



1 **Network complexity of rubber plantations is lower than tropical forests for soil**

2 **bacteria but not fungi**

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9 **Running title:** Forest conversion alters soil microbial networks

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17 **Abstract:**

18 Soil microbial communities play a crucial role in ecosystem functioning. Past
19 research has examined the effects of forest conversion on soil microbial composition
20 and diversity, but it remains unknown how networks within these communities
21 respond to forest conversion such as when tropical rainforest are replaced with rubber
22 plantations. In this study, we used Illumina sequencing and metagenome
23 shotgun sequencing to analyze bacterial and fungal community network structure in a
24 large number of soil samples from tropical rainforest and rubber plantation sites in
25 Hainan Island, China. Our results showed only a few shared network edges were
26 observed in both bacterial and fungal communities, which indicates that forest
27 conversion altered soil microbial network structure. We found a greater degree of
28 network structure and a larger number of network edges among bacterial networks in
29 samples from tropical rainforest compared to samples from rubber plantations. The
30 difference was especially pronounced during the rainy season and indicates that
31 rainforest bacterial networks were more complex than rubber plantation bacterial
32 networks. However, rubber plantations soil fungal networks showed more higher
33 links and higher network degree, suggesting that forest conversion does not reduce
34 fungal network complexity. We found that some groups of Acidobacteria were
35 keystone taxa in our tropical rainforest soils, while Actinobacteria were keystone taxa
36 in rubber plantation soils. In addition, seasonal change had a strong effect on network
37 degree, the complexity of soil bacterial and fungal network structure. In conclusion,
38 forest conversion changed soil pH and other soil properties, such as available



39 potassium (AK) and total nitrogen (TN), which resulted in changes in bacterial and
40 fungal network composition and structure.

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43 **Keyword:** Tropical rainforest, Rubber plantations, Networks, Soil microbial

44 community, Forest conversion

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49 **1. Introduction**

50 Tropical rainforest have the highest biodiversity of any ecosystem and harbor more
51 than 60% of all known plant and animal species (Dirzo and Raven, 2003). However,
52 over the past several decades, logging, mining, slash and burn agriculture have caused
53 widespread deforestation and forest degradation. Of these, the conversion of forest to
54 agriculture has caused the most forest loss (Li et al., 2007).

55 Hainan is home to a large area of tropical rainforest rich in biodiversity. It is a part
56 of the Indian-Malay rainforest system and the northern edge of the world's rainforest
57 distribution. However, rubber plantations now account for almost a quarter of the total
58 extent of vegetated areas on Hainan Island (Lan et al., 2020a).

59 The soil microbiome is highly diverse and comprises up to one quarter of Earth's
60 diversity (Wagg et al., 2019). Soil microbes play a critical role in the maintenance of
61 soil quality and function, and they represent the majority of biodiversity in terrestrial
62 ecosystems (Philippot et al., 2013). A number of studies have investigated the impact
63 of the conversion of tropical forests to rubber plantations on soil microbial
64 composition and diversity (Schneider et al., 2015; Kerfahi et al., 2016, Lan et al.,
65 2017a; 2017b; 2017c; Lan et al., 2020a; 2020b; 2020c). Studies conducted in
66 Indonesia (Schneider et al. 2015), Malaysia (Kerfahi et al. 2016) and South China
67 (Lan et al. 2017a; Lan et al. 2017b; Lan et al. 2017c) have found significant
68 differences between rubber plantations and tropical forests, specifically that the
69 diversity of soil bacteria was higher in rubber plantations than in rainforest. Compared
70 to primary forests, agricultural systems tend to have higher bacterial richness but



71 lower fungal richness ([Lan et al., 2017a](#); [Cai et al., 2018](#); [Tripathi et al., 2012](#); [Kerfahi](#)
72 [et al., 2016](#)). However, there are few studies on the effects of forest conversion on soil
73 microbial network structure.

74 Network analysis is an increasingly popular tool for investigating microbial
75 community structure, as it integrates multiple types of information and may represent
76 systems-level behavior ([Röttjers and Faust, 2018](#)). The soil microbial network is
77 viewed as a critical indicator of soil health and quality ([Kuperman et al., 2014](#)).

78 Network analysis of taxon co-occurrence patterns provides new insight into the
79 structure of complex microbial communities, insight that complements and expands
80 on the information provided by the more standard suite of analytical approaches
81 ([Barberan et al., 2012](#)). Previous work has shown that agricultural intensification can
82 reduce microbial network complexity ([Banerjee et al., 2019](#)). Logging alters soil
83 fungal network in tropical rainforests, i.e., a better-organized fungal community in the
84 select cut stands when compared with the primary stands ([Chen et al., 2019](#)). Soil
85 bacterial networks are less stable under drought than fungal networks ([De Vries et al.,](#)
86 [2018](#)). Soil networks become more connected as ecological restoration progresses
87 ([Morriën et al., 2017](#)). So far, very few studies have assessed the impact of forest
88 conversion on soil microbial networks and it is still unclear whether forest conversion
89 as well as seasonal change influences the structure and complexity of microbial
90 networks. Here we explored bacterial and fungal community network structure using
91 Illumina sequencing based on samples collected from tropical rainforest and rubber
92 plantations in Hainan Island, China. We aimed to test the hypothesis that (1) forest



93 conversion alters microbial networks by altering microbial community composition [3]
94 ([Lan et al., 2020a](#)) and that soil microbial activity is strongly influenced by plant
95 species ([Galicía and García-Oliva 2004](#)). (2) Soil microbial network structure in
96 rainforest sites is more complex and stable than in rubber plantations because natural
97 systems were more connected than artificial systems ([Morriën et al., 2017](#)). By
98 evaluating these hypotheses, we want to clarify the drivers and mechanisms that link
99 forest conversion to differences in soil microbial network structure . This study will
100 provide critical information for understanding and managing microbial communities
101 in tropical forests of China and elsewhere.

