Fierer N. Using network analysis to explore co-occurrence patterns in soil microbial communities. *ISME J.* 2012;6:343–51.
18. Banerjee S, Walder F, Büchi L, Meyer M, Held AY, Gattinger A, Keller T, Charles R, van der Heijden MGA. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME J.* 2019;13:1722–36.
19. Chen J, Xu H, He D, Li YD, Luo TS, Yang HG, Lin MX. 2019. Historical logging alters soil fungal community composition and network in a tropical rainforest. *For Ecol Manage.* 2019: 433 (5): 228–239.
20. De Vries VFT, Griffiths RI, Mark B, Hayley C, Mariangela G, Soon GH, et al. Soil bacterial networks are less stable under drought than fungal networks. *Nature Commun.* 2018;9(1):3033-.
21. Morriën E, Hannula S, Snoek L, et al. Soil networks become more connected and take up more carbon as nature restoration progresses. *Nat Commun.* 2017;8:14349.
22. Galicia L, García-Oliva F. The effects of C, N and P additions on soil microbial activity under two remnant tree species in a tropical seasonal pasture. *Appl Soil Ecol.* 2004;26(1):31–9.
23. Lopez S, Rousset F, Shaw FH, Ruth G, Shaw RG, Ophélie R. Joint effects of in? breeding and local adaptation on the evolution of genetic load after fragmentation. *Conservation and. Biology.* 2009;23:1618–27.
24. Francisco-Ortega J, Wang ZS, Wang FG, Xing FW, Liu H, Xu H, Xu WX, Luo YB, Song XQ, Gale S, Boufford DE, Maunder M, An SQ. Seed plant endemism on Hainan Island: a framework for conservation actions. *Bot Rev.* 2010;76:346–76.

25. Adams RI, Miletto M, Taylor JW, Bruns TD. Dispersal in microbes: fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances. *ISME J.* 2013;7(7):1262–73.
26. Walters W, Hyde ER, Berg-Lyons D, Ackermann G, Humphrey G, Parada A, Gilbert JA, Jansson JK, Caporaso JG, Fuhrman JA, Apprill A, Knight R. Improved bacterial 16S rRNA gene (V4 and V4-5) and fungal internal transcribed spacer marker gene primers for microbial community surveys. *mSystems.* 2016;1(1):e00009–15.
27. Sampson TR, Debelius JW, Thron T, Janssen S, Shastri GG, Ilhan ZE, Challis C, Schretter CE, Rocha S, Gradinaru V, Chesselet MF, Keshavarzian A, Shannon KM, Krajmalnik-Brown R, Wittung-Stafshede P, Knight R, Mazmanian SK. Gut microbiota regulate motor deficits and neuroinflammation in a model of Parkinson's disease. *Cell.* 2016;167(6):1469–80.
28. Qin J, Li R, Raes J, Arumugam M, Burgdorf KS, Manichanh C, Nielsen T, Pons N, Levenez F, Yamada T. A human gut microbial gene catalogue established by metagenomic sequencing. *Nature.* 2010;464:59–65.
29. Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Peña AG, Goodrich JK, Gordon JL. QIIME allows analysis of high-throughput community sequencing data. *Nat Methods.* 2010;7:335–6.
30. Edgar RC, UPARSE. Highly accurate OTU sequences from microbial amplicon reads. *Nat Methods.* 2013;10:996–8.
31. Amato KR, Yeoman CJ, Kent A, Carbonero F, Righini N, Estrada AE, Gaskins HR, Stumpf RM, Yildirim S, Torralba M, Gillis M, Wilson BA, Nelson KE, White BA, Leigh SR. Habitat degradation impacts primate gastrointestinal microbiomes. *ISME J.* 2013;7:1344–53.
32. Good IL. 1953. The population frequencies of species and the estimation of population parameters. *Biometrika* 1953; 40: 237–264.
33. Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microbiol.* 2009;75:7537–7.
34. Berry D, Widder S. Deciphering microbial interactions and detecting keystone species with co-occurrence networks. *Front Microbiol.* 2014;5:1–14.
35. Roger G, Amaral LAN. Functional cartography of complex metabolic networks. *Nature.* 2005;433:895.
36. Olesen JM, Bascompte J, Dupont YL, Jordano P. The modularity of pollination networks. *Proc Nat Acad Sci USA.* 2007;104:19891–6.
37. Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi, N.S. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature.* 2011;478:378–81.
38. Karimi B, Dequiedt S, Terrat, Sébastien, Jolivet C, Arrouays D, Wincker P, Cruaud C, Bispo A, Prévost-Bouré NC, Ranjard L. Biogeography of soil bacterial networks along a gradient of cropping intensity. *Sci Rep.* 2019;9(1):3812.

