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Climate change favours specific fungal communities in boreal peatlands

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ABSTRACT

Fungi play a pivotal role in the carbon sequestration potential of boreal peatlands through the process of decomposition. As such, climate-driven changes in the diversity and community composition of peatland fungal communities could have substantial impacts on carbon release from these ecosystems, especially in subsurface peat that represents an important global carbon stock. We used Illumina MiSeq sequencing of rDNA to examine fungal communities after 18 months in intact peatland mesocosms subjected to conditions associated with Canada's future climate, including: warming, elevated atmospheric CO_2 and lowered water table. Warming was the main driver of changes in fungal communities across three depths of the peat profile with both Ascomycota- and Basidiomycota-dominated groups becoming more homogenous under warming conditions. Specific changes in fungal functional groups, however, were temperature dependent with potential cellulose decomposers and mycorrhizal root-associated fungi from Basidiomycota dominant under warming of +4 °C, whereas there was a prevalence of potential lignocellulose decomposers and mycorrhizal root-associated fungi from Ascomycota under +8 °C warming. These climate change-induced shifts in the structure of fungal communities in favour of recalcitrant compound decomposers observed across a depth gradient, may reduce long-term carbon storage of boreal peatlands under future climate change scenarios.

1. Introduction

Soil organisms contribute significantly to the biogeochemical processes and other ecosystem-level processes of decomposition and nutrient cycling, and recent work has highlighted how multiple ecosystem-level functions are highly dependent on soil biodiversity and specifically high levels of functional diversity among soil organisms (Bardgett and van der Putten, 2014; Bradford et al., 2014; Wagg et al., 2014). In particular, the carbon sequestration potential of many ecosystems depends on the structure, function, and activity of the microbial community, which in turn is dictated by environmental factors such as soil chemistry, temperature, soil water, and nutrient availability; the quality of carbon inputs to a system also influences the microbial community composition. The largest stores of terrestrial carbon can be found in wet, cool areas of the northern hemisphere, particularly boreal peatlands, which are composed of low quality plant material and frequent anerobic conditions. Among soil microbial communities inhabiting boreal peatlands, fungi, with their broad enzymatic activities and competitive advantages over bacteria and archaea in decomposing low quality materials with high C:N ratios (Myers et al., 2012), play a significant role in mineralization of recalcitrant compounds (Thormann, 2006) that constitute more than 50% of the carbon polymers in these habitats (Turetsky et al., 2000).

Boreal peatlands are expected to experience an increase in both air and soil temperature, alongside increased atmospheric CO_2 concentrations, and a reduction in water table position under future climate change (IPCC, 2014). The sensitivity of fungal communities to their environment suggests that climate-driven changes in boreal peatlands should favor saprotrophs that benefit from warmer and drier conditions, and indeed the direct short-term effects of increased temperature on the diversity and activity of some fungal groups such as saprotrophs (generalist decomposers) has been well documented (Maheshwari et al., 2000; Peltoniemi et al., 2015; Rippon and Anderson, 1970). However, the direct effects of CO_2 enrichment on soil fungal communities are not well studied (but see Janus et al., 2005; Lipson et al., 2005), yet are hypothesized to have a weak or neutral direct effect on soil fungal communities, since soil CO_2 concentrations are far greater than predicted elevated atmospheric CO_2 levels (Schwartz and Bazzaz, 1973). Combined effects of climate warming, elevated CO_2 and water table drawdown can have synergistic effects on ecological communities (Dieleman et al., 2015). In microbial communities, while elevated temperatures can stimulate metabolic rates, a concomitant reduction in soil moisture due to warming can promote cellular energy metabolism through improved aerobic conditions favored by most fungi (Allison and Treseder, 2011; Asemaninejad et al., 2017a).

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Recently, several studies have demonstrated changes in peatland plant communities under climate change, particularly with combined effects of elevated atmospheric CO_2 and increased temperature. Laboratory (Dieleman et al., 2015) and field (Buttler et al., 2015; Weltzin et al., 2000) studies have demonstrated that non-vascular plants (e.g., mosses) are replaced by vascular plants under experimental climate change, altering litter inputs and increasing root exudates that could potentially affect fungal communities (Broeckling et al., 2008; Norby et al., 2001; Peltoniemi et al., 2012) through inputs of more labile carbon sources (Dieleman et al., 2016a). Soil fungal communities are highly associated with temporal resource pulses in the soil driven by plant root exudates (Shahzad et al., 2015), and these resource-driven changes in fungal communities may affect nutrient cycling and nutrient supply (Bardgett and van der Putten, 2014). In the long-term, shifts to mycorrhizal species associated with vascular plants could potentially drive co-evolutionary changes in plant communities through facilitating the establishment of their hosts (Bardgett and van der Putten, 2014).

Changes in fungal species richness and community composition, including relative abundances of functional groups that differ in substrate utilization, may affect different layers of peat differently. Most research on the impacts of climate change factors on fungal richness, activity and community composition in northern peatlands has focused on surface peat (Bradford et al., 2008; Lipson et al., 2005; Peltoniemi et al., 2009), while very little is known about the structure of fungal communities in peat layers beyond 15 cm depth (but see Peltoniemi et al., 2015). Although carbon dynamics in the lower horizons are less affected by climate change compared to the upper horizon (Mathieu et al., 2015), examining the combined effects of multiple drivers of climate change on the structure of the fungal communities in lower peat layers will give greater insight into future carbon dynamics in boreal peatland ecosytems.

