



Soil and tree species traits both shape soil microbial communities during early growth of Chinese subtropical forests



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ABSTRACT

A better understanding of the linkages between aboveground and belowground biotic communities is needed for more accurate predictions about how ecosystems may be altered by climate change, land management, or biodiversity loss. Soil microbes are strongly affected by multiple factors including local abiotic environmental conditions and plant characteristics. To find out how soil microbial communities respond to multiple facets of the local soil and plant environment, we analysed soil lipid profiles associated with three-year-old monocultures of 29 tree species. These species are native of the diverse subtropical forests of southeast China and greatly vary in functional traits, growth or biomass characteristics, and phylogenetic relatedness. Along with the traits of each tree species, we also determined the soil and plot characteristics in each monoculture plot and tested for phylogenetic signals in tree species-specific microbial indicators. Microbial community structure and biomass were influenced by both soil properties and plant functional traits, but were not related to the phylogenetic distances of tree species. Specifically, total microbial biomass, indicators for fungi, bacteria, and actinomycetes were positively correlated with soil pH, soil organic nitrogen, and soil moisture. Our results also indicate that leaf dry matter content and the leaf carbon to nitrogen ratio influence multivariate soil microbial community structure, and that these factors and tree growth traits (height, crown or basal diameter) positively promote the abundances of specific microbial functional groups. At the same time, a negative correlation between leaf nitrogen content and Gram positive bacterial abundance was detected, indicating plant–microbial competition for nitrogen in our system. In conclusion, even at early stages of tree growth, soil microbial community abundance and structure can be significantly influenced by plant traits, in combination with local soil characteristics.

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1. Introduction

Numerous studies have pointed out that environmental properties such as soil pH, soil texture, soil moisture, and soil nutrient

availability influence the dynamics of soil microbial communities (Fierer and Jackson, 2006; Wakelin et al., 2008; Brockett et al., 2012; Docherty et al., 2015). Soil microbial communities also have close interactions with plants, and can be affected by plant productivity, community composition, and functional traits (Bauhus et al., 1998; Buckley and Schmidt, 2002; Kao-Kniffin and Balsler, 2008; de Vries et al., 2012).

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Plant functional traits have increasingly been studied as determinants of ecosystem properties, especially for soil biogeochemical processes (Chapin, 2003; Díaz et al., 2007; de Vries et al., 2012). Plant functional traits related to growth may determine a tree species' ability to contribute to the soil carbon pool via the volume or quality of leaf litter inputs (De Deyn et al., 2008). Likewise, plant traits determining leaf litter quality and quantity influence leaf decomposition rates and other soil biogeochemical processes (Cornelissen and Thompson, 1997; Bardgett and Wardle, 2010; Eichenberg et al., 2014a). Traits associated with the leaf economic spectrum such as specific leaf area (SLA), leaf nitrogen content (LNC), or leaf dry matter content (LDMC) can also be related to belowground soil properties (Lavorel and Garnier, 2002; Garnier et al., 2004). For example, Laughlin (2011) reported that communities dominated by plant species with high LNC, SLA and low LDMC tend to have high soil nitrification potential.

There are also many ways in which plant functional traits influence the soil microbial community as drivers of these biogeochemical processes. Forest growth and canopy structure, resulting from the collective contribution of individual trees, alter microsite albedo, temperature, light penetration, humidity, and raindrop velocity; variables all known to alter microbial communities (Anderson et al., 2011; Forrester et al., 2012; Wu et al., 2012; Geißler et al., 2013). Plant functional traits have also been reported to modify the soil microbial habitat by altering resource availability (Orwin et al., 2010), pH (Wang et al., 2001; Thoms et al., 2010) and soil moisture (Brussaard et al., 2007). At a more specific level, the amount or quality of plant resource inputs, both aboveground (litter) and belowground (dead roots and rhizodeposits), influence the abundance of different fungal and bacterial groups (Wilkinson and Anderson, 2001; Scherer-Lorenzen et al., 2007; De Deyn et al., 2008; Orwin et al., 2010). For example, plant species with high SLA, high LNC, and low LDMC can result in bacterial-dominated soil microbial communities in grasslands (Orwin et al., 2010). Leaf polyphenolic compounds are another example trait that can affect the activity and composition of soil microbial communities (Hättenschwiler and Vitousek, 2000; Fierer et al., 2001).

