Title

Deforestation decreases spatial turnover and alters the network interactions in soil bacterial communities

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Deforestation decreases spatial turnover and alters the network interactions in soil bacterial communities

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Highlights

- Deforestation decreased bacterial spatial turnover rate at large geographic scale.
- Soil pH and SOM availability strongly affected bacterial spatial turnover rate.
- Bacterial networks were more intricate in primary than in secondary forests.
- Bacterial taxa tended to co-occur in secondary forest network.
- The major connectors in the secondary forest network were *Proteobacteria.*

Abstract

Despite important progress in understanding the influence of deforestation on the bacterial α diversity and community structure at local scales, little is known about deforestation impacts in terms of spatial turnover and soil bacterial community network interactions, especially at regional or global scales. To address this research gap, we examined the bacterial spatial turnover rate and the species networks in paired primary and secondary forest soils along a 3700-km north-south transect in eastern China using high-throughput 16S rRNA gene sequencing. The spatial turnover rate of bacterial communities was higher in primary foreststhan in secondary, suggesting deforestation increased biotic homogenization at a large geographic scale. Multiple regression on matrices analysis revealed that both geographic distance and soil properties (especially soil pH and organic matter availability) strongly affected bacterial spatial turnover. Through the phylogenetic molecular ecological networkapproach, we demonstrate that the bacterial network of primary forests was more intricate than in secondary forests.

This suggests that microbial species have greater niche-sharing and more interactions in primary forests as compared to secondary forests. On the other hand, the bacterial network in secondary forests was more modular, and the taxa tended to co-occur, with positive correlations accounting for 82% of all potential interactions. In conclusion, our findings demonstrate that anthropogenic deforestation has clear effects on bacterial spatial turnover and network interactions, with potential for serious consequences such as microbial diversity loss in primary forests.

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Keywords

Deforestation
Bacterial community structure
Spatial turnover rate
Microbial network interactions
Distance-decay relationship

1. Introduction

More and more primary forests are being cleared or strongly disturbed globally by human activities to make free areas for agriculture, wood production, human habitation and industry (Gómez-Acata et al., 2016). With increasing intensity of anthropogenic perturbations, more attention is being placed on secondary forests, since they may act as buffer zones and serve as a habitat for forest plants, animals and microorganisms displaced from destroyed primary forests (Brearley et al., 2004). Soil microbial communities are engineers of important biogeochemical processes and play a critical role in regulating the functions and stability of an ecosystem (Naeem and Li, 1997; Fuhrman, 2009). Many studies showed that deforestation changed soil bacterial α diversity, composition and community structure on local scales (Jesus et al., 2009; Bastida et al., 2015; Gómez-Acata et al., 2016; Wood et al., 2017). However, little is known about the effects of deforestation on spatial turnover and species interactions of bacterial community at a large spatial scale, e.g. regional, continental or global. Distance-decay relationships describe the decrease in community similarity with increasing geographic distance, with the slope reflecting the spatial species turnover rate (Nekola and White, 1999; Soininen et al., 2007; Hanson et al., 2012). This trend has been reported for microorganisms across a broad range of habitats and spatial scales (Horner-Devine et al., 2004; Martiny et al., 2006; Morlon et al., 2008; Bell,

2010; Wang et al., 2017; Zhou et al., 2008). Distance-decay relationships can be explained by two mechanisms: (1) similarity decays with distance due to environmental differences, which is attributable to niche-based community processes, with species differing in terms of their ability to adapt to environmental conditions (Nekola and White, 1999; Soininen et al., 2007); (2) community similarity declines with distance due to an organisms' limited dispersal, even if the environment is completely homogeneous (Soininen et al., 2007). There are evidences suggesting that both mechanisms are important for shaping the distance-decay relationship (Fierer and Jackson, 2006; Dini-Andreote et al., 2015; Ge et al., 2008; Chu et al., 2010; Xiong et al., 2012; Hendershot et al., 2017). However, most of these studies investigating spatial microbial community turnover rate have examined natural habitats such as those under natural forests, grasslands or marshes. Little is known about how microbial spatial turnover is affected by anthropogenic activities (e.g., long-term fertilization and elevated CO_2levels) (Liang et al., 2015; Deng et al., 2016) and only one study has focused on deforestation to date (Rodrigues et al., 2013). Rodrigues et al. (2013) found that conversion of Amazon tropical rainforest to cropland reduced the microbial turnover rate along a 10-km transect. However, it remains unclear whether deforestation influences microbial turnover rate across large spatial scales in different ecosystems and habitats. Clarifying the mechanisms that generate and maintain patterns of diversity is critical for predicting ecosystem responses to anthropogenic driven-changes.

