CHAPTER 10

Soil warming and winter snowpacks: Implications for northern forest ecosystem functioning

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Introduction

Forest ecosystem nutrient cycling is controlled to a large extent by environmental conditions, including soil and air temperature and patterns and forms of precipitation (i.e., rain, snow, and fog). Climate changes around the globe have led to increases in mean land surface temperatures (Hansen et al., 2010;

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Lawrimore et al., 2011; Jones et al., 2012; Rohde et al., 2013), altered patterns of precipitation (Smith et al., 2012), and an increased occurrence of extreme temperature and precipitation events (Hartmann et al., 2013) over the last several decades. Temperatures are expected to increase over the next century most strongly at high latitudes (Pithan and Mauritsen, 2014) and during winter months (Xia et al., 2014), which will have a large influence on seasonally snow-covered ecosystems, including many temperate and boreal forests at mid and high latitudes and elevations (Brown and Mote, 2009). While increased air temperatures in the snow-free season will likely lead to coupled increases in soil temperature, the effect of warmer winter air temperatures on soils is mediated through changes in depth and duration of snowpack in snow-covered regions (Zhang, 2005; Lawrence and Slater, 2010). For example, in some tundra regions an increased depth and/or duration of an insulating snowpack is expected to lead to warmer winter soil temperatures (Sturm et al., 2005). In contrast, in other historically snow-covered tundra, boreal, and temperate regions, snowpack depth and duration are expected to decline (Hayhoe et al., 2007; Notaro et al., 2014), leading to colder and more variable soil temperatures in winter due to the lack of insulating snow (Decker et al., 2003).

Although winter processes have typically been understudied relative to the growing season (Campbell et al., 2005; Kreyling, 2010), there is mounting evidence that biological processes in winter contribute significantly to annual fluxes of carbon (C) and nitrogen (N) (Groffman et al., 2012; Makoto et al., 2014). In addition, a growing body of literature on the effects of winter climate change demonstrates that changes in winter soil temperatures can have cascading effects on growing season ecosystem processes (Monson et al., 2006; Matzner and Borken, 2008; Wipf and Rixen, 2010; Blankinship and Hart, 2012; Bokhorst et al., 2012; Kreyling et al., 2012; Cornelissen and Makoto, 2014; Williams et al., 2014; Li et al., 2016; Song et al., 2017). Therefore understanding the mechanisms by which winter climate affects processes that control biogeochemical cycling are of considerable interest to researchers attempting to understand future ecosystem function.

In the northeastern United States, forest ecosystems make up 60% of the total regional land area (Lu et al., 2013a), are responsible for approximately 10% of the annual C sequestration by U.S. forests (Woodbury et al., 2007; Lu et al., 2013a), and can retain up to 90% of the atmospheric N deposition (Yanai et al., 2013). Over the last 5 decades, mean annual air temperatures have risen by 0.25°C per decade with an accelerated rate of 0.70°C per decade in winter (Hayhoe et al., 2007). These trends are expected to continue, with air temperatures projected to rise by an additional 0.6–4.9° C by the year 2100 (Pourmokhtarian et al., 2016). As winters have warmed, the depth of snow and number of snow-covered days have declined by approximately 4.6 cm and 8.9 days per decade (Burakowski et al., 2008). Maximum snowpack depth is expected to decline by an additional 50 cm by the year 2100 (Hayhoe et al., 2007). With a shallower and more intermittent snowpack, the frequency of soil freeze-thaw cycles in winter is projected to increase over the next century (Campbell et al., 2010). Consequently, understanding how climate change will influence ecosystem processes in the northeastern United States has become a priority research area at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire.

The HBEF, located in the southern part of the White Mountain National Forest in central New Hampshire, is part of the broader northeastern United States northern forest ecoregion. Originally established for hydrological research, long-term records of climate, hydrology, and biogeochemistry make the HBEF an ideal site to study how changes in climate may influence ecosystem processes in the northeast United States. Over the last three decades, researchers interested in the effects of warming on soils have employed a variety of methods to determine how soil temperatures will change in the future and influence ecosystem processes, including long-term data analysis, experimental manipulation, and natural climate gradient studies. Researchers at the HBEF have placed strong emphasis not only on warming, but on the indirect effects of warming on soil temperatures, which paradoxically may become colder in winter as the snowpack shrinks (Brown and DeGaetano, 2011).

Site description

History and site description

The HBEF (43°56′N, 71°45′W) was established in 1955 by the U.S. Department of Agriculture Forest Service and has been a component of the U.S. National Science Foundation's Long-Term Ecological Research Network since 1988. The HBEF covers approximately 3200 ha, encompassing a bowl-shaped valley ranging in elevation from 222 to 1105 m a.s.l. that is drained by Hubbard Brook, a tributary to the Pemigewasset River. The HBEF has hilly, occasionally steep topography and is underlain by bedrock dominated by metamorphic rock of igneous and sedimentary origin. Soils are coarse and acidic, predominantly characterized as well-drained Spodosols, more specifically, Typic Haplorthods derived from glacial till, with sandy loam textures. Vegetation is predominantly classified as northern hardwood forest on the lower slopes, dominated by *Acer saccharum* (sugar maple), *Betula alleghaniensis* (yellow birch), and *Fagus grandifolia* (American beech). Spruce-fir forest, dominated by *Picea rubens* (red spruce) and *Abies balsamea* (balsam fir), occurs at higher elevations (above c.800 m), especially on thinner, less fertile soils (Likens, 2013).

The climate at the HBEF is cool continental, characterized by long, cold winters and short, mild summers. Mean annual precipitation is 1400 mm (Bailey et al., 2003), of which about one-third is snow with an average maximum snow depth of 75 cm (Campbell et al., 2010). Snowpack typically lasts from mid-December until mid-April and shallow (<10 cm) soil frost is present for approximately two out of every three years (Campbell et al., 2010). Mean winter air temperature from December to March averages −5.7°C, with monthly temperatures ranging from an average minimum of −12.8°C during January to an average maximum of 25.5°C during July (Bailey et al. 2003).

Long-term records of meteorology, hydrology, and biogeochemistry

Long-term records from a network of meteorological, precipitation, and stream gauges have been collected since the inception of the HBEF in the mid-1950s. Meteorological data are collected continuously at the HBEF using standard methods. Air temperature has been measured at seven locations throughout the HBEF, four of which have long-term (>55 years) records. Precipitation is collected at a network of gauges distributed throughout the HBEF valley, with the oldest records dating back to 1956. There are nine gauged watersheds where continuous stream-height measurements are made in a stilling well attached to a V-notch weir. Long-term below-canopy snowpack measurements (snow depth and water equivalent) have been made at the HBEF since 1956 using a Mt. Rose snow tube. Measurements of soil frost have been made over time at a single point adjacent to snow courses using a hatchet to cut through the frozen soil and a ruler to measure the total depth to the frost line from the surface of the forest floor.

Measurements of biogeochemical pools and fluxes have also been collected at the HBEF to characterize long-term trends in ecosystem function. These include wet and dry atmospheric deposition, throughfall, aboveground biomass, litterfall, soil microbial biomass and activity, soil to atmosphere fluxes of carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4), roots, soil solution, and stream water. Combined, these data sets provide a comprehensive accounting of the principal hydrological and element fluxes for the forest ecosystems at the HBEF.

Climate trends and future projections

Analysis of meteorological records at the HBEF demonstrate that climate has changed measurably over the last half-century. Average annual air temperature has increased significantly by 0.17–0.29°C per decade (Fig. 1), with more rapid warming occurring in winter months (Campbell et al. 2007; Hamburg et al. 2013). This warming is consistent with regional trends, although warming at the HBEF is more marked (Hayhoe et al., 2007; Burakowski et al., 2008). Annual growing degree days have increased by 32.6 days per decade and thawing degree days have increased by 2.9 days per decade for January and February alone and by 10.5 days per decade for December-March. A general lengthening of the growing season has been observed over the last five decades, characterized by advancement of snowmelt (~13 days) and date of last frost (~8 days) in spring and by delays in first frost (~10 days) and establishment of measurable snowpack (~8 days) in early winter (Hamburg et al., 2013). Long-term weekly measurements of snow depth indicate that the maximum annual snowpack depth has declined by 4.8 cm per decade and the number of days with snow cover has declined by 3.9 days per decade (Fig. 2; Campbell et al. 2010), comparable to regional

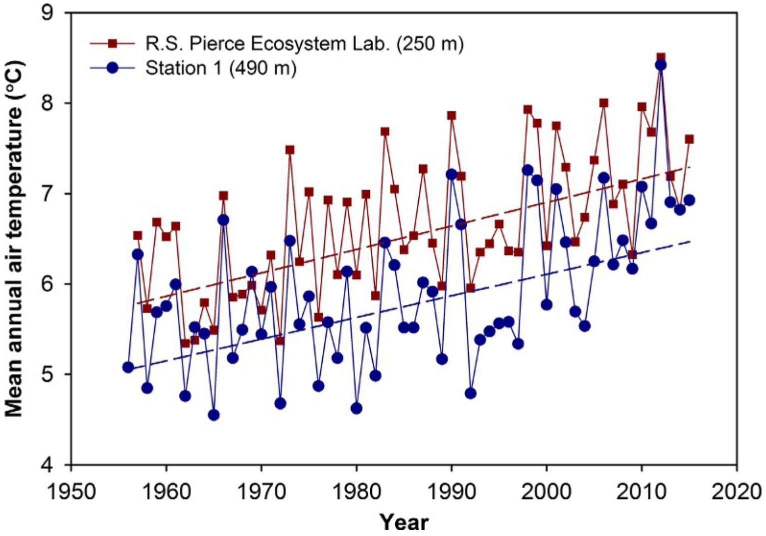

Fig. 1 Long-term records of annual air temperatures at two elevations at the HBEF.

analyses (Burakowski et al., 2008). However, there have been no significant trends in the amount of winter precipitation, indicating that factors such as faster midwinter snow melt due to warmer temperatures or more precipitation falling as rain rather than snow are responsible for changing winter snowpack conditions at the HBEF (Campbell et al., 2010). Over the long-term record, soil frost was present approximately 2 out of every 3 years with substantial year-to-year variability and no detectable trends in annual maximum soil frost depth over time (Campbell et al., 2010).

