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Effects of nitrogen addition on soil microbial diversity and methane cycling capacity depend on drainage conditions in a pine forest soil

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ABSTRACT

Two forested study sites, one well and one poorly drained, were used for investigation of the effects of variation in drainage, microclimate, and addition of inorganic nitrogen (N) on the whole soil microbial community and its methane cycling capacity. Both sites were capable of consuming and releasing large quantities of methane. The composition of the soil microbial community was investigated using the 3rd generation PhyloChip, a bacterial and archaeal 16S rRNA gene microarray. The PhyloChip was also used to target the composition of methane- and some N-cycling microorganisms. Relative abundance of functional genes involved in methane production and consumption was evaluated with qPCR.

Soil drainage condition determined the microbial community structure within and between sites. Greater community structure variation, richness of methanotrophs, and higher abundances of both methanotrophs and methanogens were all found in the poorly drained site, as was higher soil moisture and C content and methane release. In the poorly drained site, high N (67 kg NH_4NO_3 ha^{-1} yr^{-1}) increased methanotroph and methanogen abundance, overall taxonomic richness of Bacteria and Archaea, and richness of nitrifiers and methanotrophs. In the well drained site, high N decreased taxonomic richness. Results may indicate that high N concentrations stimulated oxidative reactions, including ammonia and methane oxidation and nitrification in the short term. The resultant increase in release of methane from the high N plots of the poorly-drained site may have been due to indirect inhibition of methane oxidation by the increase in other oxidative reactions. Alternatively, both methanogens and methanotrophs may have been stimulated by high N. Well-drained site high N decreased the taxonomic richness of the soil, but did not impact methane-cycling microbes. These findings begin to bridge the gap between microbial-scale community dynamics and ecosystem-scale ecological functions.
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1. Introduction

Fluctuations in greenhouse gas concentrations in the atmosphere can lead to profound climatic and environmental changes (IPCC, 2007). Methane (CH_4) is a major and growing greenhouse gas in Earth's atmosphere (Lelieveld et al., 1998). Environmental changes influence variation in soil microbial consumption and release of methane (e.g. Butterbach-Bahl and Papen, 2002; Davidson et al., 2004; Mosier et al., 2002; Adamsen and King, 1993). The CH_4 growth rate in the atmosphere slowed in the late 1980s and became erratic for at least 25 years, at a time when known anthropogenic CH_4 emissions increased and new sources continue to be discovered (Walter et al., 2006; Keppler et al., 2006). The underlying cause(s) for the unpredictable trends in atmospheric methane are disputed (Aydin et al., 2011; Kai et al., 2011). In addition to the variation in sources, biological sinks for methane in natural ecosystems are poorly understood.

Microbial metagenomic, fingerprinting and community analysis tools have revealed that the environmental gradients that shape the distribution of large organisms and large-scale elemental cycling processes may also shape some microorganism distributions and processes (Martiny et al., 2006). Using these tools, we aim to increase our understanding of how environmental gradients within ecosystems shape the microbial community as a whole. In addition, we focus on those microorganisms responsible for soil CH_4 flux in the hope that it may help explain atmospheric CH_4 trends from the bottom up.

Soil exchange of CH_4 with the atmosphere is regulated by methane producing archaea, i.e. methanogens, and methane

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oxidizing bacteria (MOB), i.e. methanotrophs. The disparate environmental requirements of these two groups, particularly with regards to oxygen level, temperature, moisture and nutrient availability, determine their distribution in the soil of a given ecosystem (Le Mer and Roger, 2001). In particular, soil inorganic nitrogen (N) addition has been found to inhibit CH_4 oxidation, except in N-limited conditions (Bodelier and Laanbroek, 2004; Aronson and Helliker, 2010). As N deposition and runoff increases (Kroeze and Seitzinger, 1998) and patterns of temperature and rainfall shift (IPCC, 2007), these changes impact microbially-mediated soil CH_4 uptake (Holmes et al., 1995).

We investigated the composition and functional characteristics of the microbial community of a sandy forest soil in the Pinelands of New Jersey and the response of this community to existing environmental variation, seasonal microclimate shifts and N treatments. Microbial genetic diversity had not been investigated previously in this location. In a review of methane consumption by terrestrial ecosystems, forests were found to consume on average more methane than all other ecosystems (Dutaur and Verchot, 2007), while wetlands are the largest source of methane to the atmosphere (Lelieveld et al., 1998). This ecosystem contains isolated riparian zones that maintain a mostly homogeneous dominant overstory vegetation distribution with the rest of the forest, minimizing plant effects on microbial diversity. The overstory consists of pitch pine (*Pinus rigida* Mill.) and oak species (*Quercus* spp.; Dighton et al., 2004),

