



Bacterial community structure of contrasting soils underlying Bornean rain forests: Inferences from microarray and next-generation sequencing methods

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ABSTRACT

Soil microbial diversity is vast, and we lack even basic understanding of how this diversity is distributed ecologically. Using pyrosequencing and microarray methods, we quantified the structure of bacterial communities in two contrasting soils underlying Bornean rain forest (clay and sandy loam) that differ markedly in soil properties, aboveground tree flora, and leaf litter decomposition rates. We found significant soil-related taxonomic and phylogenetic differences between communities that, due to their proximity, are independent of climate. Bacterial communities showed distinct compositional and taxon-abundance distributions that were significantly correlated with the structure of the overlying tree community. Richness of bacteria was greater in the more resource-rich clay soil. Phylogenetic community analyses suggested that environmental filtering may be an important mechanism of community assembly in clay, compared to niche-competition in sandy loam. The Acidobacteria were the most abundant group in clay, but the Proteobacteria dominated in sandy loam. Of the ten most abundant classes, the Actinobacteria, Betaproteobacteria, Clostridia, Bacilli, and Gammaproteobacteria were more abundant in sandy loam than clay. Our study, which is the first to quantify edaphic variation in bacterial communities using high-throughput methods in soils underlying one of the most tree species rich forests on Earth, indicates an important role of plant–soil feedbacks linking the community structure of the trees and the underlying soil microbiome. We suggest the biochemical composition of carbon and nutrient resources in plant litter and soil pH and oxygen availability as important determinants of the distribution of bacterial diversity.

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1. Introduction

Microbial diversity in soils is vast: a recent estimate suggests that a ton of soil may harbor at least one million species (Curtis et al., 2002). Of these, the microorganisms that decompose organic litter are a crucial component of global biogeochemical cycles (Burgin et al., 2011; van der Heijden et al., 2008), breaking down complex organic carbon and releasing CO₂ to the atmosphere via cellular respiration and making nutrients available to support primary production (Bardgett et al., 2009, 2008; Dubinsky et al., 2010; Nielsen et al., 2011; Reynolds et al., 2003; Zak et al., 2003). Unlike higher organisms, broad surveys of microbial diversity, including

Bacteria, Fungi, and Archaea, have historically been technologically infeasible, especially in soils, but recently developed molecular and genomic tools now open a window on the diversity and structure of these communities (Caporaso et al., 2011; Fierer et al., 2007b).

Nowhere are soil microbial communities likely to be more complex than under tropical rain forests, which house the majority of plant diversity on Earth (Dirzo and Raven, 2003). However, the factors that control the structure and composition of soil microbial communities are not well understood (Fierer and Lennon, 2011), and there is some evidence that well-established patterns of plant diversity are not necessarily predictive of those for microorganisms (Bryant et al., 2008; Fierer et al., 2011; Green et al., 2004), despite their obvious trophic linkages (Zak et al., 2003). In many plant communities, litter principally defines the resources available to decomposer microorganisms in and above the soil (Hobbie, 1992; Waldrop et al., 2006; Wieder et al., 2008). Tropical rain forests

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contribute some of the highest levels of primary production on the planet (Lewis et al., 2009; Sitch et al., 2008), much of which ultimately falls as leaf litter. The amount and diversity of leaf litter and its quality can have strong impacts on microbial community composition and function (Chapman and Newman, 2010; Nemergut et al., 2010). Leaf litter from different plant species can present dramatically different growth substrates for microorganisms (Strickland et al., 2009; Ushio et al., 2008; Wardle et al., 2009; Wu et al., 2011), due to variation in plant species' functional traits, such as leaf litter carbon and nutrient concentrations (Cornwell et al., 2008; De Deyn et al., 2008). As a result, soil microbial community composition often associates with the composition of the plants in the overlying vegetation (Slabbert et al., 2010; Yarwood et al., 2010). Abiotic environmental properties can also sharply define the composition and function of soil microbial communities. Factors such as soil temperature (Fierer et al., 2005), moisture (Hollister et al., 2010), pH (Rousk et al., 2010), nutrient availability (Cleveland et al., 2004; Cusack et al., 2011), and redox potential (DeAngelis et al., 2010) are recognized as important determinants of microbial growth and survival, and as such, can influence the structure of soil microbial communities. Despite recent advances revealing the incredible diversity of microorganisms belowground, even basic ecological identification and interpretation of these patterns, such as the associations between soil microbial community composition and the characteristics of the plant communities that these soils support, remains rudimentary at best (Fierer et al., 2007a).

As a first step towards understanding the biotic and abiotic factors that contribute to variation in microbial communities in tropical soils, we quantified the structure and composition of bacterial communities in two contrasting soils underlying Bornean rain forest. These soils share similar amounts of litterfall, but differ markedly in their rates of leaf litter decomposition (Baillie et al., 2006; Palmiotto, 1998), and represent the extremes of an edaphic gradient that strongly influences tree species composition (Davies et al., 2005). One of the soils is sandstone-derived, nutrient-depleted, and well-drained (sandy loam), and the other is shale-derived, less nutrient-depleted, and less well-drained (clay) (Table 1) (Baillie et al., 2006; Tan et al., 2009). The half-life of aggregated leaf litter on the sandy loam soil is three times longer than for litter on clay (Palmiotto, 1998). The slower rates of decomposition on sandy loam cause standing forest-floor necromass to be threefold larger than on clay (Baillie et al., 2006), resulting in higher total soil carbon (Table 1).

