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Nematode community resistant to deep soil frost in boreal forest soils

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ABSTRACT

As global climate change advances, shifts in winter precipitation are becoming more common in high latitude ecosystems, resulting in less insulating snow cover and deeper soil frost. Long-term alterations to soil frost can impact on ecosystem processes such as decomposition, microbial activity and vegetation dynamics. In this study we utilized the longest running, well-characterized soil frost manipulation experiment in a boreal forest. We measured nematode family composition and feeding group abundances at four different soil layer depths from plots that had been subjected to deep soil frost for one and 11 years. The overall abundance of nematodes and the different feeding groups were unaffected by deep soil frost. However, a higher Maturity Index was weakly associated with deep soil frost (indicative of lower nutrient enrichment and more persister nematode (i.e., K-strategist) families), likely due to the loss of nutrients and reduced inputs from inhibited decomposition. Multivariate and regression analyses showed that most nematode families were weakly associated with dominant understory plant species and strongly associated with soil organic matter (SOM). This is probably the result of higher resource availability in the control plots, which is favorable to the nematode community. These results indicate that the nematode community was more strongly driven by the long-term indirect effects of deep soil frost on SOM as opposed to the direct effects. Our findings highlight that the indirect effects of altered winter precipitation and soil frost patterns may be more important than direct winter climate effects. Further, such indirect effects on SOM and the plant community that may affect the nematode community can only be seen in long-term experiments. Finally, given the critical role nematodes play in soil food webs and carbon and nutrient cycling, our results demonstrate the necessity of considering the response of nematodes to global climate change in boreal forest soils.

1. Introduction

Over half of the land surface area in the Northern Hemisphere experiences seasonal snow cover and soil frost (Zhang et al., 2004). However, global warming has begun increasing terrestrial surface temperatures and also changing precipitation regimes (IPCC, 2013). Snowfall is occurring later, the spring melt is becoming earlier and melts during the winter are increasingly more common (Bokhorst et al., 2016; Laudon and Lofvenius, 2016). Over the next century, it is predicted that there will be 73–93 fewer days with persistent snow cover in northern Sweden (Mellander et al., 2007). Soils that are not covered by an insulating layer of snow during the winter months experience deeper penetration and increased severity of soil frost (hereafter deeper soil frost) (Stieglitz et al., 2003; Kreyling et al., 2012) and are generally exposed to more freeze-thaw cycling (Mellander et al., 2007). Therefore, as climate change advances, the role that deeper soil frost will play in shaping ecosystem functions will likely change.

Evidence is accumulating that deeper soil frost can alter biological and biogeochemical processes. In the boreal forest, deep soil frost can damage understory vegetation (Blume-Werry et al., 2016), favor fungal over bacterial growth in the soils (Haei et al., 2011), reduce soil microbial respiration (Monson et al., 2006) and lead to impaired decomposition of organic matter (Kreyling et al., 2013). Further, deep soil frost has also been shown to affect winter CO_2 fluxes across systems, likely as the result of increased mobilization of labile carbon (C) substrates caused by repeated freeze-thaw events (Brooks et al., 2011). Additionally, deeper soil frost has been shown to damage or kill fine roots in temperate and boreal ecosystems (Comerford et al., 2013; Blume-Werry et al., 2016; Reinmann and Templer, 2016), which increases organic

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matter input into the soil subsystem. Considering the important role snow plays in high latitude ecosystems, it is imperative to advance our understanding of how deeper soil frost drives ecological processes.

Nematodes are the most abundant multi-cellular animal on the planet and play an important role in driving soil nutrient and C cycling (Bardgett and Chan, 1999) making them an important guild in the soil food web (Ferris, 2010). Nematodes show considerable variability in their sensitivity to environmental disturbance, such as physical alterations to the environment or nutrient enrichment. Certain nematode taxa are considered resistant or resilient to disturbance (i.e., colonizers that are r-strategists), while others are more sensitive (i.e., persisters that are K-strategists) (Bongers, 1990). Changes to the environment that favor colonizer over persister nematodes can generate decreases in the Maturity Index, thereby making nematodes useful bioindicators (Bongers and Ferris, 1999). Notably, a microcosm experiment found that colonizer nematode groups might be particularly sensitive to changes in soil frost (Dam et al., 2012).

Additionally, dividing nematode families into feeding groups can help elucidate the role different groups play in controlling ecosystem function (Yeates et al., 1993). Partitioning nematodes into bacterial versus fungal feeders (i.e., the Channel Index) informs on fast (i.e., bacterial) and slow (i.e., fungal) soil energy channels (Ferris et al., 2001). Environmental disturbance that alters resource availability may lead to shifts in bacterial versus fungal feeding nematode groups (Kardol et al., 2010; De Long et al., 2015). Furthermore, changes to the relative abundances of these groups might affect nutrient cycling and decomposition rates (Ferris et al., 2001). Most nematode functional groups are directly or indirectly controlled by plant species (De Deyn et al., 2004; Viketoft et al., 2009) and recent studies have shown that the nematode community is affected by climate-mediated shifts in plant functional group composition (Kardol et al., 2010; Thakur et al., 2014; De Long et al., 2015). However, despite advances in how climate change affects nematodes (Hoeksema et al., 2000; Neher and Weicht, 2013; Cesarz et al., 2015), the response of nematode communities to changes in soil frost depth and the implications such responses might have for nutrient cycling and decomposition remains largely unexplored (Sulkava and Huhta, 2003; Dam et al., 2012).