102 **2. Methods**

103 **2.1 Study site**

104 This study was conducted on Hainan Island (18°10′–20°10′N and 108°37′–111°03′E),
105 south China. The total area of Hainan Island is about 34,000 km² ([Lopez et al., 2009](#)).
106 Hainan Island is the largest island within the Indo-Burma Biodiversity Hotspot in
107 tropical Asia ([Francisco-Ortega et al., 2010](#)) and has a tropical monsoon climate.
108 Hainan Island has a warm and humid climate all year round, with an average annual
109 temperature of 22-26°C. The rainy season occurs from May to October, with a total
110 precipitation of about 1500 mm, accounting for 70-90% of the total annual
111 precipitation. Only 10-30% of the total annual precipitation falls within the dry
112 season, from November to April. Rainfall is abundant, ranging from 1,000 mm to
113 2,600 mm yearly, with an average annual precipitation of 1,639 mm. The central part
114 of Hainan Island is mountainous and contains old-growth tropical rainforests and



115 monsoon forests. Rubber plantations are found on the plateaus surrounding the
116 central mountainous zone.

117 **2.2 Soil sampling**

118 We selected five rainforests as our study sites: Bangwang mountain, Diaoluo
119 mountain, Wuzhi mountain, Yinge mountain and Jianfeng mountain. Five rubber
120 plantations were selected in Haikou, Danzhou, Qiongzong, Wanning and Ledong
121 (Figure S1). More information on the study sites is provided in Table S1. For each
122 site, thirteen soil samples were collected, thus there were a total of 130 samples
123 collected between the rubber plantations and tropical rainforest per sampling interval.
124 Soil sampling was performed twice in 2018, once in the rainy season (July) and once
125 in the dry season (January). Thus, there were a total of 260 soil samples (130 per
126 forest type). Soil samples were divided into two parts: one was used to analyze soil
127 water contents, soil pH, total nitrogen, total phosphorus (TP), total potassium (TK),
128 nitrate nitrogen (NN), ammonium nitrogen (AN), available phosphorus (AP),
129 potassium (AK). The other was used for DNA extraction. Soil properties were
130 analyzed following the methods described in by Lan et al. (2020b). Soil properties of
131 the rubber plantation and rainforest sites are shown in Table S2.

132 **2.3 DNA extraction and PCR amplification**

133 Microbial DNA was extracted from 0.5 g of soil using the E.Z.N.A.® Soil DNA Kit
134 (Omega Bio-tek, Norcross, GA, U.S.) following the manufacturer's protocol. The
135 fungal ITS1 hypervariable region was amplified using the PCR primers ITS1F
136 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2R



137 (5'-GCTGCGTTCTTCATCGATGC-3') (Adams et al., 2013). For bacteria and
138 archaea, the V4 hypervariable region of the bacterial 16S rRNA gene was amplified
139 using the PCR primers 515FmodF (5'-GTGYCAGCMGCCGCGGTAA-3') and
140 806RmodR (5'-GGACTACNVGGGTWTCTAAT-3') (Walters et al., 2016; Sampson
141 et al., 2016). The PCR reactions were conducted using the following approach: an
142 initial 3 min denaturation at 95°C; followed by 27 cycles of 30s at 95°C, 30s of
143 annealing at 55°C, and 45s of elongation at 72°C; and a 10 min final extension at
144 72°C.

145 **2.4 Illumina MiSeq sequencing**

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

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

156 **2.5 Bioinformatics and data analysis**

157 Raw fastq files were demultiplexed and quality-filtered using QIIME (Caporaso et al.,
158 2010) (version 1.17). Operational Taxonomic Units (OTUs) were clustered with a



159 97% similarity cut-off using UPARSE (Edgar, 2013), and chimeric sequences were
160 identified and removed using UCHIME. Using the RDP Classifier, the phylogenetic
161 affiliation of each 16S rRNA gene and ITS gene sequence was determined using a
162 confidence threshold of 70% with the SILVA 16S rRNA database and UNITE
163 database, respectively (Amato et al., 2013). The relative abundance was determined
164 for each taxon (Good, 1953), and the Shannon and Simpson diversity indices were
165 calculated based on re-sampled sequence data using MOTHUR (Schloss et al.,
166 2009). For each site, the relative abundance of different taxa (Good, 1953) and the
167 Shannon diversity index were calculated based on re-sampled sequence data using
168 MOTHUR (Schloss et al., 2009).

169 2.6 Statistical analysis

170 For the co-occurrence network analyses, we only focus on the top 300 most abundant
171 OTUs of the two forest types. The networks of each habitat during each sampling
172 period (tropical rainforest and rubber plantations in dry season and rainy season) were
173 constructed with 65 samples each. Interactions consisted of Spearman's rank
174 correlations and co-occurrence networks were constructed using only significant
175 correlations of $\rho > 0.6$ ($P < 0.01$) (Barberan et al. 2012), because this cutoff includes
176 a range of interactions strengths (De Vries et al., 2018). The networks were then
177 visualized in R using the *igraph* package. To reveal the distribution pattern of
178 correlation coefficients, the frequency of the coefficients of $\rho > 0.3$ ($P < 0.01$) were
179 plotted. The Network Analyzer tool in Cytoscape (version 3.4.0) was used to calculate
180 network topology parameters including number of nodes, edges, degree, betweenness,



181 closeness. In order to evaluate the network differences between tropical rain forest
182 and rubber forest sites, Venn diagrams were plotted to reveal the number of shared
183 edges and unique edges which were calculated using *igraph*. Keystone OTUs were
184 selected on the basis of high network degree, high closeness centrality, and low
185 betweenness centrality as defined by Berry and Widder (2014). To evaluate the
186 proportional influence of each phylum on bacterial and fungal network structure, node
187 degrees of each phylum were calculated and bar plots were created. Correlation
188 coefficients between species and functions were calculated based on metagenomics
189 data. Here we used the top 50 most abundant species and top 50 KEGG functions
190 (pathway level 3). Then the species and function correlation network was constructed
191 on the Major bio cloud platform (<https://cloud.majorbio.com/>). To reveal the
192 relationship between microbial taxon and environment variables, two-way correlation
193 networks were also constructed on the Major bio cloud platform. The topological role
194 of each node in a network was assessed by the Z_i and P_i values, where Z_i represents
195 the nodes connectivity within a module, and P_i measures the degree of a node
196 connected with other modules (Roger and Amaral, 2005). All species can be divided
197 into four groups according to the simplified criteria (Olesen et al., 2007), namely
198 peripherals ($Z_i < 2.5$ and $P_i < 0.62$), connectors ($P_i > 0.62$), module hubs ($Z_i > 2.5$)
199 and network hubs ($Z_i > 2.5$ and $P_i > 0.62$). The Z_i and P_i values were calculated using
200 GIANT package of Cytoscape. The Z_i - P_i plot was created with *ggplot2* in R.