In addition to their disparate soil properties, the variation in decomposition rates of these soils may be due to differences in the leaf litter resources available, resulting in selection of distinct microbial communities. Supporting this hypothesis are the findings that the sandy loam and clay soils support dramatically different assemblages of tree species (Davies et al., 2005), resulting in large shifts in their leaf functional traits that are relevant for leaf litter decomposition (Russo et al., 2010; S.E. Russo, unpub. data). Relative to tree species typical of clay, fresh leaves of sandy loam specialists are significantly tougher and thicker, likely due to their total carbon contents and higher cellulose and lignin contents per unit area (S.E. Russo, unpub. data). Leaves of sandy loam specialists also have lower concentrations of N and P and greater C:N and C:P ratios (S.E. Russo, unpub. data). These differences are also likely to characterize recently fallen leaf litter, as fresh leaf and leaf litter traits are strongly correlated at this site (Kurokawa and Nakashizuka, 2008), and aggregated leaf litter on sandy loam has significantly lower concentrations of every nutrient examined (Table 1).

As a result of the strong variation between clay and sandy loam soils in the abiotic environment and the consequent effects on leaf litter resources available for microbial colonists, we predicted that soil bacterial communities would show covariation with soil type

Table 1

Properties of surface soil (0–10 cm) and leaf litterfall and decomposition for two soil types underlying Bornean rain forest. Significant differences among soil types are indicated by different lowercase letters, with standard errors following the means, when available. Abbreviations are as follows: CEC, cation exchange capacity and BS, base saturation.

Property	Soil type			Source
	Sandy loam	Clay		
Soil				
pH	4.64 ± 0.01 a	4.43 ± 0.04 b		Davies et al. (2005)
Bulk density	0.83 ± 0.04 a	0.95 ± 0.02 b		Palmiotto (1998)
CEC (cmol+/kg)	7.61	7.21		Baillie et al. (2006)
BS (%)	7.0 a	11.8 b		Baillie et al. (2006)
Total C (%)	1.90 ± 0.10 a	1.49 ± 0.12 b		Davies et al. (2005)
Total N (%)	0.093 ± 0.001 a	0.107 ± 0.003 b		Davies et al. (2005)
C:N	14.20 ± 0.80 a	10.60 ± 0.80 b		Palmiotto (1998)
Total P (mg/kg)	43.7 ± 0.7 a	133.6 ± 4.1 b		Davies et al. (2005)
Available P (mg/kg)	1.4	1.4		Baillie et al. (2006)
Exchangeable	0.12 ± 0.01 a	0.70 ± 0.04 b		Davies et al. (2005)
Mg (cmol+/kg)				
Exchangeable	0.21 ± 0.01 a	0.52 ± 0.01 b		Davies et al. (2005)
Ca (cmol+/kg)				
Exchangeable	0.12 a	0.14 b		Baillie et al. (2006)
K (cmol+/kg)				
Residual P (mg/kg)	90 a	129 b		Baillie et al. (2006)
Residual Ca (mg/kg)	133	170		Baillie et al. (2006)
Residual Mg (mg/kg)	733 a	1421 b		Baillie et al. (2006)
Residual K (mg/kg)	2356 a	4231 b		Baillie et al. (2006)
Residual Fe (mg/kg)	7808 a	14564 b		Baillie et al. (2006)
Leaf litter				
Litterfall (kg/ha-y)	6260	6550		Palmiotto (1998)
Half-life of leaf litter (y)	1.24 a	0.48 b		Palmiotto (1998)
Leaf litter nutrient input				
N (kg/ha-y)	57.00 ± 6.60	74.00 ± 3.00		Palmiotto (1998)
P (kg/ha-y)	0.89 ± 0.10	1.83 ± 0.07		Palmiotto (1998)
K (kg/ha-y)	14.30 ± 1.60	18.40 ± 0.70		Palmiotto (1998)
Ca (kg/ha-y)	15.80 ± 1.80	50.20 ± 2.00		Palmiotto (1998)
Mg (kg/ha-y)	11.30 ± 1.30	13.30 ± 0.50		Palmiotto (1998)

and, ultimately, the effects of soil type on vegetation, between the clay and sandy loam soils. Given the between-soil differences in carbon and nutrient resources, we anticipated the variation to reflect the copiotrophic–oligotrophic resource-use spectrum proposed by Fierer et al. (2007a), in which bacterial strategies exist on a continuum from copiotrophic bacteria that are abundant in nutrient-rich environments with high carbon availability to oligotrophic bacteria that are abundant in environments with low carbon availability. This would translate into communities dominated by Proteobacteria and Bacteroidetes in the more resource-rich conditions in the clay soil, compared to communities dominated by Acidobacteria in the sandy loam. Here, we explore these hypotheses by examining the community structures of sandy loam and clay soils using both taxonomic and phylogenetic analyses of 16S rRNA by pyrosequencing and microarray-based approaches. Our results show clear associations of soil bacterial community structure with soil type and the overlying tree community.

2. Materials and methods

2.1. Study system

Soil bacterial communities were characterized in Lambir Hills National Park, Sarawak, Malaysia (4°11' N, 114°01' E). The Park encompasses 6800 ha of lowland mixed dipterocarp forest with the highest tree species richness recorded in the Palaeotropics (Ashton and Hall, 1992; Lee et al., 2002). The forest is old-growth forest that has never been logged and experiences only natural forms of disturbance. Based on mortality rates, the longevity of many of the shade-tolerant tree species in this forest likely exceeds several

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