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Soil microbial community composition is correlated to soil carbon processing along a boreal wetland formation gradient

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ABSTRACT

Climate change is modifying global biogeochemical cycles. Microbial communities play an integral role in soil biogeochemical cycles; knowledge about microbial composition helps provide a mechanistic understanding of these ecosystem-level phenomena. Next generation sequencing approaches were used to investigate changes in microbial functional groups during ecosystem development, in response to climate change, in northern boreal wetlands. A gradient of wetlands that developed following permafrost degradation was used to characterize changes in the soil microbial communities that mediate C cycling: a bog representing an "undisturbed" system with intact permafrost, and a younger bog and an older bog that formed following the disturbance of permafrost thaw. Reference 16S rRNA databases and several diversity indices were used to assess structural differences among these communities, to assess relationships between soil microbial community composition and various environmental variables including redox potential and pH. Rates of potential CO_2 and CH_4 gas production were quantified to correlate sequence data with gas flux. The abundance of organic C degraders was highest in the youngest bog, suggesting higher rates of microbial processes, including potential CH_4 production. In addition, alpha diversity was also highest in the youngest bog, which seemed to be related to a more neutral pH and a lower redox potential. These results could potentially be driven by increased niche differentiation in anaerobic soils. These results suggest that ecosystem structure, which was largely driven by changes in edaphic and plant community characteristics between the "undisturbed" permafrost bog and the two bogs formed following permafrost thaw, strongly influenced microbial function.

1. Introduction

Climate change is modifying global biogeochemical cycling, often in disparate fashion [1–3]. The modification of global biogeochemical cycles is particularly evident in northern ecosystem carbon cycling [4]. Owing to thousands of years of carbon accumulation and slow rates of decomposition, boreal peatlands have been historical sinks for atmospheric carbon. However, direct and indirect effects of climate change are causing extensive degradation of permafrost in interior Alaska that are reshaping these historical carbon sinks [5]. Because ice occupies more volume than water, when ice-rich permafrost thaws, soil collapses into relic ice space; this collapse leads to inundation in low-lying areas and subsequent wetland formation. This process also leads to changes in plant community composition as part of the ecosystem state change from peat forest to peat wetland [5,6]. Given the anoxic and waterlogged conditions of these ecosystems, boreal wetlands are a significant source of atmospheric CH_4 and CO_2 and to a lesser extent N_2O [7–9]. Despite these ecosystems functioning as a long-term carbon sink, some models predict that Alaska will be a net source of greenhouse gases by the end of this

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century [10]. A unifying framework incorporating physical concepts such as thermodynamics and energy flow may help to highlight emerging patterns in response to climate change [11,12].

Soil microbial communities play an integral role in the C cycle and the metabolism of other nutrients, such as nitrogen and sulfur for energy acquisition [13]. For example, the production of CH_4, a potent greenhouse gas, is mediated by archaea—a domain of microorganisms. A better understanding of the microbial-scale conditions and processes that produce greenhouse gases will better inform models that operate at the ecosystem scale. Despite the large role that microbial communities play in nutrient cycles, less is known about microbial responses to climate change [14,15]. This is of particular concern because of the potential positive feedbacks that may enhance further climate warming. In this study, the soil microbial community was examined in Alaskan boreal wetlands that were at different stages of ecosystem development, and the soil microbes were framed as mediators of carbon (C) cycling and soil energy flow. The study venue was a gradient of developing boreal wetlands and the soil microbial community was used to provide a mechanistic understanding of changes in C cycling following a permafrost thaw disturbance at a site of actively degrading permafrost.

Rates of soil processes, such as biogeochemical cycling, may also be related to the abundance of soil microbial organisms [16,17]. Advances in tools developed specifically for analyzing soil microbial communities have streamlined workflow for analyzing millions of DNA sequences [18]. For example, next generation sequencing approaches have been used to show increases in cellulose processing microbial genes as well as denitrification and ammonification genes following permafrost thaw [19]. Advances in next generation sequencing technologies have also enhanced the ability to correlate microbial-scale mechanisms and processes with ecosystem-scale processes [17]. For example, while recent studies have shown a wide range of bacterial groups capable of degrading complex soil organic carbon (SOC) such as cellulose and hemicellulose, one recent study found that the majority of bacterial genes encoding SOC degradation enzymes are found in the bacterial phyla *Bacteroidetes, Actinobacteria*, and *Verrucomicrobia* [20]. These techniques were used in this study to investigate complex SOC-degrading community change along a permafrost thaw gradient.