Microorganisms coexist as complex arrays in many environments, and clarifying their interactions can provide insight into microbial diversity and function (Hallam and McCutcheon, 2015; Shi et al., 2016). Network analysis has proven a powerful way to study the complex community organization and member interactions in different ecological systems (Zhou et al., 2011). These interactions can be positive (e.g., mutualism) or negative (e.g., competition), and maybe depicted by a network model (Faust and Raes, 2012; Zhou et al., 2011; Deng et al., 2012), in which each node represents a species and the edge linking two nodes represent the relationship between the two species (Zhou et al., 2011; Deng et al., 2012). Network analysis can also identify keystone taxa that are critical for maintaining community structure and function (Power et al., 1996; Zhou et al., 2011; Deng et al., 2012). Recent studies have investigated microbial interactions in natural habitats or in response to human activities (e.g. elevated CO_2, oil pollution, and land use change) (Zhou et al., 2011; Liang et al., 2015; Deng et al., 2016; Ma et al., 2016), but the effects of deforestation on these interactions across large scales is unknown.

Deforestation is a very common land use change practice, which has far reaching environmental implications. With particular relevance to microbial habitats, deforestation leads to a broad number of environment modifications such as surface water losses and consequently more frequent soil drought (Bagley et al., 2014), decreased litter input and altered biochemical composition (Zou et al., 1995) and changed soil physicochemical characteristics (Gómez-Acata et al., 2016). Thus, we hypothesize that 1) deforestation may decrease the habitat differences among secondary forests, and consequently decrease the spatial microbial turnover rate at a large scale. In addition, the abundance and composition of key bacterial taxa have been shown to be sensitive to deforestation (Bastida et al., 2015; Navarrete et al., 2015; Gómez-Acata et al., 2016). Therefore, we also hypothesize that 2) deforestation may alter microbial interspecies interactions; bacterial taxa tend to present negative co-occurrence patterns as disturbance can promote microbial competition (Violle et al., 2010; Liang et al., 2015). To test these hypotheses, soil was sampled in paired primary and nearby disturbed secondary forests in nine geographic regions along a 3700-km transect to investigate whether deforestation influences microbial spatial turnover and interaction patterns.

2. Materials and methods

2.1. Study sites and field sampling

The study was conducted at nine sites across a 3700-km north-south transect of eastern China (108.9° E, 18.7° N to 123.0° E, 51.8° N; Supplementary Fig. S1). The sampling sites ranged from cold temperate coniferous forest to tropical rainforest across a northern latitudinal gradient from 51° to 18°. These sites ranged in terms of mean annual temperature from −3.67 °C to 23.2 °C, and annual precipitation from 473 to 2266 mm. Soil physicochemical characteristic differences can be found in Supplementary Table S1.

Within each primary forest site, four representative plots (30 m × 40 m) were established. Sampled primary forests were deemed well-protected national nature reserves that avoid any influence of human activities. Comparable four plots were established in nearby secondary forests which were severely disturbed by anthropogenic activities in the history. Soil was sampled from each plot by collecting 20 randomly selected cores (0–10 cm deep) that were thereafter, well mixed and homogenized. In total, 72 soil samples were collected in this study. Plant roots and leaves were carefully removed and discarded from the soil samples. A portion of each soil sample was transferred to a 50-ml centrifuge tube that was placed in an ice-box and

transferred to the laboratory. The soil tubes were stored at −80 °C for DNA extraction. The remaining soil was used for physicochemical analyses.

2.2. Soil physicochemical analyses

Soil organic carbon (SOC) and total nitrogen (TN) contents were determined with a Vario EL III Elemental Analyzer (Elementar, Langenselbold, Germany). Soil total phosphorous (TP) content was determined using the ammonium molybdate method after H_2SO_4-H_2O_2-HF digestion. Available phosphorus (AP) content was also determined using the ammonium molybdate method (no prior digestion). Particulate organic carbon (POC) content was determined according to Cambardella and Elliott (1992). The concentration of dissolved organic carbon (DOC) was determined according to Jones and Willett (2006). Humuscomposition was analyzed as reported in an earlier study (Kumada, 1988) with some modifications (Zhang et al., 2011). Soil pH was measured using a pH meter (1:2.5 w/v). Mean values for soil physicochemical properties in each forest sample are presented in Supplementary Table S2.
The soil organic matter (SOM) mineralization rate was used to represent SOM availability (Fierer and Jackson, 2006, 2007) and was estimated by measuring the rates of CO_2production over a 14-day incubation at 25 °C after adjusting soil samples to 60% water-holding capacity.