Climate projections derived from downscaled, coupled atmosphere-ocean general circulation models indicate that observed trends in air temperature will continue at the HBEF, rising 0.6–4.9°C by the end of the century (Huntington et al., 2009; Campbell et al., 2010; Pourmokhtarian et al., 2016).

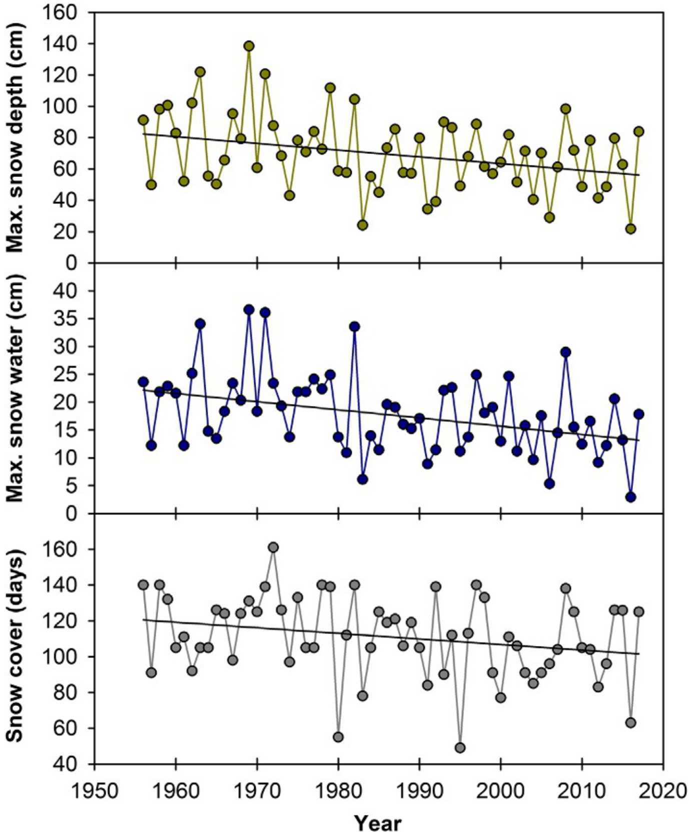

Fig. 2 Long-term records of maximum snow depth, maximum snow water content, and duration of snow-covered days at the HBEF.

Projected changes in precipitation are much more variable, ranging from a 17% decrease to a 23% increase. Researchers have used these climate projections to drive both regional and site-specific models to estimate future changes in soil frost (Campbell et al., 2010), hydrology (Campbell et al., 2011), and biogeochemistry (Pourmokhtarian et al., 2012, 2017) at the HBEF. As the climate continues to warm, maximum annual snowpack depth is projected to decline by 31–47 cm at the HBEF by 2100. Over the same time period, models indicate that snow cover duration will decline by 20–70 days and an increasing number of snow-free periods are expected due to more midwinter snowmelt events (Campbell et al., 2010). Though models project a decline in maximum depth and duration of soil frost, the number of soil freeze-thaw events are expected to increase by 1–3 events per year by the end of the century (Campbell et al., 2010).

Soil warming and winter snowpack studies

Long-term patterns in biogeochemistry

Information on long-term patterns of biogeochemical fluxes and processes provide valuable insight into how observed changes in climate over the last half-century have influenced ecosystem function at the HBEF (Rustad et al., 2012). In some cases, these data can provide verification of our classic understanding of ecosystem functioning. For example, as the length of the growing season has expanded (Hamburg et al., 2013), long-term observations of leaf phenology indicate that green canopy duration has in turn increased by approximately 10 days over the last five decades (Richardson et al., 2006). Long-term records have also pointed researchers to previously unknown relationships and raised important new questions about ecosystem function. Analysis of stream nitrate (NO_3^-) patterns from 1982 to 1993 showed an expected mean annual pattern of peak NO_3^- loss during snowmelt and lowest losses during the mid-growing season when plant N uptake is highest (Mitchell et al., 1996). Throughout the 11-year record, however, unusually high annual exports of NO_3^- coincided with very cold winters with low snowpack that suggested some role of low snow and cold soils in enhanced ecosystem N losses. In order to determine whether this pattern of winter climate driving NO_3^- leaching was supported by longer term data, Fitzhugh et al. (2003a, b) used a 27-year record (1970–97) of snow and soil frost depth to explore winter controls on stream nutrient export. Though not a significant predictor of N losses across the entire record, analysis over each decade independently found that cumulative soil frost was positively related to annual deviations of stream calcium (Ca^{2+}), magnesium (Mg^{2+}), and NO_3^- losses explaining 54%–56% of the variation in NO_3^- losses during 1979–80 and 1980–89 (Fitzhugh et al., 2003a). However, this relationship weakened during the 1990s and a series of soil-freezing events in the early years of the decade had no detectable relationship with stream NO_3^- losses (Fitzhugh et al., 2003a) and there was little evidence of NO_3^- losses following a strong soil frost event in 2006 (Judd et al., 2011). The conflicting findings regarding the relationship of soil frost and nitrate export from Hubbard Brook over time highlighted the need to better understand controls on ecosystem function to project how forest N retention and its biogeochemical controls could be altered as snowpack continues to shrink in the future, with potentially important consequences for whole-ecosystem nutrient cycling and loss.

Snow removal and soil-freezing experiments

Long-term records of ecosystem processes point to climate warming, particularly in winter, as an important control of ecosystem function. As climate changes, later development of snowpack due to warmer temperatures may counterintuitively result in colder winter soils with increased soil freezing, or "colder soils in a warmer world" (Groffman et al., 2001a; Brown and DeGaetano, 2011). Changes in winter soil freezing are likely to influence many belowground processes that could influence biogeochemical cycling, including changes in fine-root and microbial mortality, hydrologic and gaseous losses of N, and the acid-base status of drainage water. However, the mechanisms driving ecosystem responses to soil freezing are difficult to tease out of long-term data alone. Over the past two decades, a series of manipulative experiments (Groffman et al., 2001a, 2010; Templer et al., 2012) were conducted at the HBEF and elsewhere (Pilon et al., 1994; Boutin and Robitaille, 1995; Freppaz et al., 2008; Dietzel et al., 2011; Repo et al., 2011; Aanderud et al., 2013; Kreyling et al., 2013; Vankoughnett and Henry, 2014; Gavazov et al., 2017) using snow removal to simulate future winter climate warming and to determine the effects of reduced snow and persistent soil freezing on soil C and N processes, microbial activity, plant processes, and the influence of changes in soil temperatures on animal-mediated biogeochemical processes.

Experimental treatment

Snow removal experiments at the HBEF aimed to simulate a delayed onset of snowpack by manually removing natural snow accumulation by shoveling for the first 4–6 weeks of winter (Groffman et al., 2001a, 2010; Templer et al., 2012). The theory behind this manipulation is that exposure to cold winter air in the absence of an insulating layer of snow causes reductions in soil temperature and formation of soil frost. To protect the forest floor and scientific instrumentation during shoveling, and to preserve normal wintertime albedo, a few centimeters of snow was allowed to remain on treatment plots throughout the winter and snow shoes were worn by field technicians to minimize snow compaction. After 4–6 weeks of snow removal, snow was allowed to naturally accumulate on treatment plots for the duration of the winter (Groffman et al., 2001a, 2010; Templer et al., 2012).

The first snow removal experiment at the HBEF was established in 1996 (Groffman et al., 2001a, b) and consisted of two 10 × 10-m plots at each of four sites, with one plot at each site designed for snow manipulation and the other as a reference. To compare potential responses between common tree species at the HBEF, two sites dominated by sugar maple and two by yellow birch were selected (elevation range 472–648 m a.s.l.). Snow removal was conducted over two winters in 1997/1998 and 1998/1999. In 2001, a follow-up study was initiated to capture an even wider range of soil-freezing intensity by exploiting a natural elevation gradient (Groffman et al., 2010). Paired 10 × 10-m reference and snow manipulation plots were established at two low-elevation south-facing locations (at 380 and 480 m a.s.l.) and at two high-elevation north-facing locations (at 755 and 790 m a.s.l.). Although selected plots were not as purely dominated by a single tree species as in the original experiment, selected plots were broadly characterized as dominated by either yellow birch or sugar maple. Snow was removed from one of the two paired plots across the gradient for two consecutive winters in 2002/2003 and 2003/2004 (Groffman et al., 2010). A third experiment was established in 2007 (Fig. 3) with larger plots to permit evaluation of both belowground and aboveground processes and to examine longer term vegetative responses (Templer et al., 2012; Campbell et al., 2014). Four snow removal plots and four reference plots (each 13 × 13 m), each with three or more dominant or codominant sugar maple trees, were established and snow was removed from the treatment plots for five consecutive winters in 2008–14 (Sorensen et al., 2016a).

During each of these successive snow removal studies, plots were equipped with thermistors to monitor soil temperature and water content reflectometers to measure soil moisture. Approximately weekly measurements of soil frost and snow depth were also recorded. Soil frost was measured using tubes constructed from flexible PVC tubing filled with a methylene blue dye solution (Ricard et al. 1976). Snow depth was measured with either a Mt. Rose Federal

Fig. 3 Experimental snow removal plot centered on three mature sugar maple trees at the HBEF. *(Photograph by Annie Socci 2012.)*

snow core or a stationary meter stick. A variety of methods were employed across studies to capture ecosystem responses to soil freezing, including soil biogeochemical fluxes (leachates and gases), microbial community function, aboveground and belowground plant processes and nutrient pools, and animal-mediated biogeochemical cycling.