201 3. Results

202 3.1 Bacterial and fungal networks



203 Our results showed most nodes of bacterial networks (Figure 1) and fungal networks
204 (Figure 2) varied with forest type in both the dry season and rainy season. For
205 bacterial networks, there were 2559 and 2501 edges in tropical rainforest and rubber
206 plantation in dry season respectively, but these two networks only shared 262 edges,
207 accounting only about 10% the total edges (Figure 3A-B). Similarly, these networks
208 only shared 519 edges during the rainy season. For fungal networks, there were only 4
209 and 5 shared edges (i.e., no more than 5% of the total edges) in dry season and rainy
210 season, respectively (Figure 3C-D).

211 The number of edges of bacterial and fungal networks were almost equivalent
212 during the dry season. However, in rainy season, there were more edges in the
213 bacterial network in tropical rainforest than in the rubber plantation (Table 1 & Figure
214 3B). For the network structure of the fungal community, more edges were observed in
215 rubber plantations in rainy season (Table 1 & Figure 3D). Similarly, there were no
216 significant differences in both bacterial and fungal network degree between tropical
217 rainforest sites and rubber plantations in the dry season (Figure 4A, C). In the rainy
218 season, rainforest sites had higher bacterial network degree, while rubber plantations
219 showed higher fungal network degree (Figure 4B, D). For bacterial networks, more
220 nodes (OTUs) with high degree (rubber plantation had 2 nodes with degree greater
221 than 75, rainforest had 8 such nodes) of rainforest were observed during the rainy
222 season (Figure S2B). For fungal networks, 15 nodes of higher degree (degree greater
223 than 25) were observed in rubber plantations, however, only 7 such nodes existed for
224 rainforest sites (Figure S2D). These results indicate rubber plantation fungal network



225 structure was more complex than tropical rainforest during the rainy season, but that
226 the reverse was true for bacteria.

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

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

244 For bacterial groups, members of the phyla Acidobacteria, Planctomycetes and
245 Verrucomicrobia showed higher degree in the tropical rainforest sites than in rubber
246 plantations, suggesting that these taxa are strongly associated with the other members



247 of the community in tropical rainforest (Figure S5A). Members of the phyla
248 Actinobacteria showed higher degree in rubber plantations. Seasonal change also had
249 effects on network degree for soil bacterial networks. For instance, Chloroflex had
250 higher degree in rubber plantation in the dry season, but the opposite is true in the
251 rainy season. For fungal networks, members of Basidiomycota showed higher degree
252 in tropical rainforest sites during in the dry season, however, Ascomycota showed
253 higher degree in rubber plantations (Figure S5C-D) during the rainy season.

254 We used total degree of each phylum to reveal the influence of each phylum on
255 network structure (Figure 6). For bacteria, Proteobacteria, Actinobacteria and
256 Acidobacteria had a large influence on network structure (Figure 6). Acidobacteria
257 and Planctomycetes contributed more to rainforest networks than rubber plantation
258 networks. However, Actinobacteria and Chloroflex showed the opposite. For fungi,
259 Ascomycota and Basidiomycota had large influence of network structure. Both
260 Ascomycota and Basidiomycota had stronger influence on rainforest networks than
261 rubber plantation networks. The influence of Ascomycota was stronger during the
262 rainy season than in the dry season, indicating seasonal change also had impact on
263 fungal community networks.

264 **3.2 Keystone taxa**

265 Keystone OTUs of the bacterial and fungal communities were selected on the basis of
266 high degree, high closeness centrality, and low betweenness centrality. The results
267 showed that forest conversion altered the keystone taxa of bacteria and fungi. The
268 keystone taxa of bacteria were very different between rubber plantations and tropical



269 rainforest sites in both the dry season and rainy season. For bacteria, there were more
270 keystone taxa in tropical rainforest sites than in rubber plantations in both the dry
271 season and rainy season indicating that the tropical rainforest networks had higher
272 complexity. We found that some groups of Acidobacteria are keystone taxa in tropical
273 rainforest sites but disappeared after forest conversion. There were more
274 Actinobacteria bacteria in rubber plantations than in tropical rainforest sites ([Table](#)
275 [S3](#)).

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

283 **3.3 Two-ways correlation networks**

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



291 function in rubber plantations (Figure 7).

292 Two-ways correlation network analysis revealed the interaction between microbial
293 composition and environmental variables. This analysis includes different
294 environmental factors as nodes in the network, and the number of connections these
295 nodes have indicates the number of OTUs that are impacted by that environmental
296 factor (Figure 8). For bacteria, elevation had the highest network degree at 106, and
297 was followed by AK (104), soil pH (86) and TK (9). In other words, elevations, AK,
298 soil pH are all drivers of bacterial community composition. Soil pH negatively
299 correlated with most bacterial Acidobacteria OTUs. For fungi, elevation had the
300 highest network degree (61), followed by AK (51), longitude (15), and NN (11). AK
301 positively correlated with most OTUs of Basidiomycota. Relationship between OTU
302 abundance and soil pH revealed the soil pH negatively correlated with members of
303 Acidobacteria, but positively correlated with members of Chloroflexi and members of
304 Ascomycota (Figure 9). AK positively correlated with members of Planctomycetes
305 Verrucomicrobia and Basidiomycota, however negatively correlated with Chloroflexi
306 and Ascomycota.

