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Growing season soil warming may counteract trend of nitrogen oligotrophication in a northern hardwood forest

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Abstract Over the next century, many mid and high latitude temperate ecosystems are projected to experience rising growing season temperatures and increased frequency of soil freeze/thaw cycles (FTCs) due to a reduction in the depth and duration of the winter snowpack. We conducted a manipulative field experiment in a northern hardwood forest at the Hubbard Brook Experimental Forest in New Hampshire to determine the interactive effects of climate change across seasons on rates of net N mineralization, foliar N, and natural abundance foliar ^{15}N ($\delta^{15}N$) in red maple (*Acer rubrum*) trees. We warmed soils 5 °C above ambient temperatures and induced winter FTCs to simulate projected changes over the next century. Net N mineralization was dominated by ammonification and increased with warmer soil temperatures, but was not affected by soil FTCs in the previous winter. Similarly, warming led to increased foliar N concentrations and $\delta^{15}N$, with no effect of soil FTCs. Together, our results show that growing season soil warming increases soil N availability and N uptake by trees, which may offset the previously observed negative effects of a smaller snowpack and more frequent soil freezing on N cycling. We conclude that soil warming in the growing season may counteract the trend of reduced soil N availability relative to plant N demand (i.e. N oligotrophication) observed in northern hardwood forests. This research demonstrates that climate change across seasons affects N cycling in northern hardwood forests in ways that would have not been apparent from examining one season alone.

Keywords Nitrogen · Net N mineralization · Oligotrophication · Natural abundance foliar N isotopes · Northern hardwood forest

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Introduction

Similar to many other mid and high latitude temperate ecosystems, climate models project that mean annual air temperatures will rise 2.9–5.3 °C by the year 2100 relative to the 1970–1999 mean in the northeastern U.S. (Hayhoe et al. 2007). Air and soil temperatures are tightly coupled in the snow-free season (hereafter referred to as “growing season”; Smerdon et al. 2004) and as air temperatures rise, soil temperatures in the growing season will likely get warmer as well. In contrast, reductions in winter snowpack depth and duration over the next century (Reinmann et al. 2019) are projected to lower soil temperatures and increase soil freezing frequency in winter in this region (Campbell et al. 2010).

Shifts in climatic conditions can have important implications for nutrient cycling in forest ecosystems. Nitrogen (N) is an essential, but often limiting element for net primary production in temperate ecosystems (LeBauer and Treseder 2008), including northern hardwood forests of the northeastern U.S. (Vadeboncoeur 2010). While current rates of atmospheric deposition of N are elevated compared to pre-industrial levels (Galloway et al. 2008), N deposition has declined across much of North America in recent years (Lloret and Valiela 2016) due to the 1990 Clean Air Act Amendments that limit emissions of nitrogen oxides. These declines in nitrogen inputs from atmospheric deposition could exacerbate N limitation in temperate ecosystems. Simultaneously, warmer temperatures and higher atmospheric concentrations of carbon dioxide are leading to greater plant demand for N (Norby et al. 2010; Feng et al. 2015). Thus, concerns over excess N are shifting to concerns about the potential for N oligotrophication (Craine et al. 2018). Evidence of N oligotrophication, or the process by which soil N availability becomes low relative to plant N demand, has been observed in temperate forests in the U.S. and around the globe in recent years (Craine et al. 2009, 2018; Elmore et al. 2016; McLauchlan et al. 2017; Groffman et al. 2018).

Evidence of N oligotrophication includes the observation of declining natural abundance foliar $\delta^{15}N$ values (hereafter $\delta^{15}N$) globally over time, as observed through long term (37 years) data from more than 42,000 foliar samples (Craine et al. 2018). Compared to ecosystems with lower N availability and N losses, ecosystems with relatively high N availability and N losses tend to have high foliar $\delta^{15}N$ values. Elevated foliar $\delta^{15}N$ reflects that nitrate production (via nitrification) and nitrate loss (via denitrification) are fractioning processes that lead to ^{15}N enrichment of residual soil N pools available for plant uptake. Consequently, the N that is readily taken up by trees tends to be more enriched in ^{15}N in ecosystems with high rates of N cycling and loss compared to ecosystems with lower rates of N cycling and loss (Nadelhoffer and Fry 1994). Therefore, the reduction in foliar $\delta^{15}N$ observed in temperate forests around the globe over the last several years (Craine et al. 2018) provides evidence for decreased N availability and N loss in these ecosystems over time.