2.3. 16S rRNA gene amplicon sequencing and processing

DNA was extracted from 0.5 g of well-mixed soil using the PowerSoil kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The V3-V4 hypervariable regions of bacterial 16S rRNA genes were amplified using the primers 338F 5′-barcode-ACTCCTACGGGAGGCAGCAG-3′ and 806R 5′-GGACTACHVGGGTWTCTAAT-3′. PCR reactions were performed in triplicate with a 20 μL mixture containing 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, and 10 ng of template DNA. The following thermal program was used for amplification: 95 °C for 3 min, followed by 27 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s and a final extension at 72 °C for 10 min. PCR amplicons were extracted from 2% agarose gels and purified using an AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions and quantified using QuantiFluor™ -ST (Promega, USA). The purified amplicons from all samples were pooled in equimolar concentrations. Sequencing was conducted on an Illumina MiSeq platform at Majorbio BioPharm Technology Co., Ltd. (Shanghai, China).

Raw sequences >200 bp with an average quality score >20 and without ambiguous base calls were quality processed using the Quantitative Insights into Microbial Ecology (QIIME) pipeline (version 1.17). Operational taxonomic units (OTUs) were clustered with a 97% similarity cutoff using UPARSE (Edgar et al., 2011) (version 7.1 http://drive5.com/uparse/). The taxonomic assignment was performed using the Ribosomal Database Project (RDP) classifier (http://rdp.cme.msu.edu/). To correct for sampling effort (number of analyzed sequences per sample), we used a randomly selected subset of 18460 sequences per sample for subsequent analysis.

2.4. Network construction and analysis

Networks were, separately, constructed for primary and secondary forests based on 16S rRNA gene sequence data. The framework for network construction can be divided into four key steps: (1) metagenomic sequence collection, (2) data standardization, (3) pair-wise similarity estimation, and (4) adjacent matrix determination according to a random matrix theory (RMT)-based approach (Zhou et al., 2011).
Global network properties such as average degree (connectivity), average path length, and average clustering coefficient were characterized for the primary and secondary forest networks. The definitions and calculations of these indices have been previously described (Zhou et al., 2011; Deng et al., 2012). The network module is a group of highly interconnected nodes (operational taxonomic units (OTUs) in this study) with few connections outside the group (Zhou et al., 2011). Modularity describes the extent, to which nodes attain more links within their own modules than expected for random linkages. Modules were detected by the greedy modularity optimization method (Deng et al., 2012). The connectivity of each node was determined based on its within-module connectivity (Z_i) and among-module connectivity (P_i) (Guimera and Amaral, 2005). Node topologies were organized into four categories: (1) module hubs (highly connected nodes within modules, $Z_i > 2.5$); (2) network hubs (highly connected nodes within the entire network, $Z_i > 2.5$ and $P_i > 0.62$); (3) connectors (nodes connecting modules, $P_i > 0.62$), and (4) peripherals (interconnected nodes in modules with few outside connections, $Z_i < 2.5$ and $P_i < 0.62$) (Olesen et al., 2007; Zhou et al., 2011; Deng et al., 2012). Topological network features in the primary and secondary forests were compared using a Student's t-test. The above analyses were carried out using the Molecular Ecological Network Analyses pipeline (http://ieg2.ou.edu//MENA/), with the networks being prepared as graphs using Cytoscape v.2.6.2software (Cline et al., 2007).