This investigation asked: How does the soil microbial community change as a result of permafrost thaw and subsequent wetland formation, and how does this relate to functional processes? Although more is known about microbial response to climate change than a few years ago, these responses have proven to be unpredictable [21]. The objectives of this study were: 1) To investigate how soil microbial structure responded to permafrost thaw and wetland development along a space-for-time gradient, or chronosequence, of sites; 2) To measure the influence of the water table position and redox potential on microbial communities; 3) To assess changes in microbial functional groups and corresponding change in functional processes such as potential CO_2 and CH_4 production and; 4) To quantify soil microbial community diversity to assess how microbial community complexity changed following permafrost degradation. Wetland formation following permafrost thaw represents a post-disturbance ecosystem state change, and increased soil waterlogging and vegetation community change are key metrics of that ecosystem state change. Thus, shifts in microbial community abundance were expected that reflected these changes. In other words, the abundance of different bacterial and archaeal phyla would be tightly coupled to ecosystem state, or ecosystem type.

2. Methods

2.1. Site description and experimental design

The study sites were located along a gradient of wetland formation in peatlands 35 km southeast of Fairbanks, AK. The sites were in the Tanana River floodplain and contained a large number of wetlands that have developed in the last decades to centuries after permafrost degradation. A space-for-time substitution was used to test microbial community responses to permafrost thaw and state change (Table 1). Three different peatlands were selected along this successional gradient: 1) an "undisturbed" forested bog (FB) of short stature black spruce (*Picea mariana*) with a 50 cm active layer and intact permafrost; 2) a bog dominated by *Carex* sp. that formed following permafrost thaw approximately 50–80 years ago that represents a young collapse scar wetland (YCS); and 3) an older bog that thawed approximately 400–500 years ago and had higher bulk density and abundance of shrub and woody species and that represents an old collapse scar wetland (OCS). The 3 sites were located within 100–200 m from one another and experienced similar climate (Table 1; precipitation and temperature). This permafrost thaw disturbance gradient was used to quantify patterns in microbial community structure and biogeochemical function at the study sites; notably, this experimental design did not represent a generalizable pattern for wetland development and did not attempt to unravel the effects of soil and vegetation variation along the gradient of wetland formation.

2.2. Soil sampling and handling

Soils were sampled at each site along the permafrost thaw gradient by collecting five cores at each site using a sharpened steel tube (i.d. 5.4 cm) in June 2012 (when mean air temperature was 10–20 °C). Soil cores were extruded by carefully pushing the core out of the steel tube with a PVC plunger. The extracted soil cores were ~30 cm length and were subsectioned in the field at the position of the water table, where "surface" and "deep" correspond to above and below water table, respectively. The position of the water table in the forested bog was difficult to measure, so the soil cores were subdivided at a morphological change in peat structure and color. Soil core sections were subdivided and handled separately for potential gas flux experiments and molecular analyses. Soil samples that were collected above the water table were stored in sealed plastic bags and kept in a cooler on ice for transport to the lab. The samples that were collected below the water table were stored in plastic bags with bog water, to keep them anaerobic and waterlogged; they were also stored in a cooler on ice. Soils for the potential gas flux experiments were stored at 4 °C until soil incubations were conducted (within 10 days) and soil samples for DNA sequencing were stored at −20 °C until they were processed. Field redox potential was measured by inserting a redox probe 5 cm into the peat soil, and pH by inserting a pH probe 5 cm into peat soil. Redox potential and pH were quantified to investigate the influence of environmental changes along the wetland gradient on microbial community composition. To quantify total soil C and nitrogen, peat soil subsamples were oven dried 1 week at 65 °C, ground first using a Mini Wiley Mill (Thomas Scientific, Swedesboro, NJ), then ground again using a 8000D Dual Mixer/Mill (SPEX CentiPrep, Metuchen, NJ). This second grinding step was to maximize the homogeneity of the sample prior to analysis. Total C and nitrogen were quantified on a Perkin Elmer 2400 CHN Analyzer (Waltham, MA).

2.3. Potential gas flux experiments

Potential gas flux incubations were conducted by placing fresh