In congruence with the process of N oligotrophication, long term records at the Hubbard Brook Experimental Forest (HBEF) show that N availability to trees is declining, likely due to increased carbon flow from plants to soils, increased N immobilization by soil microbes, and a decreased winter snowpack with increased frequency of soil freezing that leads to diminished rates of soil N cycling (Groffman et al. 2018). Although soil freeze/thaw cycles have been shown to initially increase N availability in some ecosystems (Henry 2007; Campbell et al. 2014), after successive soil freeze/thaw cycles N availability tends to decrease due to reduced rates of N mineralization (Schimel and Clein 1996; Durán et al. 2014; Sorensen et al. 2018). Therefore, it is possible that future reductions in N availability caused by the projected increase in frequency of soil/freeze thaw cycles in winter (Durán et al. 2014; Sorensen et al. 2016) combined with decreased atmospheric N deposition (Lloret and Valiela 2016), may strengthen N oligotrophication in northern hardwood forests over time.

In contrast to soil freezing reducing N availability, warmer soil temperatures in the growing season tend to increase soil N availability via faster rates of decomposition of soil organic matter and net N mineralization (Bai et al. 2013). In a global synthesis of soil warming experiments, Bai et al. (2013) found that rates of net N mineralization increased in soils by an average of 52% with experimentally elevated soil temperatures. In forests of the northestern U.S., rates of net N mineralization increased by up to 46% in response to soil warming (Rustad et al. 2001; Melillo et al. 2002). In addition, greater rates of N availability are linked to enhanced plant N uptake, as demonstrated by increased foliar N concentrations (Butler et al. 2012). Therefore, it is possible that soil warming will strengthen N oligotrophication if N demand by plants exceeds N availability. However, it is also possible that soil warming-induced increases in N availability will weaken N oligotrophication in northern hardwood forests if N availability is bolstered enough to exceed increasing plant N demand. In summary, projected changes in climate over the next century have the potential to strengthen or weaken the trajectory of ecosystem N oligotrophication due to changes in seasonal patterns of soil temperatures and their linkages to N cycling in northern hardwood forests.

We utilized the Climate Change Across Seasons Experiment (CCASE) at the HBEF in New Hampshire to examine the combined effects of elevated soil temperatures throughout the growing season and increased frequency of soil freeze/thaw cycles in winter on N cycling in northern hardwood forests. Through laboratory incubations of soil collected from this field manipulation experiment (Sorensen et al. 2018), we found no significant differences in potential rates of net N mineralization with growing season warming and winter soil freeze/thaw cycles, but found a positive relationship between laboratory soil temperatures and potential rates of N mineralization. We also observed that increased frequency of soil freeze/thaw cycles increased soil solution ammonium concentrations, increased tree root damage, and decreased tree ammonium uptake capacity in the early growing season (Sanders-DeMott et al. 2018). These results indicate that it is essential to observe the interactive effects of changes in climate across seasons as opposed to examining changes in temperature in only one season (i.e. warmer growing season soil temperatures or increased frequency of winter soil freeze/thaw cycles) to understand potential interactive effects on N cycling from changes in climate that occur in both the growing season and winter.