2.5. Statistical analysis

A geographic distance matrix was calculated using latitudinal and longitudinal coordinates of each sampling site using a *gdist* function (R package *Imap*). Matrices of pairwise taxonomic distances between bacterial communities were analyzed using the Bray-Curtis method. The microbial spatial turnover rate were calculated by determining the slope of the distance-decay relationship (Rodrigues et al., 2013; Deng et al., 2016), which was plotted as a logarithmic similarity against a logarithmic distance with the slope obtained by linear regression. To assess the significance of the distance-decay relationship curve, we examined whether the slopes were significantly less than zero with 1000 permutations (Martiny et al., 2011). The significance of slopes between primary and secondary forests was also evaluated by permutation.
Multiple regression on matrices (MRM) was used to assess linkages between the distance-decay relationship, and measured environmental variables and geographic distance (Legendre et al., 1994). Partial regression coefficients of an MRM model provided a measure of the rate of change in microbial community similarity for variables of interest when other variables were constant (Martiny et al., 2011; Deng et al., 2016). R package *Ecodist* was used for MRM calculations (Goslee and Urban, 2007).

2.6. Data accessibility

The raw sequence data from this study were deposited in the SRA at the NCBI database with the assigned study SRP136586 and Biosamples SAMN08802961-SAMN 08803032.

3. Results

3.1. Distribution of taxa and phylotypes

Of the 72 soil samples, a total of 1,356,031 and 1,334,898 qualified sequences were obtained for the primary and secondary forests, respectively. When all samples were compared, at an equivalent sequencing depth of 18,460 per sample, soils from the primary forests showed higher OTU richness (1497) than those from the secondary forests (1360) at the 97% similarity level. The predominant phyla were *Acidobacteria*, *Actinobacteria*, Proteobacteria, *Chloroflexi* and Verrucomicrobia (relative abundance >3%) for both primary and secondary forests, which accounted for more than 84% of bacterial sequences (Table S3). In addition, the relative abundances at different taxonomical level were counted (Table S3). For example, the *Acidobacteria* and *alphaproteobacteria* are most dominant phylotypeat the

class level, and the *Rhizobiales* is the most dominant phylotype at the order level (Table S3).

3.2. Bacterial community spatial turnover rate and driving factors in primary and secondary forests

There were significant distance-decay relationships for bacterial communities in both types of forests based on the OTU level ($p < 0.001$; Fig. 1). The slope for primary forests ($r = 0.075$) was steeper than that for secondary forests ($r = 0.068$; $p < 0.001$, permutation test). At the class level, we also observed steeper slopes for primary forests ($r = 0.047$) than that for secondary forests ($r = 0.042$) (Fig. S2; $p < 0.001$, permutation test). These results suggest that spatial turnover rate of soil bacterial community is higher in primary as compared to secondary forests. The average community β diversity was lower in secondary forests than in primary forests ($p < 0.05$; Fig. S3).

