

Using landscape and depth gradients to decouple the impact of correlated environmental variables on soil microbial community composition

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Abstract

Simultaneously assessing shifts in microbial community composition along landscape and depth gradients allows us to decouple correlations among environmental variables, thus revealing underlying controls on microbial community composition. We examined how soil microbial community composition changed with depth and along a successional gradient of native prairie restoration. We predicted that carbon would be the primary control on both microbial biomass and community composition, and that deeper, low-carbon soils would be more similar to low-carbon agricultural soils than to high carbon remnant prairie soils. Soil microbial community composition was characterized using phospholipid fatty acid (PLFA) analysis, and explicitly linked to environmental data using structural equations modeling (SEM). We found that total microbial biomass declined strongly with depth, and increased with restoration age, and that changes in microbial biomass were largely attributable to changes in soil C and/or N concentrations, together with both direct and indirect impacts of root biomass and magnesium. Community composition also shifted with depth and age: the relative abundance of sulfate-reducing bacteria increased with both depth and restoration age, while gram-negative bacteria declined with depth and age. In contrast to prediction, deeper, low-C soils were more similar to high-C remnant prairie soils than to low-C agricultural soils, suggesting that carbon is not the primary control on soil microbial community composition. Instead, the effects of depth and restoration age on microbial community composition were mediated via changes in available phosphorus, exchangeable calcium, and soil water, together with a large undetermined effect of depth. Only by examining soil microbial community composition shifts across sites and down the soil column simultaneously were we able to tease apart the impact of these correlates environmental variables.

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1. Introduction

Soil microbes control many belowground processes critical to ecosystem functioning, through their influence on decomposition of organic matter, and creation of soil structure. Shifts in soil microbial community composition and abundance, in turn can significantly influence the dynamics of these essential processes. The composition of

the microbial community can be influenced by environmental perturbations, including soil management practices (Moore and de Ruyter, 1991; Bardgett et al., 1993; Cambardella and Elliot, 1994; Lovell et al., 1995; Beare, 1997; Bardgett and McAlister, 1999; Stahl et al., 1999; Zeller et al., 2001; Bailey et al., 2002; Grayston et al. 2004; Allison et al., 2005; McKinley et al., 2005). The mechanisms responsible for changes in microbial community composition have been difficult to establish, because soil variables are highly correlated. We suggest that by examining microbial community composition shifts in two dimensions simultaneously, we can decouple correlations among soil variables to reveal underlying controls.

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For example, the strong environmental gradients that occur across the landscape can parallel those that occur with depth in the soil column. However, variables that are strongly correlated in one dimension are not necessarily correlated in another. While C is highly correlated with water in surface soils, this correlation breaks down deeper in the soil column (pers. obs.). Thus, it will be possible to decouple the impact of carbon, water, and other correlated variables by simultaneously examining shifts that occur across the landscape and down the soil column.

We test this idea by examining changes in microbial community composition and environmental variables with depth at seven sites along a tallgrass prairie restoration chronosequence. Transformation of this agroecosystem soil, which had been under continuous tillage-based cultivation for the last century, to a prairie soil dominated by rhizospheric processes, results in a dramatic increase in above- and belowground plant production (Jastrow, 1987, 1996; Cook et al. 1988), litter accumulation on the soil surface, and an aggregated soil structure (Jastrow, 1987; Miller and Jastrow, 1990; Jastrow et al., 1998), together with an increase in soil carbon (Jastrow, 1996). These changes can have profound effects on soil microbial community composition (Allison et al. 2005).

Soil microbial community structure also shifts with depth (Ahl et al., 1998; Ekelund et al., 2001; Blume et al., 2002; Griffiths et al., 2003; Agnelli et al., 2004) and the strong environmental gradients that exists within a depth profile can parallel those generated across the landscape by restoration age. Depth gradients exist because resource inputs are highly stratified, entering the system either at the soil surface (in the case of litter) or strongly declining with depth (in the case of root inputs) (Feng et al., 2003; LaMontagne et al., 2003). Conversely, mineral nutrients sourced from parent material, such as inorganic phosphorus, calcium, magnesium, iron and aluminum may increase with soil depth because of protection from weathering. In addition, surface soils are more exposed to

frequent wetting and drying (Van Gestel et al., 1992; Ekelund et al., 2001), freeze/thaw cycles, and have higher levels of oxygen (Agnelli et al., 2004). These factors have been found to influence microbial community composition, with declining abundances of fungi relative to bacteria (Zelles and Bai, 1994; Blume et al., 2002; Jørgensen et al., 2002; Feng et al., 2003), and an increase in actinomycetes and gram-positive bacteria relative to gram-negative bacteria (Zelles and Bai, 1994; Feng et al., 2003; Fierer et al., 2003) with depth.

We assessed microbial community composition and biomass by using phospholipid fatty acid (PLFA) analysis, and used structural equations modeling (SEM) to determine the relative impact of environmental factors on those variables. We predicted that changes in soil carbon would have the strongest direct impact on both total microbial biomass and community composition (Ahl et al., 1998; Blume et al., 2002; Feng et al., 2003; Fierer et al., 2003), and thus that deeper, low-carbon soils will be more similar to low-carbon agricultural soils than to high-carbon remnant prairie soils (see Fig. 1). We also expected water to be important in structuring the microbial community (Ekelund et al., 2001), with water determined both by soil carbon, and by depth due to proximity to the water table. Soil pH was also expected to be an important regulator of microbial community composition, with pH in turn regulated by soil calcium (Grayston et al., 2004; Reich et al., 2005), and calcium regulated by soil texture and depth. Roots were expected to have both a direct impact on the microbial community by providing both a habitat and carbon resources, and also an indirect effect mediated through changes in soil water availability and soil carbon. In addition, phosphorus was expected to directly alter community composition by increasing the abundance of bacteria relative to fungi (Grayston et al., 2004) and by inhibiting arbuscular mycorrhizal fungi (AMF) (Marschner and Dell, 1994), and also indirectly influence community composition by increasing plant biomass. No direct effects

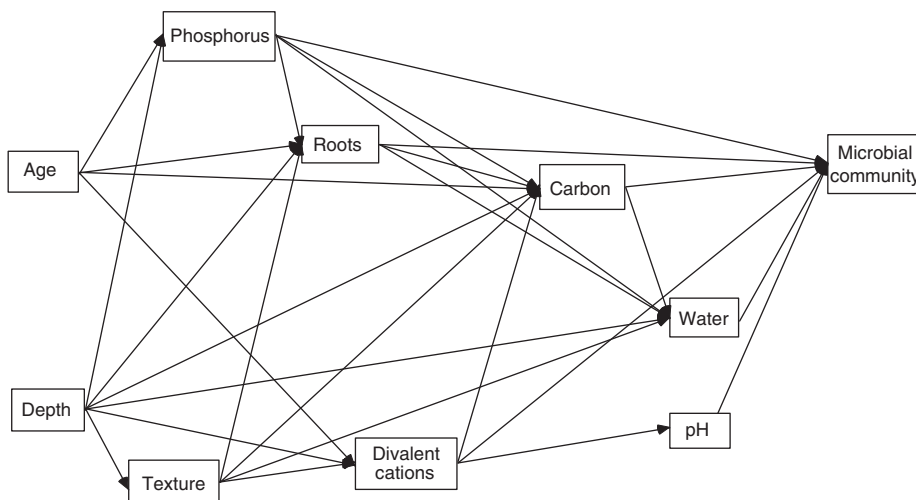


Fig. 1. Hypothetical model by which age and depth indirectly affect microbial community composition and biomass.

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