While the effects of climate change on northern hardwood forests have been explored independently in the growing season and winter, to our knowledge no studies have examined the combined effects of soil warming in the growing season and increased winter soil freeze/thaw cycles on (1) in situ net N mineralization as a measure of N availability, (2) foliar N of trees as a proxy for N uptake, and (3) natural abundance foliar $\delta^{15}N$ values to understand soil N availability relative to N losses in northern hardwood forests. We utilized the CCASE experiment to make these new measurements, which complement our existing mechanistic understanding of the effects of climate change documented in prior studies at this experiment. It is possible that the distinct effects of growing season soil warming and winter soil freeze/thaw cycles could work together to strengthen or weaken N oligotrophication; while soil freezing in winter reduces N availability by reducing N production in soils (Groffman et al. 2018), soil warming in the growing season increases soil N availability (Bai et al. 2013) and N demand by vegetation (Butler et al. 2012). If the positive effect of growing season warming on soil N availability is counteracted by negative effects of soil freeze/thaw cycles, while high N demand by trees is maintained, N oligotrophication could persist.

We hypothesized that warmer soils in the growing season increase rates of net N mineralization and foliar N concentrations (via increased N uptake), and the combination of growing season soil warming and winter soil freeze/thaw cycles together reduce rates of net N mineralization and foliar N concentrations (via reduced N uptake) in trees due to the negative effects of winter, soil freeze/thaw cycles on these processes outweighing the positive impact of growing season soil warming. We also expected foliage to have higher $\delta^{15}N$ values with growing season soil warming, possibly a result of increased soil N availability and N loss from these soils in the growing season (Sanders-DeMott et al. 2018), but lower $\delta^{15}N$ values in foliage with the combination of growing season soil warming and increased frequency of winter freeze/thaw cycles in winter possibly due to decreased N availability and N loss (Durán et al. 2014; Sorensen et al. 2016). If the effects of growing season soil warming are stronger than those of increased frequency of soil freeze/thaw cycles in winter, we may see a positive effect of climate change across seasons with enhanced net N mineralization and N uptake by trees and we would conclude that projected changes in temperature across seasons may counteract other factors inducing N oligotrophication in these ecosystems. If the effects of winter soil freeze/thaw cycles are stronger than those of increased soil temperatures in the growing season, we may see reduced rates of net N mineralization and N uptake by trees and would conclude that projected changes in temperature may instead contribute to N oligotrophication in the northern hardwood forest.

Methods

Study site

This experiment was conducted at the HBEF, a National Science Foundation Long-Term Ecological Research (NSF LTER) site located in the White Mountain National Forest in Central New Hampshire, USA (43°56′N, 71°45′W). The forest is composed primarily of northern hardwood forest species (*Acer rubrum, Acer saccharum, Betula alleghaniensis,* and *Fagus grandifolia*) with steeper slopes and higher elevations containing coniferous species (*Picea rubens, Tsuga canadensis, Pinus strobus,* and *Abies balsamea*). Soils are primarily base-poor spodosols, specifically course-loamy Typic Haplorthods, which developed in glaciofluvial sand and gravel. Depth to bedrock is on average 14 m (Winter et al. 2008). The mean annual precipitation is 1400 mm, with on average one-third falling as snow (Bailey et al. 2003; years 1969–2000). The climate is cool, humid, and continental. Winters typically have a continuous snowpack between mid-December and mid-April (Campbell et al. 2010) with winter air temperatures averaging − 4.7 °C (Bailey et al. 2003; years 1969–2000). There is soil frost in approximately two out of every three years, freezing to an average annual maximum depth of < 10 cm (Campbell et al. 2010; Fuss et al. 2016).

Climate change across seasons experiment (CCASE)

We established CCASE in summer of 2012 at HBEF (Templer et al. 2017) to examine the effects of the 5 °C increase in temperature in the snow-free season (Hayhoe et al. 2007) and rise in soil freeze/thaw cycle frequency in winter (Campbell et al. 2010) projected in this region over the next century. Soil temperature and snow-manipulation treatments are ongoing and began in December 2013. Thus, 2014 represents our first year of post-treatment data collection. Here we present results from four years of experimental manipulation.