307

308 **4. Discussion**

309 **4.1 Forest conversion reduces soil bacterial network complex**

310 Land-use changes increasingly threaten biodiversity, particularly in tropical forests
311 (Gibson et al., 2011). However, we still have little understanding of how soil
312 networks respond to forest conversion, such when rainforests are converted to rubber



313 plantations. Our results showed that forest conversion had large effects on both soil
314 bacterial and fungal networks. More edges ([Table 1](#)) and higher degree ([Figure 4](#)) of
315 tropical rainforest bacterial networks were observed, especially during the rainy
316 season, which indicates that the rainforest bacterial network was more complex than
317 the rubber plantation network. This consistent with previous observations that soil
318 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 as nature
319 restoration progresses ([Morriën et al., 2017](#)). The observed decrease in network
320 complexity and cohesion supports the hypothesis that cropping may enhance the
321 isolation of bacterial taxa ([Karimi et al., 2019](#)), which results in lower connection of
322 the network. In addition, at the microscale, the structure of tilled soils is more
323 homogeneous, and the soil pores are less connected than in soils under without tillage
324 ([Pagliai et al., 2004](#)), such as rainforest soil. In nature, soil ecosystems are highly
325 heterogeneous since soil microbial biodiversity hot spots can form spatial and
326 temporally within soil aggregates ([Bach et al., 2018](#)). This spatial heterogeneity likely
327 plays an important role for the interactions among microbes and the mechanisms by
328 which more complex and diverse communities drive various nutrient cycling
329 processes on small spatial scales ([Wagg et al., 2018](#)).

331 A large number of studies employing microbial network analysis have enriched
332 our understanding of microbial co-occurrence patterns in various soil ecosystems,
333 however, very little is known of whether differences in the structure of microbial
334 networks have consequences for microbiome functioning ([Wagg et al., 2018](#)). Our



335 results demonstrated that more species related with metabolism in natural system than
336 in the agricultural system, especially in the rainy season. This is in line with a
337 previous study conducted in Sumatra, Indonesia, which found that the transformation
338 of forest to rubber results in a 10-16% decrease in community metabolism (Barnes et
339 al., 2014). Fewer interactions between microbial species (most of them are bacteria)
340 and functions in rubber plantations demonstrated that forest conversion reduced soil
341 bacterial network complex.

342 **4.2 Forest conversion does not reduce soil fungal network complexity**

343 Surprisingly, rainforest bacterial networks were characterized by fewer edges (Table 1)
344 and lower degree (Figure 4), which means that rubber plantation bacterial networks
345 were more complex than the native forest. Although, our results were consistent with
346 previous observations which found that fungal community networks were better
347 organized disturbed forest compared to primary forest (Chen et al., 2019). Banerjee et
348 al. (2019)'s observation showed that organic agricultural fields harbored much more
349 complex fungal networks with many more keystone taxa than conventional managed
350 fields. Forest conversion resulted in shifts in fungal composition from Basidiomycota
351 to Ascomycota (Figure S7), as seen in previous investigations (Lan et al., 2020a; Lan
352 et al., 2020b). Previous work showed that Basidiomycota species show higher drought
353 sensitivity than Ascomycota species (Taniguchi et al., 2018), this would result in a
354 shift in richness and abundance of Basidiomycota species (Figure S6). Many
355 Basidiomycota species are capable of long-distance dispersal (Egidi et al. 2019, Geml
356 et al., 2012), which may result in a decrease in fungal network. This possibly



357 explained why Ascomycota OTUs contribute more to the network structure than
358 Basidiomycota (Figure 6). Overall, reduction in abundance and richness of
359 Basidiomycota species led to an increase in fungal links in rubber plantations.

360 **4.3 Forest conversion enhanced the stability of soil network**

361 The positive to negative ratio of network links indicates the balance between
362 facilitative and inhibitive relationships within a network (Karimi et al., 2017).
363 Theoretical studies, for example, predict that ecological networks that consist of weak
364 interactions are more stable than those with strong interactions (Neutel et al., 2002,
365 Coyte et al., 2015), and that compartmentalization and presence of negative
366 interactions increase the stability of networks under disturbances (Coyte et al., 2015,
367 Rooney et al., 2006, Stouffer & Bascompte 2011). In our study, more negative
368 correlations were detected in rubber plantation, indicating the network structure of
369 rubber plantation soils was more stable than rainforest soils (De Vries et al., 2018).

370 **4.4 Driver of the network structure**

371 Forest conversion results in the loss of plant diversity, plant biomass and increasing
372 soil pH (Lan et al., 2017a, 2017b). Rubber plantations had a significantly higher pH,
373 which explains the relative decrease in the abundance of Acidobacteria (Lan et al.,
374 2017a). Our results demonstrate that keystone taxa of soil microbes change after
375 forest conversion (Table 1). We found that many OTUs of Acidobacteria fit our
376 criteria as keystone species for rainforest sites, which is consistent with previous
377 findings (Banerjee et al., 2018). Unexpectedly, OTU11388 and OTU11373, both
378 Acidobacteria, were observed in rainforest soils in both the dry and rainy seasons,



379 indicating Acidobacteria were very important for rainforest soil bacterial networks
380 (Figure 6 and table S3). Higher AK concentration resulted in a higher abundance and
381 more taxa of of Actinobacteria (Figure 9), which suggests that Actinobacteria
382 contributed more in rubber plantation than in rainforest (Figure 6). Indeed, forest
383 conversion reduced the abundance of Actinobacteria OTUs (Figure S7) Due to the
384 human disturbance in rubber plantations, the soil will inevitably be slightly polluted
385 with herbicides and domestic garbage. Previous study showed member of
386 Actinobacteria were observed in contaminated soil (Jiao et al., 2016).

387 Forest conversion also increases land use intensity (Brinkmann et al., 2019),
388 including the application of fertilizer and herbicide. Herbicide application also
389 caused significant decreases in root colonization and spore biomass of arbuscular
390 mycorrhizal fungi in tropical agriculture (Zaller et al., 2014). Soil nutrient
391 concentration shows a decline around the roots of rubber plantations compared to
392 those from rainforests (Sahner et al., 2015). Our observation is no exception, for
393 instance, AK and TN concentration was significant lower in rubber plantation than in
394 samples from rainforest sites (Table S2). Higher concentration of AK reasonably
395 explained the higher contribution of Basidiomycota on the network structure (Figure
396 8B) due to AK positive association with Basidiomycota.

