Microbial community structure varies across soil organic matter aggregate pools during tropical land cover change

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ABSTRACT

Soil microorganisms regulate multiple input and loss pathways of soil carbon (C); hence, changes in microbial communities are expected to affect soil organic matter (SOM) cycling and storage. Despite this, very little is known about how microbes respond to changes in soil structure and vegetation with land use and land cover change. This study aimed to identify relationships between microbial community composition and the distribution of SOM among soil aggregate fractions to answer the following research questions: (1) Are different microbial groups associated with different SOM pools? and (2) How do these relationships differ with changes in vegetation during tropical forest succession? We measured microbial composition via phospholipid fatty acid (PLFA) analysis and C and nitrogen (N) concentrations on physically separated aggregate fractions of soils from pastures, secondary forests (40 and 90 years old) naturally regrowing on abandoned pastures, and reference or primary forests in Puerto Rico. We found different microbial communities associated with different soil aggregate fractions. Fungal to bacterial ratios decreased and gram-positive to gram-negative bacterial ratios increased with decreasing physical fraction size (from the macroaggregates to the silt and clay fractions). Microbial composition also varied with land cover type and forest successional stage, with consistent trends among soil fractions. These results show that the soil matrix and soil microsite properties play an important role in the spatial distribution of fungal and bacterial-dominated communities. The similarities in land cover effects on microbial communities at different spatial scales suggest similar controls may be influencing microbial composition with potential implications for SOM storage and turnover. In addition, the majority of C and N (relative to total soil C and fraction mass) was isolated in the macroaggregate-occluded silt and clay-sized fractions, suggesting that association with mineral surfaces, and not occlusion of particulate organic matter within aggregates, is the dominant stabilization mechanism for SOM in these highly-weathered, fine-textured soils. These results highlight the importance of soil aggregation in C storage but through mechanisms different than those reported for temperate grassland soils.

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1. Introduction

Soils provide a heterogeneous environment for microorganisms, with a non-uniform distribution of organic carbon (C) substrates and nutrients (Balser et al., 2006; Ettema and Wardle, 2002; Kögel-Knabner et al., 2008; Six et al., 2002b, 2000b). Soil aggregation processes contribute to spatial heterogeneity in soils by creating microsites that differ in resource availability (Chenu et al., 2001).

Interactions between soil organic matter (SOM) and the soil matrix are fundamental in the protection of organic compounds from complete microbial degradation and mineralization to CO_2, primarily via sorption to mineral surfaces and incorporation into soil aggregates (Lützow et al., 2006; Marschner et al., 2008; Schmidt et al., 2011; Tisdall and Oades, 1982).

The spatial distribution of soil microbes and the relationship among community composition and SOM pools with different turnover times in the soil are not well understood (Ettema and Wardle, 2002; Lodge and Cantrell, 1995; Schimel and Schaeffer, 2012; Torsvik and Øvreås, 2002). This uncertainty limits our ability to predict how changes in soil structure due to landscape

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disturbance will affect both the abundance and activity of micro-organisms and decomposition processes, and ultimately the release of C to the atmosphere. This problem is especially acute in tropical soils, which contain some of the world's largest terrestrial C reservoirs (Batjes and Sombroek, 1997; Dixon et al., 1994; Prentice et al., 2001). Year-round productivity, fast decomposition rates and dynamic land conversion contribute to rapid C exchange between tropical soils and the atmosphere (Guo and Gifford, 2002; Post and Kwon, 2000; Trumbore, 1993). Hence, understanding how changes in land use and land cover affect the distribution of SOM pools and associated microbial communities is critical for evaluating feedbacks between soils and the atmosphere and for effective management of soil resources.

Soil aggregation promotes the accumulation and persistence of organic C in several ways. Fungal hyphae, microbes and plant roots can aid in the development and stabilization of soil aggregates through the production of exudates, secondary metabolites and organic inputs that act as glue between organic and inorganic soil constituents (Tisdall and Oades, 1982; Jastrow and Miller, 1998; Wright and Upadhyaya, 1998, Six et al., 2006). SOM can become incorporated as a binding agent into a hierarchical architecture of soil aggregates (Oades and Waters, 1991; Six et al., 2004; Tisdall and Oades, 1982). In this model, large-sized aggregates or macroaggregates (2000–250 μm size class) contain recent C inputs and relatively labile C and are the most sensitive to landscape disturbance, with typical short (annual to decadal time scales) residence times in the field (Elliott, 1986; Six et al., 2004; Tisdall and Oades, 1982). SOM with longer mean residence times (centuries or older) accumulates in microaggregates (250–53 μm) and finer silt- and clay-sized aggregates (<53 μm) (Denef et al., 2007; Oades, 1984, 1988). The persistence of organic C in microaggregates has been attributed to incorporation into micropores (Bachmann et al., 2008; Lützow et al., 2006) that are inaccessible to microbes and their enzymes or where oxygen depletion slows microbial activity (Sexstone et al., 1985) as well as to interactions with clay mineral surfaces (Golchin et al., 1994; Oades, 1993; Six et al. 2000a,b; Bachmann et al., 2008). Thus, aggregation contributes to C storage by creating complex soil structure and limiting accessibility to decomposers.