There are six plots (each 11 × 13.5 m^2) at CCASE, which is dominated by red maple (*Acer rubrum*; 63 ± 7% basal area), with an understory composed of mostly American beech (*Fagus grandifolia*) saplings. There are two plots with soils warmed 5 °C above ambient temperatures ("*warmed*") between spring snowmelt (early April) and the first snowfall in November or December (hereafter referred to as the growing season); two plots with the same growing season warming treatment combined with soil freeze/thaw cycles induced in winter ("*warmed + FTC*"); and two plots with ambient soil temperature ("*reference*"). To achieve the freeze/thaw cycle treatment, snow was shoveled during the winter months to induce freezing and heating cables were used to induce thaws. In the *warmed + FTC* treatment plots only, the first snow of winter was gently packed down to maintain albedo and minimize disturbance to the forest floor with subsequent shoveling. By removing snow, we caused the soils to freeze. Soil freezing is operationally defined as soil temperature less than − 0.5 °C. After soils were frozen for 72-h, the heating cables were turned on to warm soils to 1 °C to induce a 72-h thaw. The entire process of 72-h frozen plus 72-h thawing constituted one soil freeze/thaw cycle. We achieved four freeze/thaw cycles in the winters of both 2013/2014 and 2014/2015, two in 2015/16, and one in the 2016/17 and 2017/18 winters. The frequency and duration of soil freeze/thaw cycles were chosen to mimic the four additional freeze/thaw cycles projected to occur in this region by the year 2100 (Campbell et al. 2010).

The *warmed* and *warmed + FTC* plots together make up the four "treatment" plots and are equipped with heating cables that were buried by hand 10 cm deep using a flat shovel in 2012 in parallel lines spaced 20 cm apart. *Reference* plots were similarly cut to mimic cable installation disturbance, but no cable was installed. Each plot is divided into four equal areas, each representing a quadrant. For additional technical details on experimental design, see Templer et al. (2017).

Environmental variables

We measured soil temperatures at 5, 10, and 30 cm depth (Betatherm type 10K3A1; Campbell Scientific, Logan, Utah, USA; n = 2 at 5 cm depth, n = 6 at 10 cm depth, and n = 1 at 30 cm depth for all plots) and volumetric soil moisture (m^3 H_2O m^{-3} soil volume; CS616; Campbell Scientific, Logan, Utah, USA; n = 4 per plot integrated across 0–30 cm depth) every 5 s. Half-hourly means were stored on a CR1000 multichannel data logger (Campbell Scientific, Logan, Utah, USA). In four locations per plot, weekly from December 1 through March 31 of each year, we used frost tubes (Ricard et al. 1976) to measure soil frost depth and used a meter stick inserted into snowpack to measure snow depth. Soil frost duration (i.e. number of days with frost) during winter was calculated as days when depth of soil frost was greater than 0 cm. Soil frost and snow depth measurements made in each plot throughout winter were each converted into a single continuous variable (i.e. area under the curve = AUC; Durán et al. 2014) by calculating the integral over time (i.e. x-axis = time measured in units days) of soil frost or snow depth (i.e. y-axis = depth measured in units cm) using the R package "pracma' (Borchers 2019). Data on soil frost and snow depth are presented in more detail in Templer et al. (2017) and Harrison et al. (2020).