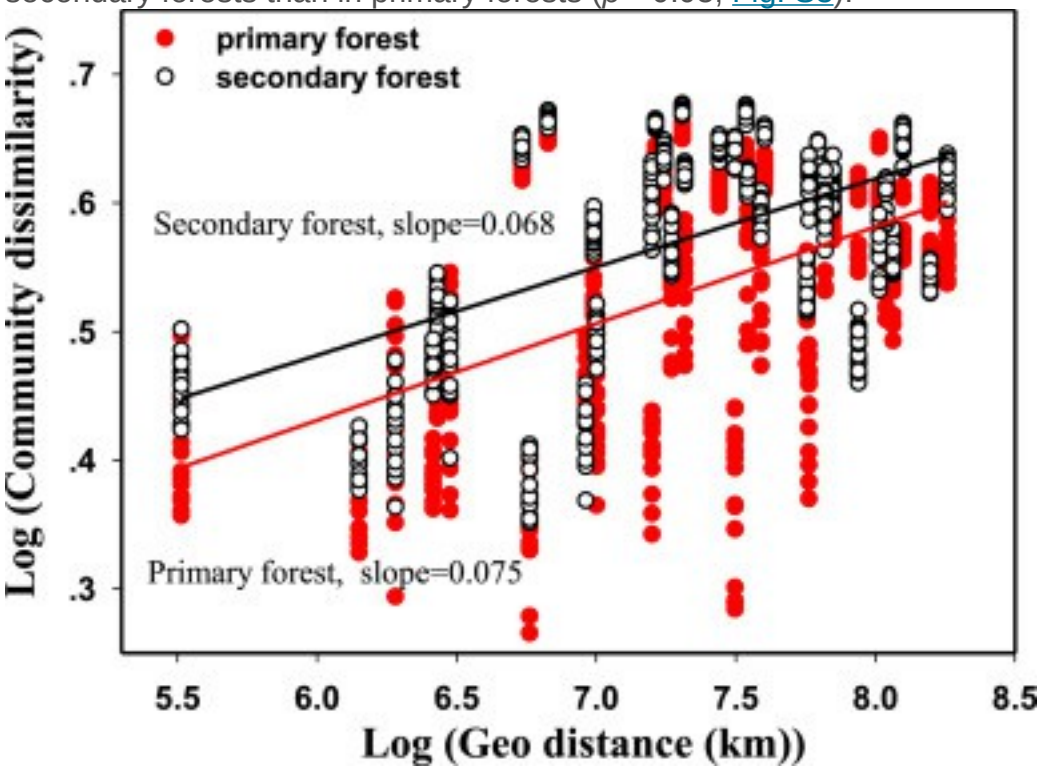

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Fig. 1. Distance-decay relationships of bacterial communities in primary and secondary forest soils.

For the geographic distances of any two samples among the nine forests, the slope of primary forestswas 0.075, and the slope of secondary forests was 0.068; the permutation test indicated that two slopes were significantly different ($p < 0.001$).

MRM was used to assess the relative contribution of geographic distance and soil properties to the observed β diversity (Table 1). A large and significant proportion of the variability in bacterial communities were explained by the MRM model (63.9% and 80.3% for primary and secondary forests, respectively; $p < 0.001$). Soil pH had the greatest influence, with partial regression coefficients of $b = 0.452$ for primary and for 1.05 secondary forests, followed by SOC_{min} ($b = 0.128–0.139$) (Table 1). Available P and geographic distance contributed minimally, but showed significant partial regression coefficients ($b = 0.024–0.037$) in both primary and secondary forests. In addition, total P content ($b = 0.131$), DOC ($b = 0.125$), and POC (b = −0.168) showed strong effects on β diversity in primary forests. Humic acid carbon (HUC) showed the significant influence on soil bacterial β diversity only in secondary forests.

Table 1. Contribution of environmental factors to the correlations by MRM on matrices analysis.

Factors	Primary forests ($R^2 = 0.639$, $p = 0.01$)		Secondary forests ($R^2 = 0.803$, $p = 0.01$)	
	Coefficient	*p*	Coefficient	*p*
distance	0.031	**0.01**[a]	0.029	**0.01**
pH	0.452	**0.01**	1.05	**0.01**
SOC[b]	−0.005	0.87	0.029	0.02
TN	−0.0017	0.98	−0.052	**0.01**
SOC:TN	0.0008	1.00	0.012	0.27
SOC_{min}	0.139	**0.01**	0.128	**0.01**
TP	0.131	**0.01**	0.039	**0.01**
AP	0.037	**0.01**	0.024	0.03
DOC	0.125	**0.01**	0.021	0.16
POC	−0.168	**0.01**	−0.119	**0.01**
HUC	−0.023	0.53	0.124	**0.01**

a

Bold indicates significant effects $p < 0.01$.

b

SOC, soil organic carbon; TN, total nitrogen; SOC_{min}, potential SOM mineralization rate; TP, total phosphorous; AP: available phosphorous; DOC, dissolved organic carbon; POC, particulate organic carbon; HUC, humic acid carbon.

3.3. Distinct bacterial networks in primary and secondary forests

The network in primary forests was larger and more complex than that in secondary forests. The primary forest contained ∼2 times more nodes and a greater number of

links among nodes with a higher average connectivity (Table 2, Fig. 2). The average geodesic distance was lower, whereas the average clustering coefficient and modularity were higher in secondary as compared to primary forest networks (Table 2; $p < 0.05$). This indicates that secondary forest networks are more modular, with closer and better-connected nodes.

Table 2. Topological properties of the empirical ecological networks (MENs) of microbial communities in primary and secondary forests and their associate random MENs.

Community	Empirical networks								Randor
	Similarity threshold (St)	Network size (n)[a]	Links	Avg. Connectivity (avgK)	Avg.path length (GD)	Avg.clustering coefficient (avgCC)	Modularity (No.of modules)	Avg.path length (GD)	Avg.c coe (av
Primary forest	0.81	142	458	6.45	3.19[b]	0.333[c]	0.433[d]	2.929 ± 0.055	0.116 ±
Secondary forest	0.81	78	161	4.13	2.89[b]	0.344[c]	0.508[d]	3.016 ± 0.082	0.093 ±

a Number of nodes in a network.

b Significant difference ($p < 0.001$) in average path length between primary and secondary forests based on the students t-test with standard deviations derived from corresponding random networks.

c Significant difference ($p < 0.001$) in average clustering coefficient between primary and secondary forests based on the students t-test with standard deviations derived from corresponding random networks.

d Significant difference ($p < 0.001$) in modularity between primary and secondary forests based on the students t-test with standard deviations derived from corresponding random networks.