397 Spatiotemporal heterogeneity can be a major driver of the abundance and
398 distribution of keystone taxa in soil which is a highly heterogeneous and multifaceted
399 environment (Mills et al., 1993; Power et al., 1996; Mouquet et al., 2013). Seasonal
400 variability determines the structural and compositional properties of microbiomes in



401 an environment, and as such, a keystone species might be present only in a specific
402 season or time period (Banerjee et al., 2018). It was interesting that more bacterial
403 OTUs were identified as connectors during the rainy season than in the dry season.
404 Connectors have been characterized as generalists (Olesen et al., 2007), and
405 generalists drive covariation among communities in a network (Chen et al., 2019).
406 Previous observation demonstrated that some keystone taxa that were found in the dry
407 season disappeared during the rainy season (Lan et al., 2018) . Seasonal changes
408 possibly explained the keystone taxa was observed in rainy season but not in dry
409 season.

410 **5. Summary**

411 Our knowledge about land-use impacts on soil ecosystems is mostly limited to
412 biodiversity and ecosystem functions, leaving uncertainty about how soil networks
413 change after forest conversion. This study is the most comprehensive report on
414 changes in network structure that occur when tropical rainforests are converted into
415 rubber forest. Our study showed that forest conversion altered both bacterial and
416 fungal soil networks, reduced bacterial network complexity and enhanced fungal
417 network complexity, especially during the rainy season. One possible reason maybe
418 that forest conversion changed soil pH and other soil properties, which altered
419 bacterial composition and subsequent network structure. Our study demonstrates the
420 impact of forest conversion for soil network structure, which has important
421 implications for ecosystem functions and health of soil ecosystems in tropical regions.

422



423

424 **Availability of data and material**

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

427 **Code availability**

428 Not applicable

429 **Authors' contributions**

430 Guoyu Lan: Conceptualization, Methodology, Writing- Reviewing and Editing;
431 Chuan Yang and Zhixiang Wu: Investigation

432 **Competing interests**

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

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446

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627 **Figure legend**

628 **Figure 1** Soil bacterial network structure of rubber plantations and tropical rainforest
629 in dry and rainy seasons. Red lines indicate positive correlation between OTUs, and
630 green indicate negative correlation. Absolute value of correlation coefficient > 0.6 , P
631 < 0.05

632 **Figure 2** Soil fungal network structure of rubber plantations and tropical rainforest in
633 dry and rainy season. Red lines indicate positive correlation between OTUs, and
634 green indicate negative correlation. Absolute value of correlation coefficient > 0.6 , P
635 < 0.05

636 **Figure 3** Soil microbial (bacterial and fungal) network of tropical rainforest and
637 rubber plantations in dry season and rainy season.

638 **Figure 4** Network degree of soil bacterial and fungal community of rubber plantations
639 (blue) and tropical rainforest (red) in dry season and rainy season.

640 **Figure 5** Frequency distributions of correlations in bacterial (a: dry season, b: rainy
641 season) and fungal (c: dry season, d: rainy season) networks of rubber plantations and
642 tropical rainforest in the dry season and rainy season. (Absolute correlation coefficient



643 greater than 0.3, $P < 0.05$) Correlations in rainforest networks are red, correlations in
644 rubber plantation networks are blue.

645 **Figure 6** Proportional influence of different phylum on bacterial and fungal network
646 structure in both dry season and rainy. The influence was the number of degrees of
647 nodes belonging to a particular phylum. (a: bacteria in dry season, b: bacteria in rainy
648 season, c: fungal in dry season, d: fungal in rainy season).

649 **Figure 7** Network of the top 50 most abundant species (based on metagenomics data)
650 and top 50 most frequent KEGG functions (pathway level 3) of rubber plantations and
651 tropical rainforest sites in dry season and rainy season. (A: rubber in dry season; B:
652 rainforest in dry season; C: rubber in rainy season; D: rainforest in rainy season) The
653 size of the node indicates the species/function abundance. A red line indicates positive
654 correlation between species/functions, and green indicates negative correlation.
655 Absolute value of correlation coefficient > 0.6 , $p < 0.05$

656 **Figure 8** Two ways correlation network of top 500 most abundant bacterial (A) and
657 fungal (B) OTUs and environmental factors. The size of the node indicates the OTU
658 abundance. A red line indicates positive correlation between species/functions, and
659 green indicates negative correlation. Absolute value of correlation coefficient > 0.5 , p
660 < 0.05 .

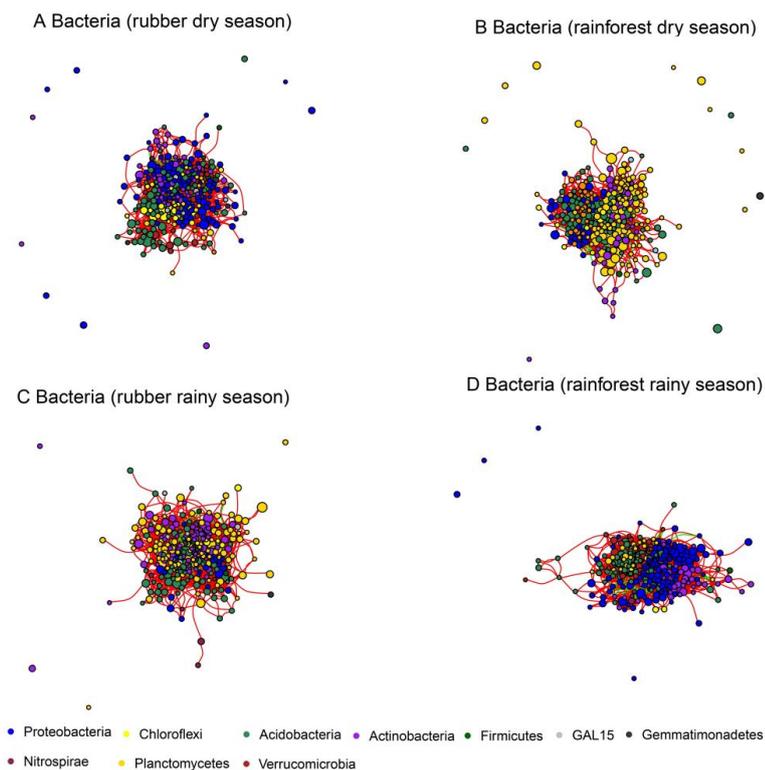
661 **Figure 9** Relationship between abundance of phylum (bacteria: A-E, I-M; fungi: F-H,
662 N-P) and soil properties (Soil pH: A-H; AK (available potassium) concentration: I-P)