Net nitrogen mineralization

Rates of net N mineralization and nitrification were measured in all six plots at CCASE using the buried bag technique (Eno 1960). We measured net N mineralization three times throughout the 2017 growing season (starting on May 18, July 13, and September 25, 2017), each representing early, peak, and late growing season, respectively. It is difficult to use soil augers to collect cores in our plots due to the buried heating cables. Instead, we collected soils in each of the four quadrants in each plot (n = 4 per plot; n = 24 total) by measuring a 10 × 10 cm area on the soil surface and gently cutting around this area into the soil, down to the organic layer, which is on average 5.2 ± 0.30 cm, but can be as deep at 10 cm (Templer et al. 2017). Half of the sample was immediately placed in a cooler (representing the initial sample); the other half was left to incubate for 28 days in the field in a polyethylene zip-top bag (representing the final sample), placed back into the hole and covered with soil. The bags allow gas exchange (e.g. oxygen and carbon dioxide), but are not permeable to water and have been shown to prevent nitrate movement (Eno 1960). Extractions were completed using 5 g of field-moist soil and 30 mL of 2 mol L^{-1} potassium chloride (KCl). The concentrations of ammonium (NH_4^+) and nitrate (NO_3^-) in soil extracts were analyzed colorimetrically for both the initial and final samples using a Versamax microplate spectrophotometer (Molecular Devices, San Jose, CA, USA; Doane and Horwáth 2003). Net ammonification was calculated as the difference in NH_4^+ in the initial sample and the final sample, divided by the incubation period (28 days). Net nitrification was calculated as the difference in NO_3^- in the initial sample and the final sample, divided by the incubation period (28 days). Net N mineralization was calculated as the difference in the sum of NH_4^+ and NO_3^- in the initial sample and the final sample, divided by the incubation period.

The organic layer is typically the most dynamic soil horizon for N cycling in temperate forests (Currie 1999). Nitrogen in mineral soils is generally less available for plant uptake, even though it comprises the largest N pool at HBEF (Yanai et al. 2013) and there is some recent evidence that plants can "mine" N stored in the mineral layer (Lovett et al. 2018). However, because in temperate forests rates of N mineralization in the organic horizon can be twice those in the mineral layer (Aber et al. 1993), and the majority of fine root biomass in hardwood forests is in the top 10 cm (Yanai et al. 2006) at Hubbard Brook, we chose to focus on the organic layer in our study.

Foliar nitrogen and natural abundance stable isotope analysis

Here we use foliar N as an indicator of plant N status and a proxy for plant N uptake (Aber et al. 1989) and we use $\delta^{15}N$ values in foliage to understand the relative rates of coupled soil N cycling and N loss via leaching or denitrification from forest ecosystems (Nadelhoffer and Fry 1994; Emmett et al. 1998; Pardo et al. 2002, 2006).

We excised three green leaves from three mature red maples in each plot in 2012–2015 and 2017–2018 from sunlit branches shot down with a shotgun; we bulked together the three leaf replicates into one sample per tree for each sampling period for analysis (n = 3 trees per plot). We collected foliage once in 2012, 2013 (pre-treatment years), and 2014 (first year post-treatment), twice in 2015, and three times in 2017 and 2018. No foliage samples were collected in 2016 and we do not have data for $\delta^{15}N$ in 2013 or 2014. Despite not having data certain years, we have enough pre-treatment and post-treatment samples to confidently conclude how our treatment affects foliar N. Samples were dried at 60 °C for 72 h and then weighed and homogenized for N concentration analysis and natural abundance $\delta^{15}N$ isotope analysis via an Isotope Ratio Mass Spectrometer (IsoPrime; GV Instruments; Wythenshave, Manchester, UK) at the Stable Isotope Laboratory at Boston University. We report all stable isotope data as natural abundance $\delta^{15}N$ values, representing the ratio between each foliar sample and that of atmospheric dinitrogen using the following equation:

$$\delta^{15}N = \{(R_{sample}/R_{standard}) - 1)\} \times 1000$$

where R_{sample} represents the sample isotope ratio ($^{15}N/^{14}N$) and $R_{standard}$ is $^{15}N/^{14}N$ for the N standard, which is atmospheric N_2 (0.0036765).

