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

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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 forests than 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 network approach, 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.

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.

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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_2 levels) (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). Humus composition 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_2 production 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