663



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

	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

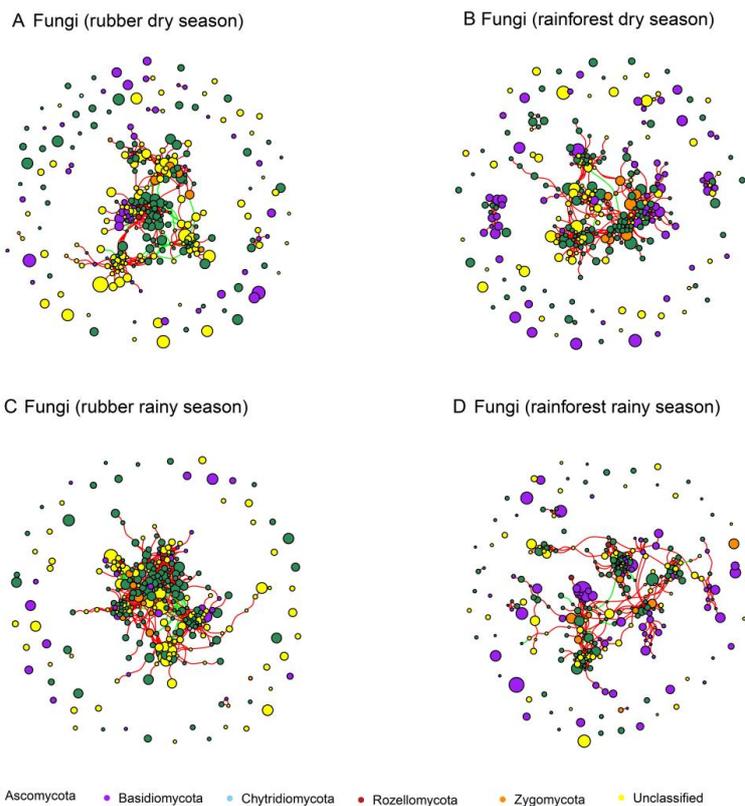


666

667 **Figure 1** Soil bacterial network structure of rubber plantations and tropical rainforest in dry and
668 rainy season. Red line indicates positive correlation between OTUs, and green indicates negative
669 correlation. Absolute value of correlation coefficient > 0.6 , $p < 0.05$

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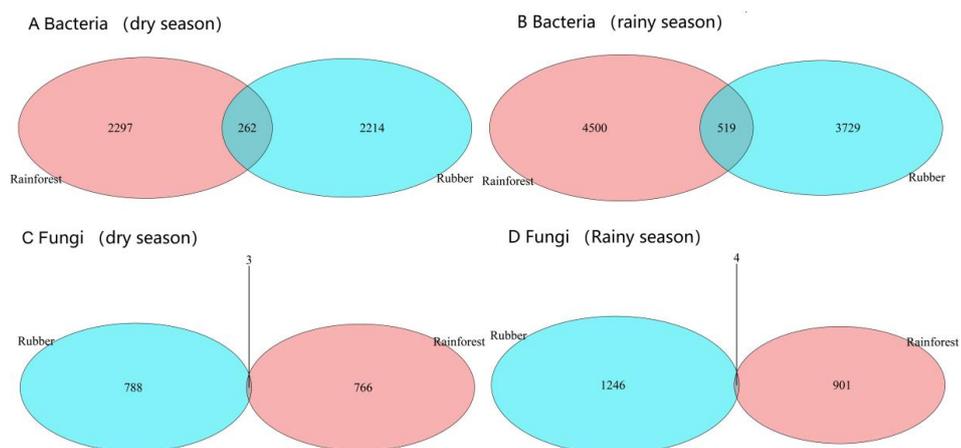
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673 **Figure 2** Soil fungal network structure of rubber plantations and tropical rainforest in dry and
674 rainy season. Red line indicates positive correlation between OTUs, and green indicates negative
675 correlation. Absolute value of correlation coefficient > 0.6 , $p < 0.05$
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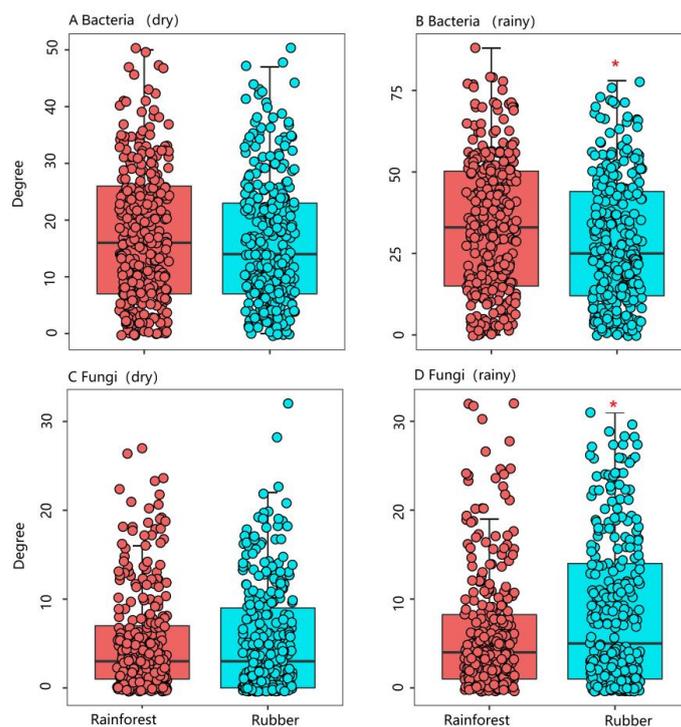
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Figure 3 Soil microbial (bacterial and fungal) network of tropical rainforest and rubber plantations in dry season and rainy season.