Results

Across all snow removal studies at the HBEF, maximum snow depth was demonstrated to be an important control on soil frost depth and snow removal treatment was an effective method for inducing soil frost (Fig. 4; Hardy et al., 2001; Cleavitt et al., 2008; Templer et al., 2012; Sorensen et al., 2016a). In the longest running experiment, which lasted 5 years (Sorensen et al., 2016a), snow removal led to an approximately twofold decrease in average maximum snow depth and over a fourfold increase in average maximum frost depth. Variation in air temperature prior to and during the snow removal period and the timing of snowpack onset resulted in significant year-to-year differences in the magnitude of the snow removal treatment across studies (Hardy et al., 2001; Cleavitt et al., 2008; Sorensen et al., 2016a). However, even relatively mild winters with low snowfall led to significant increases in soil-freezing depth and duration, suggesting that as climate shifts toward less snowfall or a shorter duration of snow on the ground, increases in soil freezing are likely (Hardy et al., 2001). Although treated plots consistently recorded slightly less soil moisture and soil water

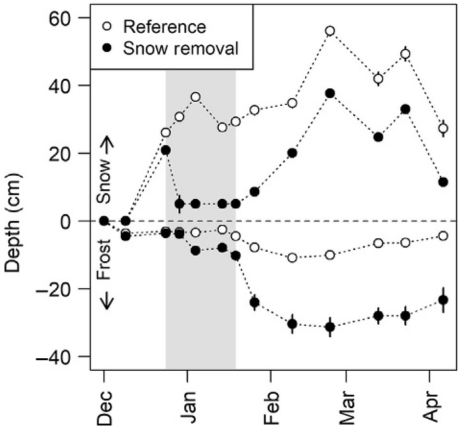

Fig. 4 Average snow and soil frost depth in reference and snow removal plots from December 2012 to April 2014. The *shaded area* represents the period of snow removal.

in spring months compared with reference plots, likely due to reduced infiltration into frozen soils (Hardy et al., 2001), any differences between reference and treatment plots subsided by the peak growing season, and often much earlier. The various plots making up these three snow removal experiments across nearly two decades at the HBEF represented a wide range of landscape positions, soil types, and elevation yet all demonstrated similar responses (i.e., increased depth and duration of soil freezing and relatively little change in soil moisture) to the snow removal treatment, although the timing and extent of the responses varied.

Soil biogeochemistry

Snow removal studies at the HBEF have generally shown that soil-freezing events can lead to increased leaching of NO_3^-, inorganic phosphorous (P_i), and base cations from soils. However, the magnitude of soil biogeochemical responses to snow removal has been variable across successive experiments. Groffman et al. (2001b) found that mild, but persistent soil freezing (minimum soil temperatures >-5°C and maximum soil frost depth <30 cm) in sugar maple and yellow birch stands in 1997–99 increased soil extractable NO_3^- across all treatment plots in summer, although this effect was only significant in the organic horizon of sugar maple stands. Soil freezing also induced accelerated leaching of N across all manipulated plots, with N losses characterized mainly by NO_3^- in sugar maple plots and by NO_3^-, ammonium (NH_4^+), and dissolved organic N in yellow birch plots (Fitzhugh et al., 2001). The average increase in N flux from organic soil resulting from snow removal was 25 kg ha^{-1} y^{-1} (Fitzhugh et al., 2001). In sugar maple stands, the increase in NO_3^- leaching was accompanied by pronounced acidification of soil solutions, as well as leaching of P_i, Ca^{2+}, and Mg^{2+} in Oa horizon solutions during the growing season (Fitzhugh et al., 2001, 2003b). A lack of P_i, Ca^{2+}, and Mg^{2+} response in yellow birch stands highlights the importance of tree species differences in modulating ecosystem responses to changing soil temperatures.

In contrast to the marked results of this initial snow removal experiment, the first follow-up experiment conducted in 2003–05, which produced more severe soil freezing (i.e., frost depth in treatment plots ranged from ~35 to 50 cm), resulted in more variable and less pronounced treatment effects on soil biogeochemistry (Groffman et al., 2010). Although soil solution concentrations of NO_3^- tended to be higher in treatment plots than in reference plots, especially those dominated by sugar maple as opposed to yellow birch, the effect was not consistently significant and concentrations (~80 μmol L^{-1}) were much lower than concentrations observed in treatment plots in the first round of experiments (~500 μmol L^{-1}). There was no significant relationship between soil-freezing intensity, as indicated by maximum soil frost depth and measured frost heaving, and NO_3^- leaching. A major difference in the second experiment was that dissolved organic carbon (DOC) increased in the treatment plots. Groffman et al. (2010) hypothesized that coupling of C and N cycling, by frost-induced mobilization of labile C driving microbial NO_3^- immobilization in soils, could be responsible for modulating the N-leaching response to soil freezing. Campbell et al. (2014) subsequently found more evidence of significant NO_3^- leaching in response to soil freezing in the third snow removal experiment conducted in sugar maple dominated stands in 2008–10. Leaching of N from mineral soil attributed to snow removal amounted to 7.0 kg N ha^{-1} in 2009 and 2.8 kg N ha^{-1} in 2010, less than N losses reported by Fitzhugh et al. (2001), but still a significant flux compared with annual DIN inputs in precipitation (5.3 kg N ha^{-1}).

In addition to the effect of snow removal and soil freezing on N-leaching losses, increased gaseous N losses caused by snow removal manipulation at the HBEF have been observed (Groffman et al., 2006, 2010). In the first snow removal study, soil freezing increased N_2O flux and decreased CH_4, especially during winter. There was no measurable effect of snow removal on CO_2 losses throughout the year. Treatment effects did not vary between tree species for N_2O, but CH_4 uptake was higher in plots dominated by yellow birch than in plots dominated by sugar maple

(Groffman et al., 2001b). In the follow-up study conducted across an elevation gradient, the response was more moderate, yet N_2O fluxes did exhibit an increase with soil freezing (Groffman et al., 2010). Trace gas fluxes were not measured in the 2008–15 snow manipulation.

Results of these studies suggest that increased soil freezing with warmer winter temperatures could lead to increased soil solution and gaseous losses of N from northern hardwood forest soils. It is possible that the variable response of N leaching in response to soil frost in these successive experiments was driven by variation in soil texture or organic layer depth among the plots chosen for manipulation or by variation in the magnitude of the applied treatments resulting from significant soil freezing occurring in reference plots, especially in the 2003–05 study (Groffman et al., 2010). Long-term trends at the HBEF also suggest that rates of nutrient cycling in soils are variable over time, and particularly high or low cycling of C and N in a given year could influence treatment responses (Groffman et al., 2010). There is particular interest in long-term trends in N oligotrophication at Hubbard Brook (Durán et al., 2016) that may make the ecosystems there less susceptible to high N losses following disturbance, like soil freezing. In any case, the variable responses across these studies clearly point to more complicated interactions between C and N cycling in soils, as well as tree species effects that raise additional questions about the biotic and abiotic mechanisms driving biogeochemical responses to soil freezing.

Microbes

Despite significant responses of soil nutrient mobilization and increased N_2O fluxes, there were no emergent effects of snow removal and soil freezing on rates of in situ N mineralization, nitrification, or denitrification, or on soil respiration in either the 1997–98 or 2002–04 snow manipulation studies. Similarly, there were no consistent treatment effects on potential net N mineralization, nitrification, and denitrification, or on microbial biomass C or N pools (Groffman et al., 2001b, 2010). Although there is no direct evidence of increased nitrification with snow removal, isotopic data from the 2008–10 study indicated that nearly all the NO_3^- in leachate from both the snow removal and reference plots was produced by nitrification (Campbell et al. 2014). To develop a more detailed understanding of microbial response to soil freezing, Sorensen et al. (2016a, b) assayed soil microbial exoenzyme activity, in addition to measuring potential microbial activity and microbial biomass C and N pools, following snow manipulation in the winters of 2012/2013 and 2013/2014. This analysis followed the third and fourth years of consecutive snow manipulation, but no significant effects were observed between treatment and reference plots when compared directly. Analysis of integrated snow depth and duration across both measured years at all plots revealed a positive relationship with microbial biomass N, exoenzyme activity, and potential soil respiration in both the organic and mineral soil (Sorensen et al., 2016a). However, although snow depth and soil frost depth were related, there was no corollary negative effect of integrated soil frost depth and duration on the same soil microbial and exoenzyme responses at the HBEF (Sorensen et al., 2016a). The lack of consistent microbial response to soil freezing suggests that changes in microbial activity alone are unlikely to account for the pulse of N leaching observed following snow removal and points to effects on vegetation and/or abiotic disruption of soil aggregates as more likely direct mechanisms for the experimental results described above.

Vegetation

Increasing evidence for the dominant role of vegetation responses in controlling observed biogeochemical consequences of soil-freezing events has largely driven the evolution of successive snow removal experiments at the HBEF. Results of snow removal studies have collectively found that snow removal-induced soil freezing leads to significant changes in patterns of root mortality, production, turnover, and function in the following growing season that alter soil C and N cycling. Tierney et al. (2001) used minirhizotron tubes to document significant overwinter fine-root mortality of both sugar maple and yellow birch roots following soil freezing in the field in the initial HBEF snow removal experiment. In the first year of treatment (1998) this elevated root mortality continued through May, the typical start of the growing season in these forests. Interestingly, although sugar maple stands exhibited a much stronger N mobilization response compared to yellow birch stands (Fitzhugh et al., 2001; Groffman et al., 2001b), there were no differences observed among species regarding root mortality. Additional soil N inputs resulting from fine-root mortality caused by soil freezing was estimated to yield an excess flux of about 0.5 g N m^{-2}, a substantial portion of the enhanced N leaching observed in response to the treatment (Fitzhugh et al. 2001). Cleavitt et al. (2008) used triphenyl-tetrazolium chloride assays of roots extracted from snow removal plots across an elevational gradient in 2008 to better understand how soil freezing affects the vitality of different classes of roots within the soil profile. The assay provides a quantitative measure of the proportion of living cells per unit root dry mass and indicated that first- and second-order roots in the organic soil were most susceptible to reduced vitality following soil freezing, while third- and fourth-order roots in the organic soil and all mineral soil roots examined were unaffected by the treatment. Low-order roots (e.g., first- and second-order) in the organic horizon are critical to water and nutrient uptake and their increased mortality likely reduces the ability of trees to take up nutrients in early spring. Unlike the prior study, Cleavitt et al. (2008) found that sites dominated by sugar maple trees showed the strongest reduction in root vitality, regardless of the relative severity of soil freezing across plots in the study, indicating an influence of tree species on susceptibility to freezing damage.