Statistical analyses

All statistical analyses were conducted in R Studio v 1.0.44 (R Development Core Team 2014). In addition, we considered the *reference, warmed,* and *warmed + FTC* treatments as independent categorical variables in all of our analyses. Plot differences in winter environmental variables (i.e. maximum snow depth, maximum soil frost depth, soil frost duration, snow duration, and soil frost AUC) were assessed using separate ANOVAs within each year. A linear mixed effects (LME) model was used to test the effects of treatment on rates of N cycling (net ammonification, nitrification, and mineralization), foliar N, and $\delta^{15}N$ for each sampling period separately (i.e., early, peak, or late) and for the average of the entire growing season. We used quadrant nested within plot for soil samples and tree nested within plot for leaf samples as random effects in the LME to account for repeated sampling within a plot, and treatment as the fixed effect. We also tested the effect of sampling period (i.e. early, peak, or late) on rates of N cycling (net ammonification, nitrification, and mineralization), foliar N, and $\delta^{15}N$ using an LME with quadrant or tree within plot as the random effect and sampling period as the fixed effect. We also examined foliar N and $\delta^{15}N$, separately, to see if N concentrations and isotopic composition differed between treatments for a given year from 2012 and 2013 (pre-treatment) to 2018 using an LME with tree within plot as the random effect and treatment as the fixed effect for each. For all models that examined treatment as a fixed effect, we included both treatments to explore the interactive effects of our treatments, even when the treatments had similar results and model selection favored including *warmed* plots alone.

The relationships between average soil temperature at 5 cm depth during each incubation period and rates of N cycling, foliar N, or $\delta^{15}N$ were examined using an LME with quadrant or tree nested within plot for the 2017 growing season. We also examined the relationship separately between: (1) foliar N and net N mineralization; (2) $\delta^{15}N$ and net N mineralization; and (3) foliar N and $\delta^{15}N$ using LMEs with quadrant or tree nested within plot for each treatment and each season.

We assessed all data for normality and equal variance by examining residuals plotted against predictors and confirmed that all data were normally distributed and no data transformations were necessary. We used the package “nlme” in R (Pinheiro et al. 2012) for all linear mixed effects models and calculated the marginal R^2 values to describe the proportion of variance explained by the fixed effects using the R package “piecewiseSEM” (Lefcheck 2016). All post-hoc pairwise comparisons among treatments used the R package “lsmeans” (Lenth 2016). A larger number of plots ($n > 2$ plots) would have improved our statistical power, but was not feasible due to logistical and economic constraints on experimental design. Therefore, we report all p-values and do not apply a strict $\alpha = 0.05$ cutoff in describing our results.

Results

Growing Season and Winter Environmental Variables

Details about environmental variables for 2014–2017 are described in Templer et al. (2017) and Harrison et al. (2020). Briefly, experimental treatments elevated soil temperatures approximately 5 °C in the *warmed* and *warmed + FTC* plots during the growing season and between two and four freeze–thaw cycles were induced during winter in the *warmed + FTC* plots throughout the duration of the experiment. Here we go into more detail about environmental variables in 2017 as this is the year we collected soil samples to measure net N mineralization. In 2017 there were significant increases in growing season soil temperatures in the *warmed* and *warmed + FTC* plots by 4.99 ± 0.02 °C and 4.88 ± 0.08 °C, respectively, compared to the *reference* plots throughout the growing season (April 14 to November 15). Soil moisture integrated over the top 30 cm of soil was not affected by the soil temperature treatments in the 2017 growing season ($p = 0.88$) or the 2016/2017 winter ($p = 0.32$), which is consistent with all post-treatment years (2014 on). In the 2014/2015, 2015/2016, and 2016/2017 winters, snow removal led to lower snow depths and snow AUC, as well as lower minimum winter soil temperatures, greater maximum soil frost depths, greater soil frost AUC, number of soil freeze/thaw cycles, and soil frost duration in the *warmed + FTC* plots (Templer et al. 2017; Harrison et al. 2020).

Net Nitrogen Mineralization

Net nitrification rates in the forest soils were generally low, ranging from 0–0.70 μg N g soil^{-1} day^{-1}, compared to net ammonification rates that ranged from 0–5.78 μg N g soil^{-1} day^{-1}. Overall, net ammonification made up over 99% of net N mineralization, and this proportion did not vary significantly by treatment ($p = 0.40$) or with timing throughout the growing season ($p = 0.57$). In addition, we did not observe any significant differences in soil moisture between our samples processed for net N mineralization (all time periods $p > 0.10$).