Below-ground microbial diversity is subject to multiple anthropogenic disturbances and stressors, thus it is important for ecologists to understand how the structure of soil microbial communities, in particular fungi, will be affected by changes in their environment (Wolters et al., 2000). Accordingly, the general objective of our study was to assess the impacts of combined climate change factors (increased temperature, elevated atmospheric CO_2 and lowered water table) on fungal richness, diversity and community composition across a depth gradient of peat soil in boreal peatlands. The work we present here builds on previously published results using a large-scale mesocosm approach demonstrating plant community shifts and changes to dissolved organic carbon dynamics (Dieleman et al., 2015, 2016a), decreases in the average body size of the microarthropod communities (Lindo, 2015), and increased rate of microbial successional change associated with degradative succession of *Sphagnum* peat substrate in litter bags (Asemaninejad et al., 2017a) under warming. In this study we examine 1) whether fungal richness and diversity in the surface (0–5 cm) peat and subsurface peat fractions (roughly 10–15 cm and 30–35 cm) are similarly affected by climate change factors, 2) the functional turnover in the fungal community across this depth gradient, and 3) whether climate-driven changes in fungal community composition can be attributed to observed changes in plant functional groups over 18 months of experimental manipulation.

2. Material and methods

2.1. Experimental design

In August 2012, one hundred intact peat monoliths (25 cm diameter; 40 cm deep; 25 kg) covered by *Sphagnum* mosses, herbaceous and shrubby vegetation, were collected from relatively uniform lawn areas in a nutrient-poor fen in northern Ontario, Canada (48°21′N, 85°21′W). Each monolith contained characteristic plant species of the system, mainly dominated by different species of *Sphagnum* mosses (*S. angustifolium* (C. Jens. ex Russ.) C. Jens., *S. fallax* (Klinggr.) Klinggr., *S. fuscum* (Schimp.) Klinggr., and *S. magellanicum* Brid.), with at least one *Chamaedaphne calyculata* (L.) Moench (as the dominant shrub in the sampling site) and sparse distribution of sedges such as *Carex magellanica* Lam. and *C. disperma* Dewey. Each monolith was transferred to a 19 L pail with an ABS fitting port attached to a French drain system and a clear plastic hose held vertically to maintain the water table treatment (see Dieleman et al., 2015 for full mesocosm design). All mesocosms were transported to Western University's Biotron Environmental Climate Change Research Centre in London, Ontario, and kept under seasonal temperatures and light conditions for three months recovery. After three months, four mesocosms that did not recover were discarded, 12 mesocosms were destructively sampled, and 84 mesocosms went into the experimental treatments. Fourteen mesocosms were positioned randomly in each of six custom-designed, state-of-the-art, environmentally controlled chambers set at three temperature treatments ('ambient' (Control), ambient +4 °C and ambient +8 °C), crossed with two atmospheric CO_2 regimes (430 ppm (Control), 750 ppm), with seven replicates in each chamber under saturated conditions (water table 5 cm from the peat surface (Control)) and seven replicates under lowered water table conditions (water table 20 cm from the peat surface). As it is predicted that boreal regions of Canada will experience temperature increases of more than +8 °C by 2100 (IPCC, 2014), we chose corresponding experimental conditions across this range of temperature. The 'ambient' temperature conditions were programmed to match the 5 year average daily maximum and minimum temperatures between April and October for London, Ontario with a constant slope between highs and lows corresponding to the actual time points, recorded for any given day. The average ambient temperature for this period of time was 16.9 °C (see Lindo, 2015 for full temperature regime), which is slightly higher than temperatures observed at the sampling location. Full simulation of winter conditions was not logistically possible as temperatures below 10 °C could not be reliably maintained, so between November and March, 'ambient' conditions were set at 11.5 °C, with +4 °C and +8 °C offsets in other chambers. The specific environmental conditions for the 84 mesocosms placed in experimental chambers was regulated and maintained using a fully automated system (ARGUS Control Systems Ltd., White Rock, BC, Canada). Every six months, all the mesocosms within each chamber and their related experimental treatment were randomly moved to another chamber to prevent any potential chamber effects.

2.2. Initial and final destructive sampling

At the start of the experiment (T_0 - December 2012), 12 mesocosms were destructively sampled by splitting the monolith vertically and collecting 125 cm^3 of wet peat from the centre of each monolith at three different depths (upper 0–5 cm, middle 15–20 cm, and bottom 30–35 cm) to measure fungal communities and biochemical properties of the peat prior to treatment. After 18 months (T_{18}), at the end of second growing season, three mesocosms from each treatment were destructively harvested using the same protocols as in the initial sampling. All samples were stored in air-tight plastic bags at −80 °C until processed.

2.3. DNA extraction and PCR protocols

The initial and final destructively harvested peat samples were freeze dried for 48 h, homogenized and approximately 0.5 g (dwt) submerged in liquid nitrogen and ground using mortar and pestle. A Zymo Soil DNA isolation kit was used to extract total genomic DNA from 25 mg (dwt) of each sample according to manufacturer's instructions (Zymo Research Corporation). The extracted DNA were normalized to 20 ng per μL, then stored at −20 °C for downstream PCR amplifications.

Two sets of primers were used to capture major fungal groups present in peat samples: LSU200A-F (AACKGCGAGTGAAGCRGYA)/LSU476A-R