The mechanism causing fine-root mortality following persistent soil freezing remains unclear. Evidence from Tierney et al. (2001) suggests that cold temperatures alone are not sufficient to induce the magnitude of root mortality observed in the field. They transplanted seedlings from the HBEF into 1-m-diameter pots filled with soil and exposed them to freezing temperatures comparable to those experienced in the snow removal plots in 1998–99, but under controlled conditions. The controlled temperature manipulation did not result in significant root mortality and they concluded that frost heaving of intact soil, rather than temperature alone, is an important driver of root mortality observed in the field. Cleavitt et al. (2008) tested this hypothesis by removing frozen roots from snow removal plots in the winter of 2008 and subjecting a subset to artificial frost heave by mechanically stretching frozen roots in the lab to a comparable offset as measured frost heave in the field. They found no difference in measured tensile strength between roots that were frozen and mechanically stretched and those roots that were simply frozen, pointing to temperature sensitivity as the dominant driver of root damage. These contrasting conclusions indicate that a combination of cold temperature threshold and physical disruption of the soil aggregation surrounding roots in situ are both important for controlling root response to soil freezing and suggest that not only soil freezing, but the timing and frequency of freeze-thaw events could be significant.

Subsequent studies showed that snow removal caused sublethal damage to living roots that altered plant root function. Comerford et al. (2013) sampled organic layer roots from sugar maple stands following snow removal in the winter of 2009/2010. Living roots were sorted from dead roots based on visual inspection and then measured for relative electrolyte leakage, a metric of cellular membrane damage to root cells. They found that roots that had survived overwinter soil freezing in the snow removal plots exhibited a 37% increase in damage relative to those in reference plots. Root damage and mortality caused by soil freezing was demonstrated to directly alter plant function by reducing uptake of soil nutrients in early spring (Campbell et al., 2014). Using the nutrient depletion method (BassiriRad et al., 1999), rates of in situ uptake of NO_3^- and NH_4^+ were measured for sugar maple fine roots throughout the growing season in 2010 and 2011. Roots from snow removal plots took up 36% less NH_4^+, well established as the preferred form of mineral N for sugar maple trees (Templer and Dawson, 2004; Lucash et al., 2005; Socci and Templer, 2011), than roots in reference plots. There were no changes observed in root NO_3^- uptake, which remained near zero throughout the sampling period (Campbell et al., 2014). These measurements do not account for potential changes in root-mychorrizal fungal associations as a result of snow removal, although Cleavitt et al. (2008) did not find any evidence of reduced mychorrizal associations in the prior snow removal study. The observed reduction in N uptake by roots, particularly in the early growing season, overlapped temporally with elevated N-leaching losses, providing evidence that soil N losses due to soil freezing are driven by changes in vegetation.

Additional root responses to snow removal suggest that soil freezing may alter plant interactions not only with N, but with other important nutrients and water. Sugar maple fine roots subjected to snow removal exhibited reductions in concentrations of biogenic silica, an important nutrient for tissue support and protection against stressors (Maguire et al., 2017). Decreasing biogenic silica content likely reflects a reduction in root uptake of dissolved silica from soil water and could decrease the capacity of trees to search for and adsorb water and other nutrients in addition to N (Maguire et al., 2017). Continuous growing season measurements in 2010 and 2011 of sap flow, or upward water movement through tree boles, showed no response to soil freezing in sugar maple trees when averaged across the entire growing season. However, across the 2 years of measurements a seasonal treatment response emerged. Though not consistent across all measured trees, soil freezing tended to reduce sap flow in the early growing season and accelerate sap flow later in the growing season (Socci, 2012). It is possible that recovery of sap flow later in the growing season is driven by accelerated fine-root production in June and July (Tierney et al., 2001; Cleavitt et al., 2008), thought to be a compensatory response following significant root mortality after soil freezing. These results suggest that despite reduced root nutrient content and decreased nutrient uptake in spring, sugar maple trees may acclimate to frost-induced damage and recover some reduced function during the growing season.

Evidence indicates that the negative effects of soil freezing on root health and function have implications for aboveground plant processes at the HBEF.

Snow removal caused changes in growing season chemistry of sugar maple foliage, including decreased Ca^{2+} to aluminum (Al) ratios and elevated starch and total nonstructural carbohydrate concentrations (Comerford et al., 2013). Rather than a direct result of root damage, Comerford et al. (2013) hypothesized that increased foliar Al results from freeze-induced soil acidification and increased bioavailability of Al in soils. Subsequent increases in plant uptake of Al could be responsible for altering tree carbon relations, causing a buildup of starch in foliage and explaining reduced woody growth in terminal shoots (Comerford et al., 2013). Reinmann et al. (unpublished data) collected tree cores from experimental sugar maple trees in 2015 and documented significant and persistent declines in radial growth of sugar maple following five consecutive years of snow removal (2009–13) relative to reference trees. This reduced growth continued for the year after snow manipulation was completed (2014). Although the drivers of negative growth response to snow removal cannot be attributed directly to a specific mechanism, it is likely that a combination of factors resulting from snow removal and soil freezing, including root damage, reduced nutrient uptake, and changes in soil nutrient availability interact to reduce sugar maple growth.

Fauna

Aside from the direct effects on plant, microbial, and soil biogeochemistry, changes in snowpack depth and duration may influence higher order trophic interactions between and within species in significant ways (Penczykowski et al., 2017). Snow manipulation experiments at the HBEF have provided a lens through which we can examine how fauna, both small and large, respond to a reduced snowpack and soil freezing and further influence C and N cycling, as well as ecosystem structure. Soil fauna, including arthropods, thrive within the forest floor and play an important role in the decomposition of organic matter. Although there were no apparent changes in microbial activity (Groffman et al., 2010), rates of sugar maple litter decomposition were reduced with soil freezing in 2002–04, suggesting that unmeasured activity of soil fauna could be responsible for the observed delay in decomposition (Christenson et al., 2010). In the subsequent snow removal experiment, colder soil temperatures altered the community of soil arthropods relative to reference plots in 2009 and 2010 by reducing the abundance of several important taxa, including Araneae, Pseudoscorpionida, Hymenoptera, Collembola, adult Coleoptera, and larval Diptera, and increasing the abundance of Hemiptera (Templer et al., 2012). Changes in arthropod abundance led to a 30% decline in arthropod richness and 22% decline in

Simpson's index of diversity during the two subsequent growing seasons. Taken together, these results indicate that colder soils in winter in a changing climate could cause declines in arthropod abundance that may slow rates of organic matter decomposition and lead to shifts in arthropod community structure over time.

By changing the physical structure of the aboveground winter environment, snow removal can also influence overwinter browsing behavior of larger fauna. Large herbivores influence ecosystem processes through feedbacks to C and N cycling both directly, through consumption of plant tissue and deposition of fecal matter, and indirectly, through selective browsing of tree species with distinct biogeochemical roles (Sirotnak and Huntly, 2000; Bardgett and Wardle, 2003). To investigate how moose activity and soil freezing impact N dynamics and tree species response, Christenson et al. (2014) established 48 pairs of 2 × 2-m experimental plots at the HBEF containing at least three saplings of the same species (sugar maple, balsam fir, or *Viburnum*). Within each species, plots were assigned to a fully replicated design to experience all possible combinations of snow removal, mechanical clipping of saplings to simulate browsing, and addition of ^{15}N labeled moose feces. To evaluate the effect of snow removal on moose browsing behavior, researchers also established 12 paired 1 × 15-m transects and removed snow from one of each pair (Christenson et al., 2014). Browsing intensity of each of the three species of interest were monitored in the snow removal and reference transects throughout the winter of 2004/2005. They found that snow removal led to increased moose browsing on balsam fir relative to sugar maple or *Viburnum* when snow was removed, indicating that the increased accessibility to balsam fir saplings with reduced snowpack will cause increased overwinter herbivory damage to this species (Christenson et al., 2014). While applied soil freezing alone did not induce changes in soil pH, soil C and N, or potential net C and N mineralization or nitrification, the combined effects of moose fecal additional, simulated browsing, and soil freezing increased NO_3^- leaching in plots dominated by sugar maple and balsam fir (Christenson et al., 2014), highlighting the importance of plant species—specific function in biogeochemical responses to winter climate change.

In another snow removal experiment at the HBEF, researchers removed snow from five groups of buried pots planted with sugar and red maple saplings for varying lengths of time (2–10 weeks) in the winter of 2014, inducing variation in depth and duration of winter snowpack (Sanders-DeMott et al., 2018a). They found that snowpack reduction decreased rates of stem herbivory by small rodents in winter, suggesting that alleviation of aboveground stem damage in winters with reduced snowpack may offset the root damage incurred from soil freezing in winters with low snowpack. Reduced herbivory is also likely to have differential effects on different tree species, depending on how susceptible different species are to winter browsing. Together, these findings suggest that declines in snow depth can lead to a cascade of ecosystem responses across trophic levels that influence soil biogeochemistry and may cause shifts in plant community assemblages due to differential susceptibility to the combined stressors of winter climate change.