39. Pagliai M, Vignozzi N, Pellegrini S. Soil structure and the effect of management practices. *Soil Tillage Res.* 2004;79:131–43.
40. Bach EM, Williams RJ, Hargreaves SK, Yang F, Hofmockel KS. Greatest soil microbial diversity found in micro-habitats. *Soil Biol Biochem.* 2018;118:217–26.
41. Barnes AD, Jochum M, Mumme S, Haneda NF, Farajallah A, Widarto TH, Brose U. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nat Commun.* 2014;5:5351.
42. Taniguchi T, Kitajima K, Douhan GW, Yamanaka N, Allen MF. A pulse of summer precipitation after the dry season triggers changes in ectomycorrhizal formation, diversity, and community composition in a Mediterranean forest in California, USA. *Mycorrhiza.* 2018;28(7):665–77.
43. Egidi E, Delgado-Baquerizo M, Plett JM, Wang J, Eldridge DJ, Bardgett RD, Maestre FT, Singh BK. A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat Commun.* 2019;10:2369.
44. Geml J, Timling I, Robinson CH, Lennon N, Nusbaum HC, Brochmann C, Noordeloos ME, Taylor DL. An arctic community of symbiotic fungi assembled by dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. *J Biogeogr.* 2012;39:74–88.
45. Karimi B, Maron PA, Chemidlin-Prevost Boure N, Bernard N, Gilbert D, Ranjard, L. Microbial diversity and ecological networks as indicators of environmental quality. *Environ Chem Lett.* 2017;15:265–81.
46. Neutel AM, Heesterbeek JAP, de Ruiter PC. Stability in real food webs: weak links in long loops. *Science.* 2002;296:1120–3.
47. Coyte KZ, Schluter J, Foster KR. The ecology of the microbiome: networks, competition, and stability. *Science.* 2015;350:663–6.
48. Rooney N, McCann K, Gellner G, Moore JC. Structural asymmetry and the stability of diverse food webs. *Nature.* 2006;442:265–9.
49. Stouffer DB, Bascompte J. Compartmentalization increases food-web persistence. *Proc. Natl Acad. Sci. USA.* 2011;108:3648–3652.
50. Banerjee S, Schlaeppi K, van der Heijden. M.G.A. Keystone taxa as drivers of microbiome structure and functioning. *Nat Rev Microbiol.* 2018;16:567–76.
51. Jiao S, Liu ZS, Lin YB, Yang J, Chen WM, Wei GH. Bacterial communities in oil contaminated soils: biogeography and co- occurrence patterns. *Soil Biol Biochem.* 2016;98:64–73.
52. Brinkmann N, Schneider D, Sahner J, Ballauff J, Edy N, Barus H, Irawan B, Budi SW, Qaim M, Danie R, Polle A. Intensive tropical land use massively shifts soil fungal communities. *Sci Rep.* 2019;9:3403.
53. Zaller JG, Heigl F, Ruess L, Grabmaier A. Glyphosate herbicide affects belowground interactions between earthworms and symbiotic mycorrhizal fungi in a model ecosystem. *Sci Rep.* 2014;4:5634.
54. Sahner J, Budi SW, Barus H, Edy N, Meyer M, Corré MD, Polle A. Degradation of root community traits as indicator for transformation of tropical lowland rain forests into oil palm and rubber plantations. *Plos One.* 2015;10(9):e0138077.

55. Mills LS, Soulé ME, Doak DF. The keystone- species concept in ecology and conservation. *Bioscience*. 1993;43:219–24.

56. Power M, Tilman D, Estes J, Menge B, Bond W, Mills S, Daily G, Castilla J, Lubchenco J, Paine R, Power M, Tilman D, Estes J, Menge B, Bond W, Mills L, Daily G, Castilla J, Lubchenco J, Paine R. Challenges in the quest for keystones. *Bioscience*. 1996;46:609–20.

57. Mouquet N, Gravel D, Massol F, Calcagno V. Extending the concept of keystone species to communities and ecosystems. *Ecol Lett*. 2013;16:1–8.

58. Lan GY, Li YW, Lesueur D, Wu ZX, Xie GS. Seasonal changes impact soil bacterial communities in a rubber plantation on Hainan Island China. *Sci Total Environ*. 2018;626c:826–34.

Tables

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

	Bacteria				Fungi			
	Rubber	Rainforest	Rubber	Rainforest	Rubber	Rainforest	Rubber	Rainforest
	Dry	Dry	Rainy	Rainy	Dry	Dry	Rainy	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

Figures

Figure 1

Soil bacterial network structure of rubber plantations and tropical rainforest in dry and rainy seasons. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient > 0.6 , $P < 0.05$

A Fungi (rubber dry season)

B Fungi (rainforest dry season)

C Fungi (rubber rainy season)

D Fungi (rainforest rainy season)

● Ascomycota ● Basidiomycota ● Chytridiomycota ● Rozellomycota ● Zygomycota ● Unclassified

Figure 2

Soil fungal network structure of rubber plantations and tropical rainforest in dry and rainy season. Red lines indicate positive correlation between OTUs, and green indicate negative correlation. Absolute value of correlation coefficient > 0.6 , $P < 0.05$

Figure 3

Soil microbial (bacterial and fungal) network of tropical rainforest and rubber plantations in dry season and rainy season.

Figure 4

Network degree of soil bacterial and fungal community of rubber plantations (blue) and tropical rainforest (red) in dry season and rainy season.

Figure 5

Frequency distributions of correlations in bacterial (a: dry season, b: rainy season) and fungal (c: dry season, d: rainy season) networks of rubber plantations and tropical rainforest in the dry season and rainy season. (Absolute correlation coefficient greater than 0.3, $P < 0.05$) Correlations in rainforest networks are red, correlations in rubber plantation networks are blue.

Figure 6

Proportional influence of different phylum on bacterial and fungal network structure in both dry season and rainy. 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 7

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 dry season and rainy season. (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 , $p < 0.05$

A Bacteria

B Fungi

Figure 8

Two ways correlation network of top 500 most abundant bacterial (A) and fungal (B) OTUs and environmental factors. The size of the node indicates the OTU abundance. A red line indicates positive correlation between species/functions, and green indicates negative correlation. Absolute value of correlation coefficient >

Figure 9

Relationship between abundance of phylum (bacteria: A-E, I-M; fungi: F-H, N-P) and soil properties (Soil pH: A-H; AK (available potassium) concentration: I-P)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementalInformation.docx](#)