To our knowledge, only one study to date has investigated the effect of deep soil frost on soil nematodes and this work only considered total nematode abundance after one winter of deep soil frost in the boreal forest (Sulkava and Huhta, 2003). In the current paper, we utilized the world's longest running, well-characterized soil frost manipulation experiment (Haei et al., 2010, 2011, 2012, 2013; Kreyling et al., 2012, 2013; Blume-Werry et al., 2016) along a stretch of riparian boreal forest in northern Sweden. We measured nematode community composition and feeding group abundances at different soil layer depths in soils that had been subjected to deep soil frost for one and 11 years in order to test the following hypotheses: 1) Deep soil frost will have similar overall abundances of nematodes to control plot soils because nematodes from boreal soils are able to tolerate deep soil frost (Sulkava and Huhta, 2003); 2) Deep soil frost plots will have a higher Maturity Index and a higher Channel Index (i.e., increased fungal to bacterial feeding nematodes leading to slower nutrient cycling). This is because deep soil frost will inhibit overall microbial growth (Monson et al., 2006), thereby promoting a higher Maturity Index (Bongers and Ferris, 1999). Further, despite overall decreases in microbial growth, fungal growth will be favored over bacterial growth (Haei et al., 2011), thereby promoting a higher Channel Index; 3) Deep soil frost will indirectly negatively impact upon all nematode feeding groups abundances via a reduction of the understory vegetation (Blume-Werry et al., 2016), which strongly dictates nematode community composition (Kardol et al., 2010; De Long et al., 2015). In all cases, the strongest effects were expected in plots exposed to deep soil frost for 11 years and in the shallowest soil layers where nematodes are most active (Ou et al., 2005) and the frost is most severe. Exploring how the nematode community is driven by changes to soil frost depth is essential for understanding how the ecosystem processes they control will respond to altered winter climate regimes.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted in a riparian boreal forest near a first order stream in the Krycklan catchment in Svartberget Experimental Forest (64°14′N, 19°46′E). Bedrock consists of Svecofennian metasediments/metagraywacke (Laudon et al., 2013) and soils are predominantly ferric podzols developed on glacial till. Soil pH increases with increasing soil depth from 4.0 to 5.2 from 10 to 65 cm (Kreyling et al., 2013). The forest consists primarily of *Picea abies* and *Pinus sylvestris*, with an understory dominated by the dwarf shrubs *Vaccinium myrtillus* and *V. vitis-idaea* and the feather mosses *Hylocomium splendens* and *Pleurozium schreberi* (Forsum et al., 2008). Mean annual air temperature between 1980 and 2010 was 1.8 °C, with average January and July temperatures of −9.5 °C and 14.7 °C, respectively (Laudon et al., 2013). Snow cover lasts for approximately 167 days per year from mid November to early May and snow depth ranges between 42 and 113 cm (1980–2015) (Laudon and Lofvenius, 2016). Soil frost depth ranges from 2.5–79 cm (measurements taken from a nearby snow-covered reference location between 1992 and 2007). All climatic measurements were taken at the climate station at the Svartberget Experimental Forest.

Soil frost manipulation treatments were initiated in 2002 and the experimental design is described in full by Haei et al. (2010). Extensive measurements have been taken in these plots on the vegetation (Kreyling et al., 2012), microbial communities and microbial respiration/decomposition (Haei et al., 2011; Kreyling et al., 2013) and dissolved organic C processes (Haei et al., 2010, 2012), which can be readily linked to the results of the current experiment. Ammonium concentrations have been found to decrease with soil depth (from 0.131 to 0.037 mg per g dry weight soil from 0 to 60 cm) and were unaffected by soil frost treatment; see below (Kreyling et al., 2012). Briefly, two different soil frost treatments were replicated three times each in 9 m^2 plots: deep soil frost and ambient soil frost (control). During the winter months, the deep soil frost plots were covered with a transparent roof (2.5 m above each plot) to prevent snow from accumulating underneath and the control plots were exposed to ambient conditions. At the end of winter each year the snow that had accumulated on the roof above each deep soil frost treatment plot was transferred to the surface of the corresponding plot before melting in order to ensure comparable water balance between the plots. For this experiment, three additional 9 m^2 deep soil frost plots were created nearby in autumn 2012 to compare the effects of short-term (one-year) versus long-term (11-year) deep soil frost on the nematode community.

Temperature measurements from probes placed at 10, 25, 40 and 60 cm depths in the plots showed that soil temperatures during the winter were strongly reduced in the deep soil frost plots compared to the control plots. Without snow, soil frost was on average deeper (49 ± 6 cm versus 29 ± 3 cm, mean ± standard deviation), persisted over twice as long (118 ± 4 days at 10 cm depth versus 56 ± 4 days), delayed thawing by 6 days at the soil surface and 26 days at 10 cm depth, and soil temperatures were