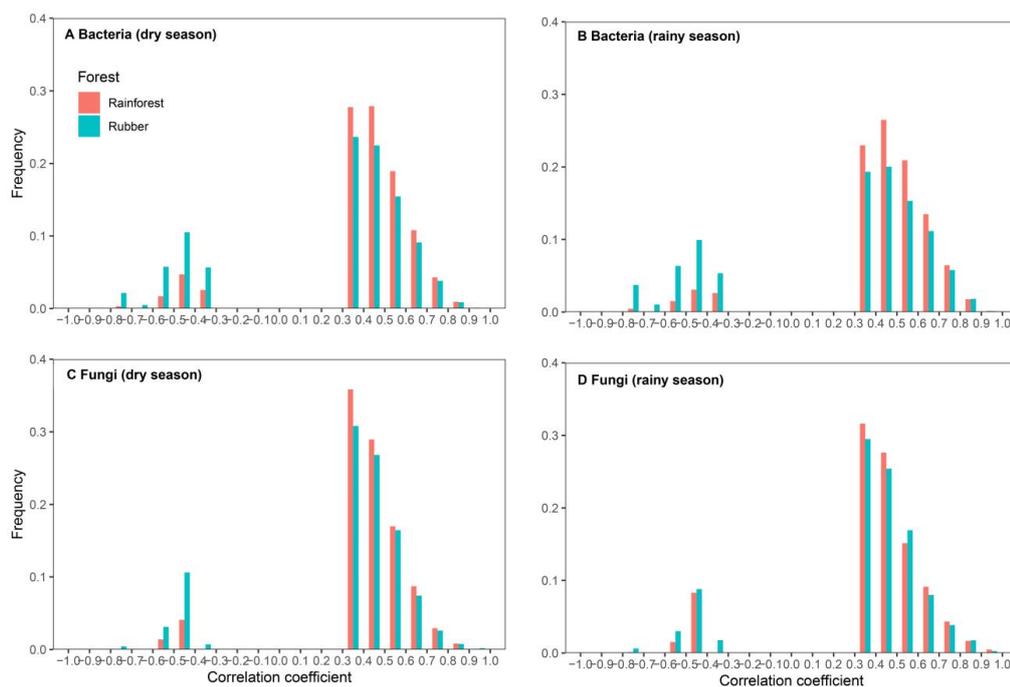


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Figure 4 Network degree betweenness of soil bacterial and fungal community of rubber plantations (blue) and tropical rainforest (red) in dry season and rainy season.



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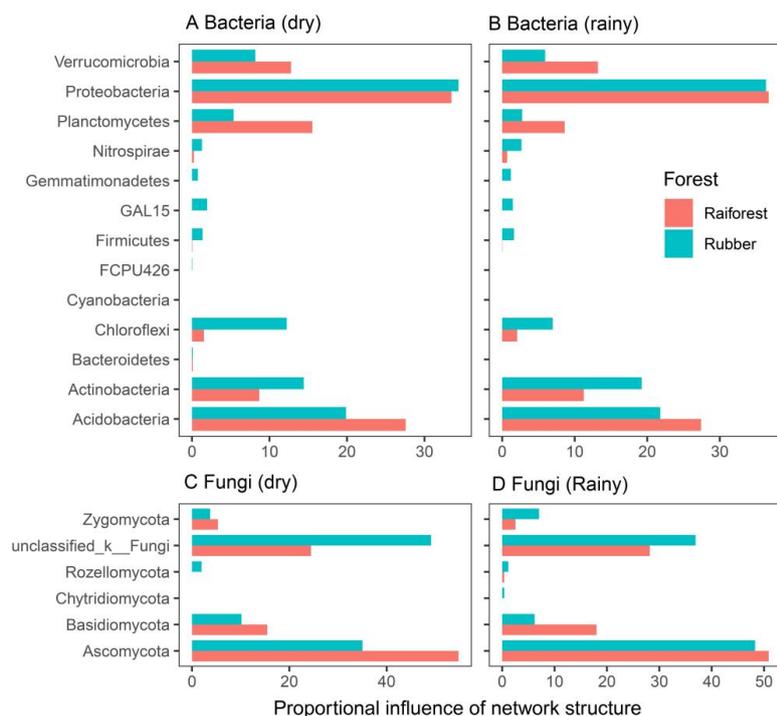


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689 **Figure 5** Frequency distributions of correlations in bacterial (a: dry season, b: rainy season) and
690 fungal (c: dry season, d: rainy season) networks of rubber plantations and tropical rainforest in dry
691 season and rainy season. (Absolute correlation coefficient greater than 0.3, $p < 0.05$) Correlations
692 in rainforest networks are red, correlations in rubber plantation networks are blue.
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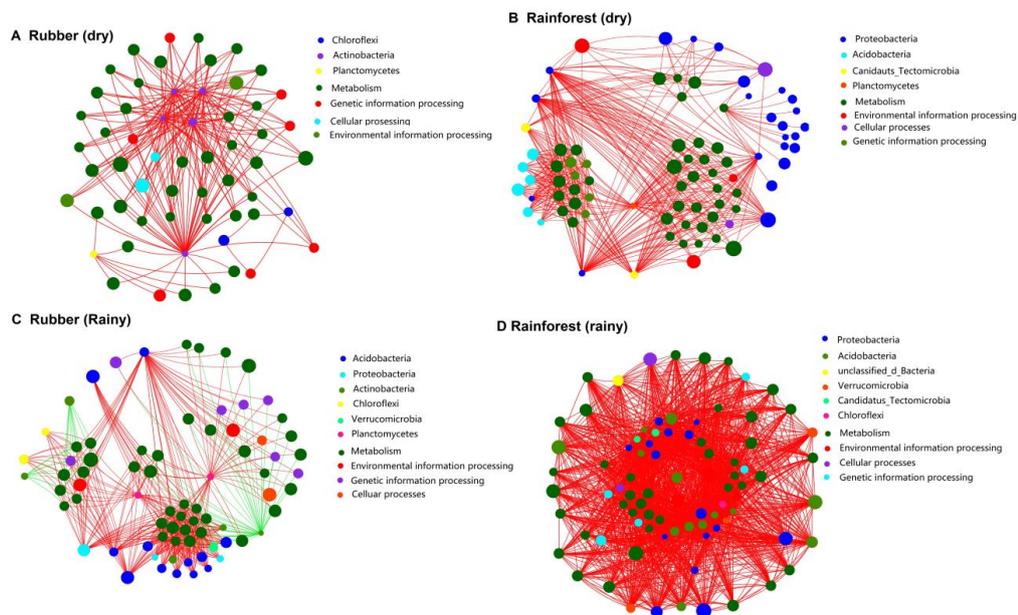