From a broader perspective than individual traits, related tree species could possibly cultivate similar microbial communities through plant–microbial coevolution. This idea of plant–microbial coevolution, and plant selection of a specific rhizosphere microbial community, has been demonstrated for some pathogenic fungi (Liu et al., 2012) and perhaps the most widespread, or well known, association is the symbiosis between plants and mycorrhizal fungi (Hoeksema, 2010; Buscot, 2015). Evidence of complementary traits coevolving between plants and arbuscular mycorrhizal fungi are well documented, such as the development of different functional roles across different arbuscular mycorrhizal fungal (AMF) lineages that colonize different hosts (Maherali and Klironomos, 2007). In turn host plants have evolved to provide a more hospitable environment for fungi (Brundrett, 2002). Despite this established knowledge regarding specific plant–microbe interactions based on plant species relatedness, few studies have investigated whether plant phylogenetic relatedness affects the soil microbial community in a more general way. Moreover, because most studies that have explored the effects of plant functional traits on microbial communities have only incorporated a low number of tree species or few plant species traits, the relative importance of different traits or of phylogenetic conservatism are less well understood.

The influence of plant characteristics on soil microbial communities may be modified by local soil characteristics, and soil and plant characteristics could interact in unexpected ways to mediate soil microbial communities (De Deyn et al., 2008; Orwin et al., 2010). Recent studies of plant–soil interactions have

demonstrated that soil properties play a crucial role on the interactions between plant species and soil microbial communities (Innes et al., 2004; De Deyn et al., 2009; Harrison and Bardgett, 2010). In light of this interplay in influence of soil and plant characteristics, it's likely that in early successional systems where plants are just becoming established, soil characteristics will play a dominant role in driving soil community dynamics with plant traits playing a larger role as plant communities become developed. In general, little is known about the relative importance of traits across a wide range of plant species during plant development, their related plant functional traits, or how local soil characteristics alter the development of soil microbial communities.

In this study we examined the effects of plant traits, specific tree species, tree phylogeny and soil conditions on microbial community structure in the context of highly diverse subtropical forests. We conducted this study across 29 tree species grown in monocultures, for a broad examination of aboveground–belowground relationships during early tree growth. Specifically, we tested the following four hypotheses: (1) Soil properties have a strong impact on soil microbial community composition, and predominantly explain the variation in microbial structure and abundance in the early stage of tree reforestation. (2) Plant traits influence soil microbial community composition and biomass, but to a lesser extent than soil properties. (3) Soil microbial communities differ in association with different tree species through identity effects (the collective sum of their traits). (4) Soil microbial communities are more similar in association with more closely related tree species. In other words there will be a phylogenetic signal present in tree-associated soil microbial communities.

2. Material and methods

2.1. Study sites

The study sites are located in a subtropical forest in south-east China, Jiangxi province, near the town of Xingangshan (29.08–29.11° N, 117.90–117.93° E). The sites are part of a large scale forest biodiversity and ecosystem function (BEF) experiment, Biodiversity Ecosystem Function-China (BEF-China, Bruelheide et al., 2014). The full experiment includes a total of 566 plots allocated to two study sites (site A and site B). On both experimental sites, the original forests were clear-cut in 2009. Site A plots were planted and established in March 2009, and site B plots were planted in March 2010. We focused on a subset of 29 intensively studied monoculture plots in order to compare our microbial data to tree species-specific datasets on plant and soil characteristics.

The experimental region is characterized by a subtropical climate with a warm, rainy summer and a cool, dry winter. Mean annual rainfall in this area is 1821 mm (peaking in May to June) and mean temperature is 16.7 °C (Yang et al., 2013). Soils are Cambisols and Cambisol derivatives, with Regosols on ridges and crests (Geißler et al., 2012). The natural regional vegetation is dominated by broad-leaved forests that are extremely species-rich. Dominant plant species are *Quercus glauca* (previously *Cyclobalanopsis glauca*, adapted to the taxonomy given by Zanne et al., 2014), *Castanopsis eyrei*, *Daphniphyllum oldhamii*, and *Lithocarpus glaber* (Bruelheide et al., 2011, 2014). The 29 plant species included in this study are listed in Table 3 and Table S1.

2.2. Soil sampling and soil properties

Soil samples were taken from monoculture plots of the listed 29 tree species between October and November in 2011 (site A) and October in 2012 (site B), respectively. This was done to ensure that

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