Natural climate gradient studies

While snow removal studies at the HBEF have provided valuable insight into the importance of winter climate on both overwinter and growing season processes, this class of experiment has implicit artifacts that limit our capacity to project how ecosystems will respond to the complex interactions among winter and growing season warming. First, snow removal may generate overly extreme reductions in soil temperature since winter air temperatures will rise concurrently with reductions in snowpack and thus modulate soil cooling (Henry, 2008). While exposed soils are indeed projected to become colder in winter, models project an increase in soil temperature variability and not necessarily deep, sustained soil freezing (Henry, 2008; Campbell et al., 2010). Additionally, though warming has been most pronounced in winter, growing season air temperatures have risen by approximately 1°C over the last 5 decades and climate models indicate another 0.6–4.9°C of warming by 2100 at the HBEF (Campbell et al., 2011; Pourmokhtarian et al., 2016). Therefore in addition to winter climate, warmer growing seasons, shifts in seasonal transitions, and altered precipitation patterns are likely to influence ecosystem responses to climate change. To develop a more complete understanding of how ecosystem processes respond to a warmer climate in a more naturally occurring annual cycle, researchers have exploited natural gradients of climate across an elevation range at the HBEF. Gradient studies provide insight into how ecosystem processes vary with climate by enabling researchers to observe a range of climate scenarios without introducing artificial treatments that manipulate only a small suite of variables in isolation and inherently lack the complexity of climate. The diverse landscape of the HBEF provides for examination of ecosystem processes across similar forest communities in variable climates which are within the range of projected changes over the next 50–100 years (Pourmokhtarian et al., 2016).

Description of climate gradients at Hubbard Brook

At the HBEF, two climate gradient studies have been conducted to explore how winter snow depth, soil freezing, and associated ecosystem processes vary with elevation, serving as proxies for climate. The first climate gradient study at the HBEF was established in 2002 and the design consisted of four 10 × 10-m plots, two at low-elevation south-facing sites at the HBEF valley bottom (380 and 480 m a.s.l.), and two high-elevation north-facing sites (755 and 790 m a.s.l.). These sites also served as reference plots for the snow removal experiment across an elevation gradient described above (Groffman et al., 2010). Although plots spanned a range of elevations and the maximum distance between plots was approximately 8 km, all were located in northern hardwood forest stands dominated by similar species, including sugar maple and yellow birch, with similar soil pH, organic layer depth, and soil C:N ratios (Groffman et al., 2009).

An additional gradient study with 20 independent plots was established in 2010 with 12 high-elevation north-facing plots and 8 low-elevation south-facing plots spanning an elevation gradient from 375 to 775 m a.s.l. (Durán et al., 2014). The range of air temperatures across the gradient was within the projected increase in temperature over the next century (Hayhoe et al., 2007). The gradient had relatively little variation in soils or vegetation and all plots were dominated by sugar maple.

In similar fashion to the snow removal experiments, each plot in both gradient experiments was measured for snow depth during the winter using either a Federal snow sampling tube or meter stick, as well as for frost depth with a methylene blue dye frost tube (Ricard et al., 1976). Plots were also equipped with soil temperature and moisture sensors. In these studies, snowpack accumulated naturally in all plots without any experimental manipulation. Variation across plots was due only to the naturally occurring climate gradient and its influence on temperature, snow depth, and frost depth.

Results

The elevation gradients at the HBEF provided significant variation in air temperature and snow depth. Snowpack at low-elevation sites developed later, and to shallower depths than at high-elevation sites, facilitating the development and maintenance of soil frost at low elevations (Groffman et al., 2009; Durán et al., 2014). Low-elevation plots experienced 1.5–2.5°C warmer air temperatures, within the 2.1–5.3°C range of warming projected for the northeast United States over the next century (Hayhoe et al., 2007; Groffman et al., 2009; Durán et al., 2014). The effect of elevation on soil frost was also significant, although less consistent across studies due to the influence of snowfall timing and the severity of winter (Groffman et al., 2009; Durán et al., 2014). In 2003, frost depth was significantly deeper at low-elevation plots than high-elevation plots when there was an early onset of snowpack. In fact, there was almost no soil frost (<4 cm) recorded at upper elevation plots in that year. However, in 2004 snowpack did not set in until later in December when soils across elevations had already become much colder than the prior year. Frost penetrated much deeper across all plots in the gradient with the later onset of snowpack in 2004, although lower elevation sites experienced significantly deeper frost (Groffman et al., 2009).

Durán et al. (2014) found that in the winters of 2011–12 decreasing elevation was significantly related to the integrated metrics of reduced snow depth and snow water equivalent, as well as increased winter soil temperature variability across all plots, although elevation was not significantly related to integrated soil frost depth. In addition to temperature effects, Groffman et al. (2009) found that lower elevation plots tended to have drier soils, although this relationship was not significant in the 2010–12 gradient study (Durán et al. 2014). The results across both gradient studies generally support the hypothesis that a climate change that causes reduced snowfall will lead to reduced insulation of soil, decreased and more variable winter soil temperatures, and increased soil freezing, even with concurrent warming of winter air.

Soil biogeochemistry

Unlike the results of snow removal experiments, increasing soil frost depth across the elevation gradient did not affect rates of measured NO_3^- leaching at the HBEF (Fuss et al., 2016). However, increased soil frost at low-elevation plots was significantly related to an increase in DOC leaching from organic soils (Fuss et al., 2016). These findings build upon those of Groffman et al. (2010) who suggested that coupling of C and N biogeochemistry may be responsible for the inconsistent response of N losses to soil freezing, as mobilization of labile C may suppress NO_3^- losses through microbial immobilization of N. There were also no observed differences in soil CO_2 or N_2O losses with soil-freezing variation across the elevation gradient, in contrast to findings from snow removal manipulations (Morse et al., 2015).

Microbes

Lower elevation plots at the HBEF that generally experienced less snow, deeper soil frost, and reduced soil moisture had lower rates of potential net N mineralization and nitrification, pools of soil NO_3^-, and microbial biomass N compared with high-elevation plots (Groffman et al., 2009; Durán et al., 2014, 2016) and reduced in situ rates of N mineralization and nitrification in both winter and the growing season (Groffman et al., 2009; Durán et al., 2016). Differences in N pools and fluxes were consistent for all soil horizons, but sensitivity to climate variation increased with soil depth, highlighting the need to assess soil response to climate change throughout the soil profile (Duran et al., 2017). However, microbial exoenzyme activity was only weakly related to elevation, snow, or soil frost, but showed a stronger, positive correlation with soil moisture (Sorensen et al., 2016b). Patterns of N cycling throughout the year across the gradient suggest that the response of in situ N cycling in winter is more sensitive to soil temperature, while rates in summer are more strongly controlled by soil moisture (Groffman et al., 2009). Thus the combination of both warmer, drier soils in the growing season with reduced snowpack and colder soils with increased temperature variability in the winter may lead to slower N cycling and reduced soil N availability with climate change. In support of findings from the gradient studies, Durán et al. (2016) found that patterns of reduced N cycling rates and N availability have been observed over time with recent climate change (since 1973) at the HBEF.

Vegetation

Root response to variation in climate across the elevation gradient was assessed using root exclusion cores buried for up to 29 months across the range of plots. Sorensen et al. (2016b) found that root ingrowth was positively related to integrated measures of soil frost across the gradient and low-elevation sites that experienced more frost had 40% more root ingrowth than high-elevation sites. These results are consistent with field experiments showing stimulated root production following snow removal and soil freezing (Tierney et al., 2001; Cleavitt et al., 2008), indicating that trees may respond to frost-induced damage and mortality with compensatory root growth in the following growing season. Increased root production in lower elevation sites was correlated with a 30% reduction in nitrification rates (Sorensen et al., 2016b). This coupling of plant and microbial dynamics indicates a potential negative feedback of increased soil freezing on mineral N production as greater compensatory root growth may reduce nitrification rates via plant-microbe N competition, resulting in lower N availability to trees in northern hardwood forests.

Soil warming and freeze-thaw cycles: Climate change across seasons experiment

Although gradient studies provide valuable insight into how ecosystem processes vary with climate, they are constrained by the range in climate that can occur across an elevation gradient while maintaining similar site characteristics (e.g., soils and vegetation). Controlled experiments allow for greater control over climatic treatments and provide an opportunity to identify mechanistic relationships by manipulating specific environmental drivers. Although the projected reduction of snow cover and associated soil freezing is an important driver of ecosystem response to climate change at the HBEF, soil warming during the snow-free season will also likely play an important role in ecosystem processes in the future. Soil-warming studies conducted in other temperate forest ecosystems in the northeast region (McHale et al., 1998; Rustad and Fernandez, 1998; Melillo et al., 2011) and around the globe have typically applied soil-warming treatments either in the growing season only or consistently throughout the year, including the winter (Sanders-DeMott and Templer, 2017). These studies suggest that warming soils causes the acceleration of N and C cycles (Rustad et al., 2001; Lu et al., 2013b) and can lead to overall increases in uptake and retention of N by forest trees (Melillo et al., 2011). Results of warming studies are in direct contrast to findings from winter climate manipulation and gradient studies at the HBEF, indicating reduced nutrient uptake by damaged tree roots (Campbell et al., 2014) and slower C and N cycling rates with colder winter soils (Groffman et al., 2010; Durán et al., 2016). The interaction of reduced snowpack and colder soils in winter with warmer soil in the growing season is likely to cause ecosystem responses that could be antagonistic or synergistic, which would not be apparent from examining one season alone. The Climate Change Across Seasons Experiment (CCASE; Templer et al. 2017) was initiated in 2012 to determine whether the interacting effects of colder soils with increased temperature variability in winter and warmer soils in the growing season on nutrient cycling are distinct from either of these changes in isolation.