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696 **Figure 6** Proportional influence of different phylum on bacterial and fungal network structure in
697 both dry season and rainy. The influence was the number of degrees of nodes belonging to a
698 particular phylum. (a: bacteria in dry season, b: bacteria in rainy season, c: fungal in dry season, d:
699 fungal in rainy season).

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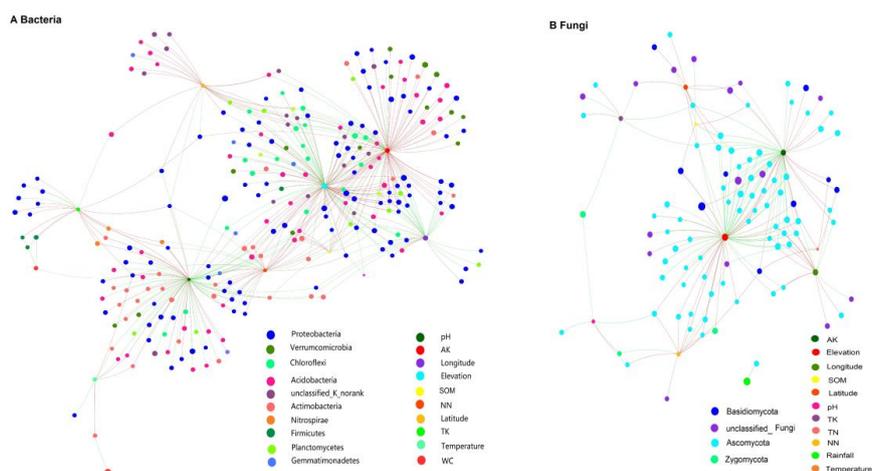
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703 **Figure 7** Network of the top 50 abundant species (based on metagenomics data) and top 50
704 abundant KEGG function (pathway level 3) of rubber plantations and tropical rainforest in dry
705 season and rainy season. (A: rubber in dry season; B: rainforest in dry season; C: rubber in rainy
706 season; D: rainforest in rainy season) The size of the node indicates the species/function
707 abundance. Red line indicates positive correlation between species/functions, and green indicates
708 negative correlation. Absolute value of correlation coefficient > 0.6 , $p < 0.05$

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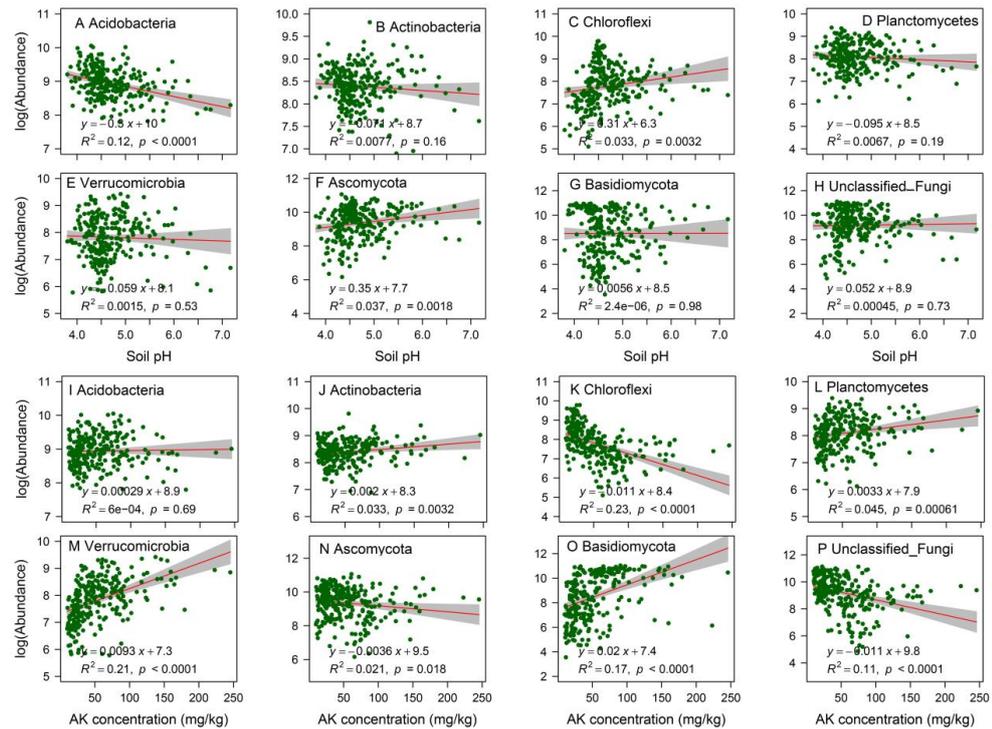
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712 **Figure 8** Two ways correlation network of top 500 abundant bacterial (A) and fungal (B) OTU
713 and environmental factors. The size of the node indicates the OTU abundance. Red line indicates
714 positive correlation between species/functions, and green indicates negative correlation. Absolute
715 value of correlation coefficient > 0.5 , $p < 0.05$.

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718

719 **Figure 9** Relationship between abundance of phylum (bacteria: A-E, I-M; fungi: F-H,

720 N-P) and soil properties (Soil pH: A-H; AK (available potassium) concentration: I-P)