Rates of net N mineralization averaged across the 2017 growing season were significantly higher in plots with growing season soil warming (*warmed* and *warmed + FTC* plots) compared with *reference* plots (Fig. 1a; 63.27 ± 3.19% and 87.86 ± 2.78% higher in *warmed* and *warmed + FTC*, respectively, than *reference* plots; $p = 0.09$). Warmed plots tended to have higher rates of net N mineralization at every sampling date, but were significant in the late growing season only (27.89 ± 20.37% and 88.31 ± 10.19% increase in the *warmed* and *warmed + FTC* plots relative to the *reference* plots, respectively; $p = 0.04$). Rates of net N mineralization across all plots were 1.5 and 3.1-fold higher in the peak growing season compared to the early and late growing seasons, respectively (Fig. 1b; $p < 0.0001$). There was not a significant interaction between experimental treatment and timing of sampling (Fig. 1b; $p = 0.13$).

Across all plots, soil temperatures and rates of net N mineralization across the entire growing season ($p = 0.75$) and the early and peak growing season ($p = 0.28$ and 0.26, respectively) were not significantly related. In the late growing season, however, there was a statistically significant positive relationship between average soil temperatures and rates of net N mineralization ($p = 0.033$; Fig. 2a).

Foliar Nitrogen and Natural Abundance $\delta^{15}N$

In 2017, foliar N concentrations related positively with soil temperatures across the entire growing season (Fig. 2b; $p = 0.01$), and in the early ($p = 0.02$), peak ($p = 0.02$), and late growing seasons ($p = 0.04$). In addition, foliar N concentrations were significantly higher, by 11–21%, in the peak compared to the early and late growing seasons in 2017 and 2018 across all plots ($p = 0.05$), the two years for which we collected foliage from three distinct time periods throughout the growing season. There was a significant positive relationship between net N mineralization and foliar N concentrations in 2017 across all plots (Fig. 2d; $p = 0.0015$).

Foliar δ^{15}N values were positively related to soil temperatures (Fig. 2c; $p < 0.01$), but not related to net N mineralization (Fig. 2e; $p = 0.18$).

Before treatments began, there were no differences in foliar N concentrations (Fig. 3a; $p = 0.94$ and $p = 0.23$ across all plots in 2012 and 2013, respectively) or δ^{15}N values (Fig. 3b; $p = 0.19$ for 2012, the only pretreatment year with δ^{15}N data). Foliar N increased in the *warmed* and *warmed + FTC* plots compared to *reference* plots in all treatment years (2014–2018; $p = 0.001$). Specifically, in 2014 there were significant increases in foliar N concentrations in the *warmed + FTC* plots, relative to trees in *reference* and *warmed* plots ($p < 0.001$). Beginning in 2015, foliar N concentrations were significantly higher in all treatment plots (*warmed* and *warmed + FTC* plots) compared to *reference* plots ($p = 0.001$ in 2016 and $p < 0.001$ in 2017 and 2018). Foliage was more enriched in δ^{15}N the *warmed* and *warmed + FTC* plots compared to *reference* plots between 2015 and 2018 (Fig. 3b, $p < 0.001$ overall and for 2015, 2017, and 2018). There was a statistically significant positive relationship between foliar N concentration and δ^{15}N in all post-treatment years between 2014 and 2018 (Fig. 4; $p = 0.08$).