Experimental treatment

The CCASE experiment was established at approximately 250 m a.s.l. in an *Acer rubrum* (red maple) stand at the HBEF (Templer et al., 2017). The experiment consists of six plots: two manipulations and a reference. Two plots experience a soil warming of +5°C above ambient soil temperatures during the snow-free season (typically late April to late November), two experience a soil warming of +5°C during the snow-free season coupled with soil freeze-thaw cycles in winter, and the two reference plots experience ambient soil temperatures year-round. Temperature treatments began in the winter of 2013/2014 and are ongoing. The four plots that experience warming were each equipped with heating cables, which were installed by cutting the soil with a flat shovel to a depth of 10 cm and burying cable into the cut. Reference plots were similarly cut to mimic the cable installation disturbance, but no cable was installed. Winter soil freeze-thaw cycles at CCASE are achieved by manually removing snow to expose the soils to below-freezing air temperatures and induce soil freezing. After soils have been frozen for 3 days, the heating cables are turned on to thaw soils to 1°C for an additional 3 days, comprising 1 freeze-thaw cycle. At the onset of the snow-free season—operationally defined as the time at which all snow and soil frost has melted and daily soil temperatures begin a natural ramping up, tracking air temperatures (Groffman et al., 2012; Contosta et al., 2016)—soil warming begins in both the warmed and warmed plus freeze-thaw treatment plots. Once triggered, the heating cables are used to maintain soil temperatures at +5°C above ambient soil temperatures throughout the snow-free season (Fig. 5).

Results

By combining snow removal manipulation with soil heating cables, researchers successfully created freeze-thaw cycles in winter and elevated

Fig. 5 Infrared image of soil heating cables warming the forest floor at CCASE. *(Photograph by Jon Chapell, Science Metrics LLC, 2015.)*

snow-free season soil temperatures by 5°C (Fig. 6) for four consecutive years (2014–17) with treatments ongoing. There were no effects of warming or snow removal on soil moisture integrated across the top 30 cm of soil (Templer et al., 2017), but organic layer soil moisture was reduced in the early growing season for both warmed and warmed plus freeze-thaw cycle treatments (Sorensen et al., 2018). Although most previous studies that have examined forest responses to warming have focused on warming in the growing season only or on consistent warming throughout the year (Sanders-DeMott and Templer, 2017), by including the projected changes in winter climate that are distinct from mean annual warming in the snow-free season, ecosystem responses that are not captured by warming alone have been observed.

Microbes

Soil freeze-thaw cycles caused an approximate twofold increase in both soil and ion-exchange resin extractable inorganic N in the organic soil during the period following snowmelt through commencement of leaf-out (Sorensen et al., 2018, Sanders-DeMott et al., 2018b). During the same period, microbial biomass N declined by 85% and there were significant declines in exoenzyme activity and microbial respiration in plots that had experienced overwinter soil freeze-thaw cycles combined with warming (Sorensen et al., 2018). In contrast, there were no treatment effects on

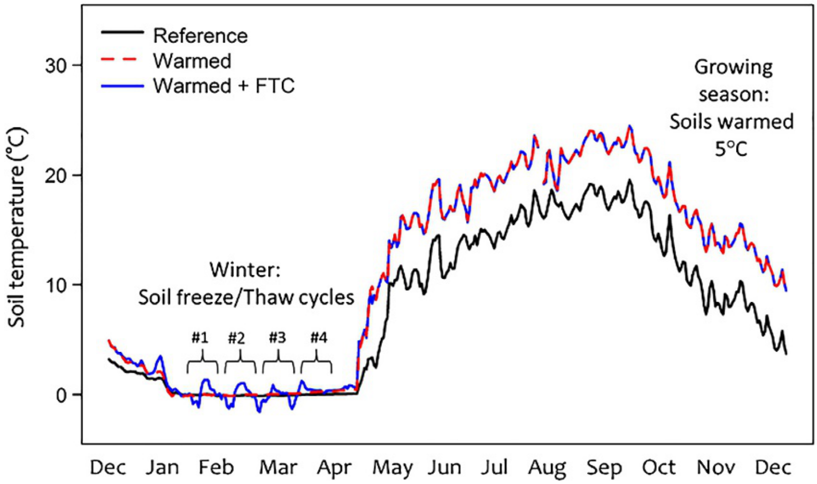

Fig. 6 Soil temperatures at a depth of 10 cm at the Climate Change Across Seasons Experiment (CCASE) from December 2013 to December 2014.

potential N mineralization throughout the growing season and snow-free soil warming alone had no influence on exoenzyme activity. Rates of microbial respiration in both treatments that experienced warming (regardless of whether freeze-thaw treatment in winter was applied) were reduced in the later growing season, perhaps due to reduced soil moisture (Sorensen et al., 2018). These results suggest that positive feedbacks between warming and rates of soil C and N cycling that have been observed in previous soil-warming studies may be partially mitigated by an increased frequency of winter soil freeze-thaw cycles, which decrease microbial biomass and activity.

Vegetation

Similar to findings from snow removal experiments that created persistent soil freezing during winter (Tierney et al., 2001; Cleavitt et al., 2008; Comerford et al., 2013), the applied soil freeze-thaw cycles caused overwinter damage to tree roots as measured by relative electrolyte leakage (Sanders-DeMott et al., 2018b). Freeze-thaw cycle damage also resulted in changes to root function, with a 42% decline in potential N uptake capacity by damaged roots in the early growing season. To better determine the mechanisms of root damage, Sanders-DeMott et al. (2018a) established a parallel study with sugar maple and red maple saplings planted in buried pots at the HBEF to test the effect of freeze-thaw frequency on root health. From 2013 to 2015, variation in soil freezing (persistent freezing or either two, four, six, or eight freeze-thaw cycles) was applied to saplings using snow removal and buried heating cables. Persistent soil freezing caused significant damage to both sugar and red maple roots, while only sugar maple roots were increasingly damaged by successive freeze-thaw cycles. This provides more evidence that sugar maple is particularly susceptible to damage from soil freezing (Tierney et al., 2001; Cleavitt et al., 2008; Comerford et al., 2013), although other tree species are certainly impacted by cold winter soils (Tierney et al., 2001; Cleavitt et al., 2008).

Although previous studies on elevated soil temperatures have found evidence of increased plant uptake of N (Gessler et al., 2004; Melillo et al., 2011), at the HBEF warmer soils both with and without freeze-thaw cycles in winter had significant declines in potential root N uptake during the peak growing season (Sanders-DeMott et al., 2018b). The mechanism driving this shift in N uptake is unclear but suggests that growing season warming will lead to changes in root function that interact with winter climate change. Combined with evidence that climate change will lead to slower cycling of N and reduced availability of soil nutrients to plants in the growing season (Durán et al., 2016), this suggests that changes in root function with warming could exacerbate the increased stress of plant N demand with changing climate.

Summary of findings

Three decades of research at the HBEF indicate that warming winters with less snowpack will have profound influences on the cycling of nutrients among soils, microbes, vegetation, and fauna. Reduced snow and increased soil freezing cause damage to plant roots, altering root function by reducing the uptake of nutrients and enhancing root production in the following growing season. Although the effects of soil freezing on enhancing N losses through leaching varied among and within differing research approaches (e.g., snow removal and elevation gradients), there is evidence to suggest that a complex interplay between mobilization of labile soil C and ecosystem losses of N, due to declines in plant uptake and/or decomposition of dead roots, exerts an influence over soil N losses following soil-freezing events. Despite limited responses of microbial biomass and activity to snow removal, elevation gradient studies and long-term trends indicate that warmer annual temperature cycles, including but not limited to reduced snowpack in winter, are associated with slower rates of N cycling throughout the year, potentially a result of the combination of winter freezing and summer warming and drying of soils. These studies also point to the considerable role of plant species in modulating ecosystem response to climate change over time considering differential sensitivities to freezing damage, susceptibility to herbivory, and competition with microbes for available nutrients in the soil. Taken together, these results indicate that shifts in forest ecosystem function due to climate change are mediated through a combination of winter and growing season dynamics that lead to a suite of effects governed by a complicated interplay among soil biogeochemistry, microbes, vegetation, and fauna.

Implications and future directions

Climate change poses a significant threat to the current strength of C and N sinks in terrestrial ecosystems. The body of work from the HBEF demonstrates that understanding winter ecosystem function in seasonally snow-covered ecosystems is critical to projecting how climate change across seasons will influence forests. By leveraging long-term records of climate and biogeochemistry, natural variation in landscape and species composition, and the infrastructure to conduct and maintain large-scale and long-term experiments, researchers at the HBEF have identified important controls that warming temperatures have on ecosystem processes that shed light on how climate change will affect future northern forest ecosystems. As climate at the HBEF continues to change, long-term data on climate and biogeochemistry will continue to reveal information that enhances our understanding of ecosystem function.

Research to date on climate change at the HBEF has raised many important questions about fundamental ecosystem relationships among the environment and biogeochemical cycling. Applying results of winter climate change studies to process-based ecosystem models will further test our understanding of the differing sensitivities of interacting ecosystem processes under future scenarios, and likely generate additional questions about drivers of long-term ecosystem change. Future directions of research at the HBEF involve developing a deeper understanding of the mechanisms driving long-term trends in watershed-scale nutrient and water fluxes through new and continued measurements, exploring how seasonal transitions are changing to influence timing of phenological events and nutrient transformations, and examining the responses of ecosystem processes and ecosystem resilience to increasing frequency of extreme events, such as ice storms and droughts, through manipulative experiments, observation, and modeling. By continuing to build on the decades of foundational research at the HBEF utilizing multiple approaches to examine the many distinct, yet synergistic, manifestations of climate change in northern forest ecosystems, we will improve our understanding of the integrated responses of ecosystems to future climate change.

References

Aanderud, Z.T., Jones, S.E., Schoolmaster, D.R., Fierer, N., Lennon, J.T., 2013. Sensitivity of soil respiration and microbial communities to altered snowfall. Soil Biol. Biochem. 57, 217–227.