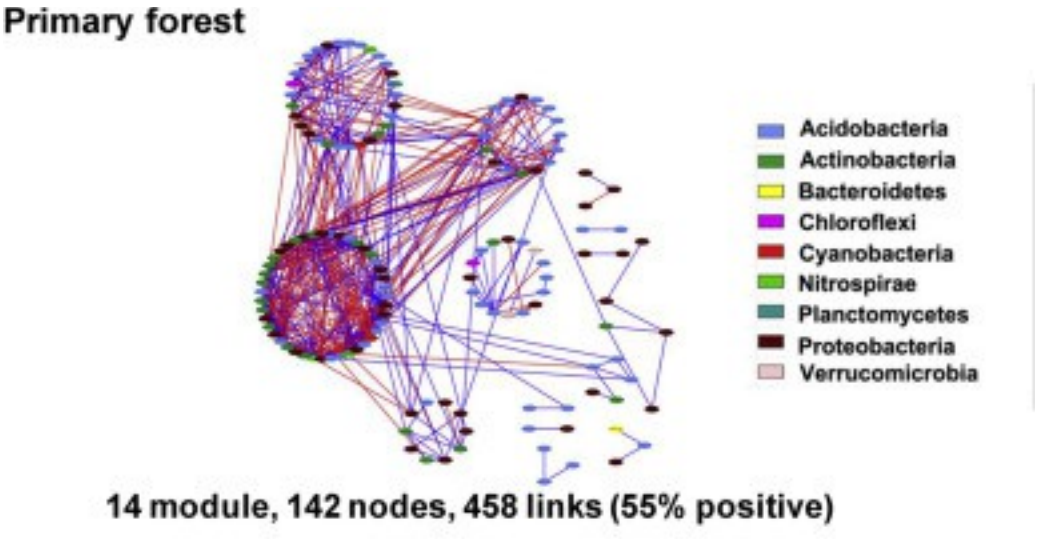

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Fig. 2. Network interactions in primary and secondary forest soils.
Colors of nodes indicate different major phyla. A red link indicates negative interaction between two individual nodes, whereas a blue link indicates positive interaction. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

A total of 458 links were identified in primary forests, including 255 (55%) positive and 203 (45%) negative interactions (Fig. 2). In contrast, bacterial taxa tended to co-occur in secondary forest networks, with positive correlations accounting for 82% of potential interactions observed (Fig. 2). We assessed possible topological roles of taxa in the

networks based on Z_i and P_i values. The majority of nodes in the two networks were peripheral, and most of their links were inside the modules (Fig. 3). Only one node, belonging to phylum *Acidobacteria*, was identified as a module hub in the primary forest network (Fig. 3). Four nodes were classified as connectors in the primary forest network: one each belonging to *Acidobacteria* and *Actinobacteria* and two belonging to *Proteobacteria* (Fig. 3). Four of five identified connectors in the secondary forest network were *Proteobacteria* (primarily *Alphaproteobacteria*) and one was *Acidobacteria* (Fig. 3).