Heterogeneity in drainage conditions, like that found at this site, is overlooked in most *in situ* trace gas flux investigations and climate models (Werner et al., 2003), but is relevant at microbial scales. The purpose of this study was to bridge the gap between ecosystem and microbial scale analysis by assessing how similar (or different) the diversity, functional capacity, and functions of the microbial community were in these two soils in close proximity and with similar vegetation, but different hydrology. In addition, we investigated how these different microbial communities responded to two different N perturbations relevant to the location, one reflecting projected regional increases in N deposition, the other the low level of fertilization used in local agriculture. We expected that the communities would overlap in taxa between 25 and 50%, but that their functional capacities, in terms of the number of copies of key methane-cycling genes, would differ with hydrology and show different responses to N addition, as did the methane flux profiles (Aronson et al., 2012). We used quantitative polymerase chain reaction (qPCR) to evaluate the functional capacity of the soil, i.e. the number of microbes present that could perform methane-cycling, a key ecosystem function. To assess microbial community composition, we used the PhyloChip, a DNA microarray targeting the 16S gene across bacteria and archaea (Hazen et al., 2010). The PhyloChip is a tool created for comparison of diversity among samples in that it can minimize the sampling artifacts associated with random sampling processes (Zhou et al., 2008) and was used to compare large-scale diversity trends between soil drainages and N treatments, while focusing on the diversity of key functional species.

2. Materials and methods

2.1. Site description and N manipulations

The field site and manipulations have been previously described (Aronson et al., 2012) and will be briefly summarized here. Measurements were made in a sandy pine forest soil in New Jersey, USA (39°55′N, 74°35′W) during the summer and fall of 2009. The average annual temperature is 12.3 °C and precipitation is 1143 mm. The study location consisted of two sites separated by 30–40 m, each containing 18 plots: one well drained at an elevation of 30 m asl, 7 m above the water table, and the other poorly drained at an elevation of 23 m asl, with the water table located within 5 cm of the soil surface. The sites differed in soil and drainage characteristics: the well-drained site was considered an "excessively drained" sand of the Evesboro series, which consists of Mesic, coated Lamellic Quartzipsamments covered by an organic (O) horizon (Krumins et al., 2009); the poorly-drained site was a Fluvaquent with a large O horizon of variable depth, sometimes topped with peat (Aronson et al., 2012). However, the sites shared overstory species of trees, dominated by oak and pine spp., as described by Krumins et al. (2009). The understory in the well-drained site consisted of small patches of mixed grasses and herbaceous species, while that of the riparian site contained a denser mixture of ericaceous shrubs, e.g. blueberry (*Vaccinium* spp.) and sedges (*Carex* spp.).

Research on the soil CH_4 cycle in the Pinelands showed large fluxes of CH_4 into and out of the soil, with great variation both within and between sites, which correlated with many soil characteristics (Table 1). Both well- (upper) and poorly-drained (lower) sites were capable of consuming and releasing large quantities of CH_4, which demonstrated the presence of both MOB and methanogens within the soil column. Varied CH_4 flux responses to N addition in this site suggest that ammonia oxidizing bacteria (AOB) or nitrifying bacteria may also play an indirect role in the CH_4 cycle (Aronson et al., 2012).

Starting in June 2009, soil sampling was performed on a given block of 12 randomly selected plots, six upper and six lower, in a

Table 1
Relationship between CH_4 flux and environmental variables (reproduced from Aronson et al. 2012, with pH added). Single variable linear regression intercepts and coefficients of variation (of the form $y = mx + b$) for the impact of environmental variables (left column) on CH_4 flux (mg CH_4 m^{-2} h^{-1}) of all observations. The estimates are bounded by standard errors.

Environmental variable	Slope (m)	Intercept (b)	Sample size (n)	R^2 value	p-Values
Bulk density (g cc^{-1})	−94.2 ± 12.7	65.6 ± 12.8	36	$R^2 = 0.103$	<0.0001
% C content June	3.2 ± 0.6	−118.6 ± 21.6	36	$R^2 = 0.062$	<0.0001
% C content October	3.0 ± 0.5	−80.2 ± 13.6	36	$R^2 = 0.084$	<0.0001
% N content June	75.3 ± 19.9	−91.2 ± 23.5	36	$R^2 = 0.030$	<0.0002
% N content October	86.2 ± 14.3	−69.8 ± 13.0	36	$R^2 = 0.072$	<0.0001
Soil moisture (ml H_2O ml^{-1} soil)	366.4 ± 44.0	−107.0 ± 14.0	480	$R^2 = 0.127$	<0.0001
Soil water potential (MPa)	14963.8 ± 3468.9	124.5 ± 22.4	480	$R^2 = 0.073$	<0.0001
Soil temperature (°C)	−4.5 ± 1.2	96.0 ± 29.6	480	$R^2 = 0.028$	<0.0002
Soil NH_4 content (mg N g^{-1} dry soil)	0.6 ± 0.3	−25.5 ± 11.2	430	$R^2 = 0.013$	0.019
Soil $NO_2 + NO_3$ content (mg N g^{-1} dry soil)	0.9 ± 0.4	−17.8 ± 9.6	430	$R^2 = 0.013$	0.020
Soil pH	0.00001 ± 0.0003	3.2 ± 0.05	25	$R^2 = 0.0001$	0.967

Notes: Soil temperature, moisture and NH_4 and $NO_2 + NO_3$ content regressions are from individual plots on all dates/times of CH_4 flux measurements; bulk density is given for the top 15 cm of soil, while all other measurements are for the top 10 cm of soil; % N and C content are given for the very first pre-fertilization date of all plots (June) and for the last fertilization date of all plots (October); soil pH regression is for all soil samples used for PhyloChip analyses.

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