Bailey, A.S., Hornbeck, J.W., Campbell, J.L., Eagar, C., 2003. Hydrometeorological Database for Hubbard Brook Experimental Forest: 1955–2000. Gen. Tech. Rep. NE-305. U. S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA 36 pp.

Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84, 2258–2268.

BassiriRad, H., Prior, S., Norby, R., Rogers, H., 1999. A field method of determining NH_4^+ and NO_3^- uptake kinetics in intact roots: effects of CO_2 enrichment on trees and crop species. Plant Soil 217, 195–204.

Blankinship, J.C., Hart, S.C., 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere 3, 1.

Bokhorst, S., Bjerke, J.W., Tømmervik, H., Preece, C., Phoenix, G.K., 2012. Ecosystem response to climatic change: the importance of the cold season. Ambio 41, 246–255.

Boutin, R., Robitaille, G., 1995. Increased soil nitrate losses under mature sugar maple trees affected by experimentally induced deep frost. Can. J. For. Res. 25, 588–602.

Brown, P.J., DeGaetano, A.T., 2011. A paradox of cooling winter soil surface temperatures in a warming northeastern United States. Agric. For. Meteorol. 151, 947–956.

Brown, R.D., Mote, P.W., 2009. The response of Northern Hemisphere snow cover to a changing climate. J. Clim. 22, 2124–2145.

Burakowski, E.A., Wake, C.P., Braswell, B., Brown, D.P., 2008. Trends in wintertime climate in the northeastern United States: 1965–2005. J. Geophys. Res. Atmos. 113, 1–12.

Campbell, J., Mitchell, M., Groffman, P.M., Christenson, M., Hardy, J.P., 2005. Winter in northeastern North America: a critical period for ecological processes. Front. Ecol. Environ. 3, 314–322.

Campbell, J.L., Driscoll, C.T., Eagar, C., et al., 2007. Long-Term Trends From Ecosystem Research at the Hubbard Brook Experimental Forest. Gen. Tech. Rep. NRS-17. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA 41 pp.

Campbell, J.L., Ollinger, S.V., Flerchinger, G.N., Wicklein, H., Hayhoe, K., Bailey, A.S., 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. Hydrol. Process. 24, 2465–2480.

Campbell, J.L., Driscoll, C.T., Pourmokhtarian, A., Hayhoe, K., 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, United States. Water Resour. Res. 47, 1–15.

Campbell, J.L., Socci, A.M., Templer, P.H., 2014. Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. Glob. Chang. Biol. 20, 2663–2673.

Christenson, L.M., Mitchell, M.J., Groffman, P.M., Lovett, G.M., 2010. Winter climate change implications for decomposition in northeastern forests: comparisons of sugar maple litter with herbivore fecal inputs. Glob. Chang. Biol. 16, 2589–2601.

Christenson, L.M., Mitchell, M.J., Groffman, P.M., Lovett, G.M., 2014. Cascading effects of climate change on forest ecosystems: biogeochemical links between trees and moose in the Northeast USA. Ecosystems 17, 442–457.

Cleavitt, N.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Henry, K.S., Driscoll, C., 2008. Effects of soil freezing on fine roots in a northern hardwood forest. Can. J. For. Res. 38, 82–91.

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., Wallin, K.F., 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia 171, 261–269.

Contosta, A.R., Adolph, A., Burchsted, D., et al., 2016. A longer vernal window: the role of winter coldness and snowpack in driving spring transitions and lags. Glob. Chang. Biol. 1–16.

Cornelissen, J.H.C., Makoto, K., 2014. Winter climate change, plant traits and nutrient and carbon cycling in cold biomes. Ecol. Res. 29, 517–527.

Decker, K.L.M., Wang, D., Waite, C., Scherbatskoy, T., 2003. Snow removal and ambient air temperature effects on forest soil temperatures in Northern Vermont. Soil Sci. Soc. Am. J. 67, 1234–1242.

Dietzel, R., Wolfe, D., Thies, J.E., 2011. The influence of winter soil cover on spring nitrous oxide emissions from an agricultural soil. Soil Biol. Biochem. 43, 1989–1991.

Duran, J., Morse, J.L., Rodríguez, A., et al., 2017. Differential sensitivity to climate change of C and N cycling processes across soil horizons in a northern hardwood forest. Soil Biol. Biochem. 107, 77–84.

Durán, J., Morse, J.L., Groffman, P.M., et al., 2014. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Glob. Chang. Biol. 20, 3568–3577.

Durán, J., Morse, J.L., Groffman, P.M., et al., 2016. Climate change decreases nitrogen pools and mineralization rates in northern hardwood forests (Ed. Peters DPC). Ecosphere 7, e01251.

Fitzhugh, R., Driscoll, C., Groffman, P.M., Tierney, G.L., 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. Biogeochemistry 56, 215–238.

Fitzhugh, R.D., Likens, G.E., Driscoll, C., Mitchell, M.J., Groffman, P.M., Fahey, T.J., Hardy, J.P., 2003a. Role of soil freezing events in interannual patterns of stream chemistry at the Hubbard Brook Experimental Forest, New Hampshire. Environ. Sci. Technol. 37, 1575–1580.

Fitzhugh, R.D., Driscoll, C., Groffman, P.M., Tierney, G.L., Fahey, T.J., Hardy, J.P., 2003b. Soil freezing and the acid-base chemistry of soil solutions in a Northern Hardwood Forest. Soil Sci. Soc. Am. J. 1897–1908.

Freppaz, M., Celi, L., Marchelli, M., Zanini, E., 2008. Snow r emoval and its influence on temperature and N dynamics in alpine soils (Vallée d'Aoste, northwest Italy). J. Plant Nutr. Soil Sci. 171, 672–680.

Fuss, C.B., Driscoll, C.T., Groffman, P.M., et al., 2016. Nitrate and dissolved organic carbon mobilization in response to soil freezing variability. Biogeochemistry 131, 35–47.

Gavazov, K., Ingrisch, J., Hasibeder, R., et al., 2017. Winter ecology of a subalpine grassland: effects of snow removal on soil respiration, microbial structure and function. Sci. Total Environ. 590–591, 316–324.

Gessler, A., Kopriva, S., Rennenberg, H., 2004. Regulation of nitrate uptake at the whole-tree level: interaction between nitrogen compounds, cytokinins and carbon metabolism. Tree Physiol. 24, 1313–1321.

Groffman, P.M., Driscoll, C., Fahey, T.J., Hardy, J.P., Ross, D., Tierney, G.L., Filtzhugh, R.D., 2001a. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56, 135–150.

Groffman, P.M., Driscoll, C., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., Tierney, G.L., 2001b. Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. Biogeochemistry 56, 191–213.

Groffman, P.M., Hardy, J.P., Discoll, C.T., Fahey, T.J., 2006. Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. Glob. Chang. Biol. 12, 1748–1760.

Groffman, P.M., Hardy, J.P., Fisk, M.C., Fahey, T.J., Driscoll, C.T., 2009. Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. Ecosystems 12, 927–943.

Groffman, P.M., Hardy, J.P., Fashu-Kanu, S., Driscoll, C., Cleavitt, N.L., Fahey, T.J., Fisk, M.C., 2010. Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape. Biogeochemistry 102, 223–238.

Groffman, P.M., Rustad, L.E., Templer, P.H., et al., 2012. Long-term integrated studies show complex and surprising effects of climate change in the Northern Hardwood Forest. Bioscience 62, 1056–1066.

Hamburg, S.P., Vadeboncoeur, M.A., Richardson, A.D., Bailey, A.S., 2013. Climate change at the ecosystem scale: a 50-year record in New Hampshire. Clim. Chang. 116, 457–477.

Hansen, J., Ruedy, R., Sato, M., Lo, K., 2010. Global surface temperature change. Rev. Geophys. 48, RG4004.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., et al., 2001. Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry 56, 151–174.

Hartmann, D., Klein Tank, A., Rusticucci, M., et al., 2013. Chapter 2: Observations: atmosphere and surface. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hayhoe, K., Wake, C.P., Huntington, T.G., et al., 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Clim. Dyn. 28, 381–407.

Henry, H.A.L., 2008. Climate change and soil freezing dynamics: historical trends and projected changes. Clim. Change 87, 421–434.

Huntington, T.G., Richardson, A.D., Mcguire, K.J., Hayhoe, K., 2009. Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystems. Can. J. For. Res. 39, 199–212.

Jones, P.D., Lister, D.H., Osborn, T.J., Harpham, C., Salmon, M., Morice, C.P., 2012. Hemispheric and large-scale land-surface air temperature variations: an extensive revision and an update to 2010. J. Geophys. Res. Atmos. 117.

Judd, K.E., Likens, G.E., Buso, D.C., Bailey, A.S., 2011. Minimal response in watershed nitrate export to severe soil frost raises questions about nutrient dynamics in the Hubbard Brook experimental forest. Biogeochemistry 106, 443–459.

Kreyling, J., 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 91, 1939–1948.

Kreyling, J., Haei, M., Laudon, H., 2012. Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. Oecologia 168, 577–587.

Kreyling, J., Haei, M., Laudon, H., 2013. Snow removal reduces annual cellulose decomposition in a riparian boreal forest. Can. J. Soil Sci. 93, 427–433.

Lawrence, D.M., Slater, A.G., 2010. The contribution of snow condition trends to future ground climate. Clim. Dyn. 34, 969–981.

Lawrimore, J.H., Menne, M.J., Gleason, B.E., Williams, C.N., Wuertz, D.B., Vose, R.S., Rennie, J., 2011. An overview of the Global Historical Climatology Network monthly mean temperature data set, version 3. J. Geophys. Res. Atmos. 116D19121.

Li, W., Wu, J., Bai, E., et al., 2016. Response of terrestrial nitrogen dynamics to snow cover change: a meta-analysis of experimental manipulation. Soil Biol. Biochem. 100, 51–58.