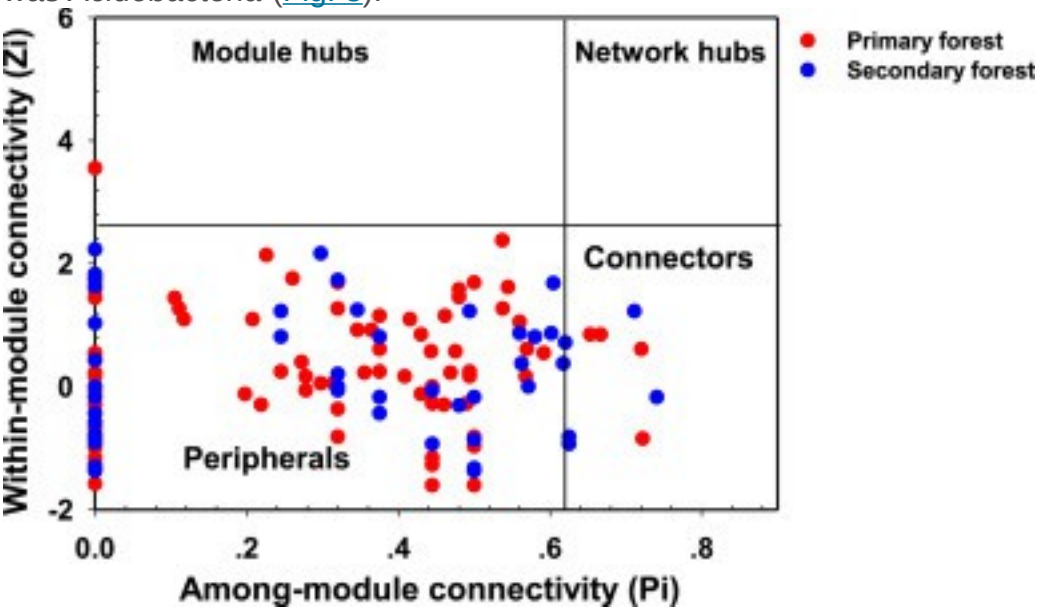

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Fig. 3. ***Z*-P plot showing the classification of nodes to identify putative keystone species in primary and secondary forests**.
Each symbol represents an OTU. Modules hubs have Zi > 2.5, whereas connectors have Pi > 0.62. One module hub was classified as *Acidobacteria* in the primary forest network. Four connectors in the primary forest network: one each belonging to *Acidobacteria* and *Actinobacteria* and two belonging to *Proteobacteria*. Four connectors in the secondary forest network were *Proteobacteria* (primarily *Alphaproteobacteria*) and one connector was *Acidobacteria*.

4. Discussion

4.1. Effects of deforestation on bacterial community spatial turnover rate

Understanding the patterns of microbial diversity and the mechanisms that maintain them are critical for predicting the response of an ecosystem to environmental changes.

Our hypothesis that bacterial community similarity decreased with increasing distance in both primary and secondary forests (Fig. 1) was verified. Furthermore, the bacterial spatial turnover rate was reduced by deforestation (Fig. 1), resulting in more similar bacterial communities over space. Changes in β diversity can be caused by environmental variations and efficient dispersal (Martiny et al., 2006; Ramette and Tiedje, 2007; Ge et al., 2008; Hendershot et al., 2017). Indeed, we found that a large and significant proportion of the variability in β diversity is explained by environmental variation and geographic distance (R^2 = 0.64 and 0.80; Table 2). However, based on the MRM model, environmental factorshad strong effects on bacterial community similarity with high partial regression coefficients(Table 2). This suggests that environmental selection plays an important role in shaping the similarity of bacterial communities spatially after deforestation. Among environmental factors, soil pH was the most important factor with a partial regression coefficient of b = 0.45–1.05, followed by SOC_{min} (b = 0.128–0.139) (Table 1). Consequently, changes in soil pH and SOM availability (as determined by SOM mineralization) caused by deforestation are major contributors to the decrease in β diversity. This is in agreement with previous studies demonstrating the importance of soil pH in influencing bacterial diversity on a large spatial scale (Fierer and Jackson, 2006; Liu et al., 2014; Chu et al., 2010; Griffiths et al., 2011; Rousk et al., 2010) and showing that SOC availability combined with taxa traits (e.g., abundance and distribution of dominant taxonomic groups) determines geographic distribution patterns (Fierer et al., 2007; Tian et al., 2018).

An increase in spatial similarity of bacterial communities following deforestation indicates spatial biotic homogenization, which offers a simple prediction of the human impact on global biodiversity (Olden and Poff, 2003). Biotic homogenization describes the gradual transition to nonnative-dominated communities which results in increased spatial and temporal similarity in the taxonomic characteristics of once-disparate biota (Olden and Poff, 2003). Biotic homogenization of macro-organisms (e.g., plants and animals) is a common outcome of ecosystem conversion (McKinney and Lockwood, 1999; Smart et al., 2006), but is seldom investigated in microorganisms (Rodrigues et al., 2013). Biotic homogenization of microorganisms can occur through loss of taxa with restricted geographic ranges (endemic taxa) or invasion of taxa with broad spatial ranges (Olden and Poff, 2003). There was no evidence for invasion by broadly distributed microbial taxa in this study, but we found that the deforestation reduced endemic taxa (Supplementary Fig. S4). This study purely focuses on the effects of deforestation on soil bacterial communities. However, it should be noted that soil fungi are also critical components of microbial communities and play crucial functional