Research on microbial abundance among soil aggregates and particle-size fractions has revealed variable results in the spatial distribution of biomass and community members (Kandeler et al., 1999; Poll et al., 2003; Schutter and Dick, 2002; Torsvik and Øvreås, 2002). Greater microbial biomass or abundance has been reported the smallest-sized fractions, i.e. silt and clay (Kandeler et al., 1999, 2000; Monrozier et al., 1991; Poll et al., 2003; Qin et al., 2010) and the coarser or larger-sized fractions (Briar et al., 2011; Chiu et al., 2006; Huygens et al., 2008). Some authors have reported decreased fungal abundance (Chiu et al., 2006; Huygens et al., 2008) and fungal-to-bacterial ratio (Kandeler et al., 2000; Poll et al., 2003; Briar et al., 2011) with decreasing particle size, whereas others have found no change among soil physical fractions (Huygens et al., 2008; Chiu et al., 2006). The high variability in results among studies may be due to soil-specific properties such as mineralogy and differences in soil C and nutrient content (Chiu et al., 2006), or to differences in the methods used to characterize microbial biomass and community composition. Most studies on the relationship between soil physical fractions and microbial communities have been conducted in temperate, agricultural soils, so their applicability to other ecosystems is limited. Further work across environmental gradients and a diversity of soil types will increase understanding of the relationship between soil structure and microbial biomass, composition and, ultimately, function.

Microorganisms play an important role in the fate of C in soils through their contribution to SOM decomposition processes (Cotrufo et al., 2013; McGuire and Treseder, 2009; Wieder et al., 2013). Different microbial groups preferentially use different sources and amounts of C (Kramer and Gleixner, 2006, 2008; Paterson et al., 2008). Therefore, changes in the relative abundance of key microbial groups in soils may alter SOM cycling and storage (Six et al., 2006; Waring et al., 2013). For example, fungal-dominated communities are thought to enhance soil C sequestration due to increased biomass and higher growth efficiencies compared to bacterial-dominated communities (Bailey et al., 2002; Holland and Coleman, 1987; Jastrow et al., 2007; Rousk and Bååth, 2007; Six et al., 2006; Zhao et al., 2005). Fungal byproducts and necromass have been shown to have slower rates of decomposition relative to bacterial biomass and residues (Guggenberger et al., 1999; Martin and Haider, 1986; Six et al., 2006). An increase in soil fungal-to-bacterial abundance is therefore expected to lead to greater soil C accumulation.

The aim of our research was to evaluate shifts in microbial community composition with aggregate-associated SOM pools during tropical secondary forest succession on abandoned pastures. The geographic expansion of post-agricultural forests in the tropics (Grau and Aide, 2008; Meiyappan and Jain, 2012) provides the opportunity to examine the role of microorganisms in the fate of SOM with changes in vegetation. Our research questions were: (1) Are different microbial groups associated with different SOM pools? and (2) How do these relationships differ with changes in vegetation during tropical forest succession? To test the relationship among microbial composition, soil aggregate fractions and soil C and N pools, we measured microbial biomass and composition via phospholipid fatty acid-fatty acid methyl ester analysis in the following physically-isolated soil aggregate fractions: (1) macroaggregates (2000–250 μm), microaggregates (250–53 μm), (2) macroaggregate-occluded microaggregates (250–53 μm), (3) macroaggregate-occluded and silt and clay (<53 μm) fractions, and (4) free silt and clay-sized fractions (<53 μm) in surface soils collected from active pastures, secondary forests and reference primary forests in Puerto Rico.

Understanding how microbial communities respond to disturbance and ecosystem recovery is important for predicting effects of changes in land use and land cover on belowground C pools and nutrient availability. This study also provides new insights into spatial patterns of microbial distribution in Oxisols, which are characteristic of highly-weathered tropical landscapes and are grossly underrepresented in the literature on soil aggregation and microbial ecology. We are aware of only one other study investigating microbial composition in physical soil fractions in tropical soils (Blaud et al., 2012), despite their important role in the global C cycle.

2. Methods

2.1. Field site description

This study was conducted on an established long-term replicated successional chronosequence consisting of active pastures, secondary forests growing on abandoned pastures, and primary reference forest sites that have not been under pasture or agricultural use in the Sierra de Cayey of southeastern Puerto Rico (18°01′ N, 66°05′ W)(Marín-Spiotta et al., 2007, 2009). Forest vegetation differed along the reforestation chronosequence, with the first 30–40 years of succession on abandoned pastures dominated by the early successional tree *Tabebuia heterophylla*. Late secondary forests had a mixed-species canopy, whereas the primary forests had high abundances of the tabonuco tree *Dacryodes excelsa* and the palm *Prestoea acuminata var. montana*, characteristic of montane forests in the subtropical wet forest life zone. All