Likens, G.E., 2013. Biogeochemistry of a Forested Ecosystem. Springer New York, New York, NY.

Lu, X., Melillo, J.M., Kicklighter, D., et al., 2013a. A contemporary carbon balance for the northeast region of the United States. Environ. Sci. Technol. 47, 13230–13238.

Lu, M., Zhou, X., Yang, Q., et al., 2013b. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. Ecology 94, 726–738.

Lucash, M.S., Joslin, J.D., Yanai, R., 2005. Temporal variation in nutrient uptake capacity by intact roots of mature loblolly pine. Plant Soil 272, 253–262.

Maguire, T.J., Templer, P.H., Battles, J.J., Fulweiler, R.W., 2017. Winter climate change and fine root biogenic silica in sugar maple trees (*Acer saccharum*): implications for silica in the Anthropocene. J. Geophys. Res. Biogeosci. 122, 708–715.

Makoto, K., Kajimoto, T., Koyama, L., Kudo, G., Shibata, H., Yanai, Y., Cornelissen, J.H.C., 2014. Winter climate change in plant-soil systems: summary of recent findings and future perspectives. Ecol. Res. 29, 593–606.

Matzner, E., Borken, W., 2008. Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. Eur. J. Soil Sci. 59, 274–284.

McHale, P.J., Mitchell, M.J., Bowles, F.P., 1998. Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition. Can. J. For. Res. 28, 1365–1372.

Melillo, J.M., Butler, S., Johnson, J., et al., 2011. Soil warming, carbon-nitrogen interactions, and forest carbon budgets. Proc. Natl. Acad. Sci. 108, 9508–9512.

Mitchell, M.J., Driscoll, C.T., Kahl, J.S., Likens, G.E., Murdoch, P.S., Pardo, L.H., 1996. Climatic control of nitrate loss from forested watersheds in the Northeast United States. Environ. Sci. Technol. 30, 2609–2612.

Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A., Delany, A.C., Williams, M.W., Schmidt, S.K., 2006. Winter forest soil respiration controlled by climate and microbial community composition. Nature 439, 711–714.

Morse, J.L., Duran, J., Groffman, P.M., 2015. Soil denitrification fluxes in a Northern Hardwood Forest: the importance of snowmelt and implications for ecosystem N budgets. Ecosystems 18, 520–532.

Notaro, M., Lorenz, D., Hoving, C., Schummer, M., 2014. Twenty-first-century projections of snowfall and winter severity across central-eastern North America. J. Clim. 27, 6526–6550.

Penczykowski, R.M., Connolly, B.M., Barton, B.T., 2017. Winter is Changing: Trophic Interactions Under Altered Snow Regimes. Food Webs.

Pilon, C.E., Cote, B., Fyles, J.W., 1994. Effect of snow removal on leaf water potential, soil moisture, leaf and soil nutrient status and leaf peroxidase activity of sugar maple. Plant Soil 162, 81–88.

Pithan, F., Mauritsen, T., 2014. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nat. Geosci. 7, 181–184.

Pourmokhtarian, A., Driscoll, C.T., Campbell, J.L., Hayhoe, K., 2012. Modeling potential hydrochemical responses to climate change and increasing CO_2 at the Hubbard Brook Experimental Forest using a dynamic biogeochemical model (PnET-BGC). Water Resour. Res. 48.

Pourmokhtarian, A., Driscoll, C.T., Campbell, J.L., Hayhoe, K., Stoner, A.M.K., 2016. The effects of climate downscaling technique and observational data set on modeled ecological responses. Ecol. Appl. 26, 1321–1337.

Pourmokhtarian, A., Driscoll, C.T., Campbell, J.L., et al., 2017. Modeled ecohydrological responses to climate change at seven small watersheds in the northeastern United States. Glob. Chang. Biol. 23, 840–856.

Repo, T., Roitto, M., Sutinen, S., 2011. Does the removal of snowpack and the consequent changes in soil frost affect the physiology of Norway spruce needles? Environ. Exp. Bot. 72, 387–396.

Ricard, J., Tobiasson, W., Greatorex, A., 1976. The Field Assembled Frost Gage. Technical Note. Cold Regions Research and Engineering Laboratory.

Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W., O'Keefe, J., 2006. Phenology of a northern hardwood forest canopy. Glob. Chang. Biol. 12, 1174–1188.

Rohde, R., Muller, R.A., Jacobsen, R., et al., 2013. A new estimate of the average Earth surface land temperature spanning 1753 to 2011. Geoinform. Geostat. 1, 2.

Rustad, L.E., Fernandez, I.J., 1998. Soil warming: consequences for foliar litter decay in a spruce-fir forest in Maine, USA. Soil Sci. Soc. Am. J. 62, 1072–1080.

Rustad, L.E., Campbell, J.L., Marion, G.M., et al., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Rustad, L., Campbell, J., Dukes, J.S., Huntington, T., Lambert, K.F., Mohan, J., Rodenhouse, N., 2012. Changing Climate, Changing Forests: The Impacts of Climate Change on Forests of the Northeastern United States and Eastern Canada. Gen. Tech. Rep. NRS-99. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA 48 pp.

Sanders-DeMott, R., Templer, P.H., 2017. What about winter? Integrating the missing season into climate change experiments in seasonally snow covered ecosystems. Methods Ecol. Evol. 8, 1183–1191.

Sanders-DeMott, R., McNellis, R., Jabouri, M., Templer, P.H., 2018a. Snow depth, soil temperature, and plant-herbivore interactions mediate plant response to climate change. J. Ecol. 106, 1508–1519.

Sanders-DeMott, R., Sorensen, P.O., Reinmann, A.B., Templer, P.H., 2018b. Growing season warming and winter freeze-thaw cycles reduce root nitrogen uptake capacity and increase soil solution nitrogen in a northern forest ecosystem. Biogeochemistry 137, 337–349.

Sirotnak, J.M., Huntly, N.J., 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. Ecology 81, 78–87.

Smith, T.M., Arkin, P.A., Ren, L., Shen, S.S.P., 2012. Improved reconstruction of global precipitation since 1900. J. Atmos. Ocean. Technol. 29, 1505–1517.

Socci, A.M., 2012. Impact of winter climate change on nutrient and water uptake in a northern forest ecosystem. PhD Thesis. Boston University, ProQuest Dissertations and Theses Database. UMI No. 3500678.

Socci, A.M., Templer, P.H., 2011. Temporal patterns of inorganic nitrogen uptake by mature sugar maple (*Acer saccharum Marsh*.) and red spruce (*Picea rubens Sarg*.) trees using two common approaches. Plant Soil 4, 141–152.

Song, Y., Zou, Y., Wang, G., Yu, X., 2017. Altered soil carbon and nitrogen cycles due to the freeze-thaw effect: a meta-analysis. Soil Biol. Biochem. 109, 35–49.

Sorensen, P.O., Templer, P.H., Finzi, A.C., 2016a. Contrasting effects of winter snowpack and soil frost on growing season microbial biomass and enzyme activity in two mixed-hardwood forests. Biogeochemistry 128, 141–154.

Sorensen, P.O., Templer, P.H., Christenson, L.M., et al., 2016b. Reduced snow cover alters root-microbe interactions and decreases nitrification rates in a Northern Hardwood Forest. Ecology 97, 3359–3368.

Sorensen, P.O., Finzi, A.C., Giasson, M.-A., Reinmann, A.B., Sanders-DeMott, R., Templer, P.H., 2018. Winter soil freeze-thaw cycles lead to reductions in soil microbial biomass and activity not compensated for by soil warming. Soil Biol. Biochem. 116, 39–47.

Sturm, M., Schimel, J.P., Michaelson, G., et al., 2005. Winter biological processes could help convert arctic Tundra to Shrubland. Bioscience 55, 17.

Templer, P.H., Dawson, T.E., 2004. Nitrogen uptake by four tree species of the Catskill Mountains, New York: implications for forest N dynamics. Plant Soil 262, 251–261.

Templer, P.H., Schiller, A.F., Fuller, N.W., Socci, A.M., Campbell, J.L., Drake, J.E., Kunz, T.H., 2012. Impact of a reduced winter snowpack on litter arthropod abundance and diversity in a Northern Hardwood Forest Ecosystem. Biol. Fertil. Soils 413–424.

Templer, P.H., Reinmann, A.B., Sanders-DeMott, R., et al., 2017. Climate Change Across Seasons Experiment (CCASE): a new method for simulating future climate in seasonally snow-covered ecosystems. PLoS One 12e0171928.

Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., Driscoll, C.T., 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry 56, 175–190.

Vankoughnett, M.R., Henry, H.A.L., 2014. Soil freezing and N deposition: transient vs multi-year effects on plant productivity and relative species abundance. New Phytol. 202, 1277–1285.

Williams, C.M., HAL, H., Sinclair, B.J., 2014. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol. Rev. 90, 214–235.

Wipf, S., Rixen, C., 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Res. 29, 95–109.

Woodbury, P.B., Smith, J.E., Heath, L.S., 2007. Carbon sequestration in the U.S. Forest Sector from 1990 to 2010. For. Ecol. Manag. 241, 14–27.

Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., Wan, S., 2014. Terrestrial carbon cycle affected by non-uniform climate warming. Nat. Geosci. 7, 173–180.

Yanai, R.D., Vadeboncoeur, M.A., Hamburg, S.P., et al., 2013. From missing source to missing sink: long-term changes in the nitrogen budget of a Northern Hardwood Forest. Environ. Sci. Technol. 47, 11440–11448.

Zhang, T., 2005. Influence of the seasonal snow cover on the ground thermal regime: an overview. Rev. Geophys. 43, RG4002.

ECOSYSTEM CONSEQUENCES OF SOIL WARMING

Microbes, vegetation, fauna, and soil biogeochemistry

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