roles in forest soils (Peay et al., 2008; He et al., 2017). In contrast to bacterial communities, the fungal communities are more strongly affected by the vegetation (Peay et al., 2013). Therefore, it is expected that the effect of soil variables on fungal communities is less than that on bacterial composition. Nevertheless, further studies are necessary to investigate whether deforestation reduces fungal diversity and spatial turnover across a large scale. Biotic homogenization is now regarded as one of the most prominent forms of global biotic impoverishment. The long-term impact of diversity loss resulting from deforestation is unknown; additional studies are necessary to clarify the mechanisms underlying current trends to guide conservation efforts.

4.2. Effects of deforestation on bacterial network interactions

Understanding interactions between microbial taxon can reveal the structure of complex microbial communities across spatial gradients (Barberán et al., 2012). The RMT-based approach (which provides objectively defined thresholds for network construction) was used to model phylogenetic molecular ecological networks (Fig. 2) (Zhou et al., 2011; Deng et al., 2012). Soil bacterial communities in primary forests formed larger (i.e., more nodes and links) and more complex (i.e., higher average K value) networks than those in secondary forests (Table 2 and Fig. 2). Greater network complexity can stabilize communities with mixed interaction types (Mougi and Kondoh, 2012; Liang et al., 2015); on the other hand, deforestation can reduce the stability of microbial communities.

Microbial networks in secondary forests were more modular than those in primary forests (Fig. 2). Modularity measures the connectivity between nodes within their own modules that would not occur by chance (Zhou et al., 2011; Deng et al., 2012). In ecology, a module is a group of species that interact strongly among themselves but little with species in other modules (known as compartmentalization) (Olesen et al., 2007). The modularity increased in secondary forests; meanwhile, the constituent nodes were more highly connected (Table 2and Fig. 2). This indicates that functional association and/or phylogenetic clustering of closely related species was higher in deforested areas. Interestingly, we found that covariation within modules was predominantly positive (82%) in secondary forests, suggesting the occurrence of extensive mutualism or commensalism (Faust and Raes, 2012). This disagrees with studies reporting that increasing disturbance promotes interspecies competition (Violle et al., 2010; Liang et al., 2015), although this has been contradicted by others (Grime, 1979; Huston, 1979). This result is also not consistent with our second hypothesis. Secondary forests have a higher SOC availability than primary forests (student's t-

test = 0.04, Table S2), presumably, a resource-rich environment reduced competitive pressures after deforestation (Dini-Andreote et al., 2015). This is supported by our finding that the main keystone nodes (OTUs) of secondary forests networks were *Proteobacteria* (Fig. 3). According to the growth processes of a network, keystone nodes are recognized as initiating components in networks (Barabási, 2009; Ma et al., 2016). *Proteobacteria* are mainly copiotrophic; they are the initial metabolizers of labile carbon, and are therefore more abundant in soils with higher organic matter availability (Fierer et al., 2007). However, the extent of positive interactions among natural populations of bacteria is still debated (Morris et al., 2012; Ren et al., 2015).

5. Conclusions

In conclusion, deforestation decreased the bacterial community spatial turnover rate, indicating biotic homogenization. We identified distinct topological features of networks in soils of primary and secondary forests. The microbial network was larger and more complex in the soils of primary as compared to secondary forests, indicating greater potential for microbial interactions and niche-sharing. Taxonomic groups in secondary forests tended to be modular, and species were more closely connected than those in primary forestnetworks. Keystone species shifted to predominantly *Proteobacteria* after deforestation. Soil pH and SOM availability were the most important factors for the observed microbial β diversity and networks interactions. Taken together, these findings provide a better understanding of the relationship between soil bacterial diversity and forest ecosystems, as well as a framework for predicting continental-scale microbial responses to anthropogenic activities. Future studies are necessary to investigate the influence of deforestation on temporal dynamics of bacterial communities and their networks across large scales. Additionally, studies of the long-term influence of the loss of diversity after deforestation on forest ecosystem function are required.

Conflicts of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

The following is the supplementary data related to this article:

Download Word document (471KB)Help with docx files

Supplementary material.

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