Discussion

Our results show that the projected increase in soil temperatures during the growing season in this region may counteract the negative effects of a smaller winter snowpack and greater frequency of soil freeze/thaw cycles that induce lower N availability and contribute to N oligotrophication in northern hardwood forests. We found that warmer growing season soil temperatures led to increased rates of net N mineralization, higher foliar N concentrations, and more enriched δ^{15}N in foliage, and none of these N responses were

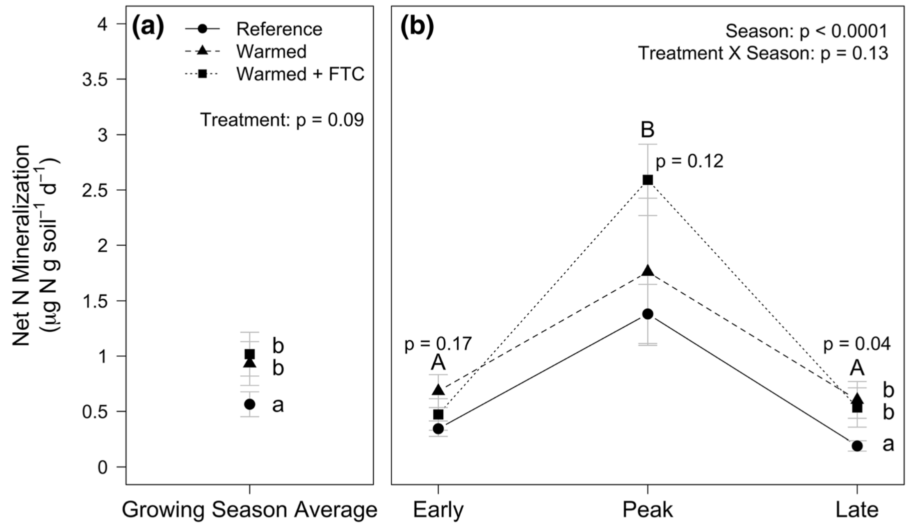

Fig. 1 Net nitrogen mineralization (Panel a) across the entire growing season in 2017 for each treatment, and (Panel b) in the early (mid-May), peak (mid-July), and late (late-September) growing season in 2017. Error bars represent standard error of the means. In Panel b different uppercase letters represent statistically significant differences across the entire growing season and different lowercase letters represent statistically significant differences across treatments, respectively. *p*-values are shown for differences in treatment across the entire growing season, within each sampling date, differences in seasonal rates, and the interaction between treatment and season

reduced by soil freeze/thaw cycles in winter. The similar response from plots with experimental soil warming with or without winter freeze/thaw cycles demonstrates that soil temperatures in the growing season are more critical than in winter in controlling these facets of the N cycle. These results suggest that soil N availability and uptake by trees are likely to increase with warmer temperatures, despite the projected increase in soil freeze/thaw cycles in winter over the next century.

Similar to Sorensen et al. (2018), we did not use $\alpha = 0.05$. Our choice in a higher alpha value (0.10) is in contrast to some of our other publications from the CCASE study (Templer et al. 2017; Sanders-DeMott et al. 2018) that use $\alpha = 0.05$ in reporting results. It is possible the foliar N and net N mineralization responses observed here respond differently to growing season soil warming and winter soil freeze/thaw cycles compared to soil temperature, snow depth, soil frost depth, root damage and N uptake capacity, and soil solution N, which were all statistically significant at $p < 0.05$ (Templer et al. 2017; Sanders-DeMott et al. 2018).

Soil nitrogen cycling

The increased rates of net N mineralization observed with soil warming in the growing season (*warmed* and *warmed + FTC* plots) was expected as this relationship has been demonstrated using laboratory incubations of soils collected from CCASE (Sorensen et al. 2018) and in other warming experiments in temperate forests around the globe (Rustad et al. 2001; Melillo et al. 2002; Bai et al. 2013). Our high rates of net ammonification relative to net nitrification align with past measurements of potential rates of soil N cycling (Sorensen et al. 2018) and soil N solution (Sanders-DeMott et al. 2018) at CCASE, further showing that these soils contain more ammonium compared to nitrate.

Laboratory measurements of CCASE field soils showed no significant differences in potential rates of net N mineralization with growing season soil warming and winter soil freeze/thaw cycles after one year of treatment (Sorensen et al. 2018). In contrast to these findings, we found that rates of net N mineralization increased in response to in situ soil warming in the growing season. The trend of increased rates of net N mineralization with soil warming was also observed in those plots with increased frequency of soil freeze/

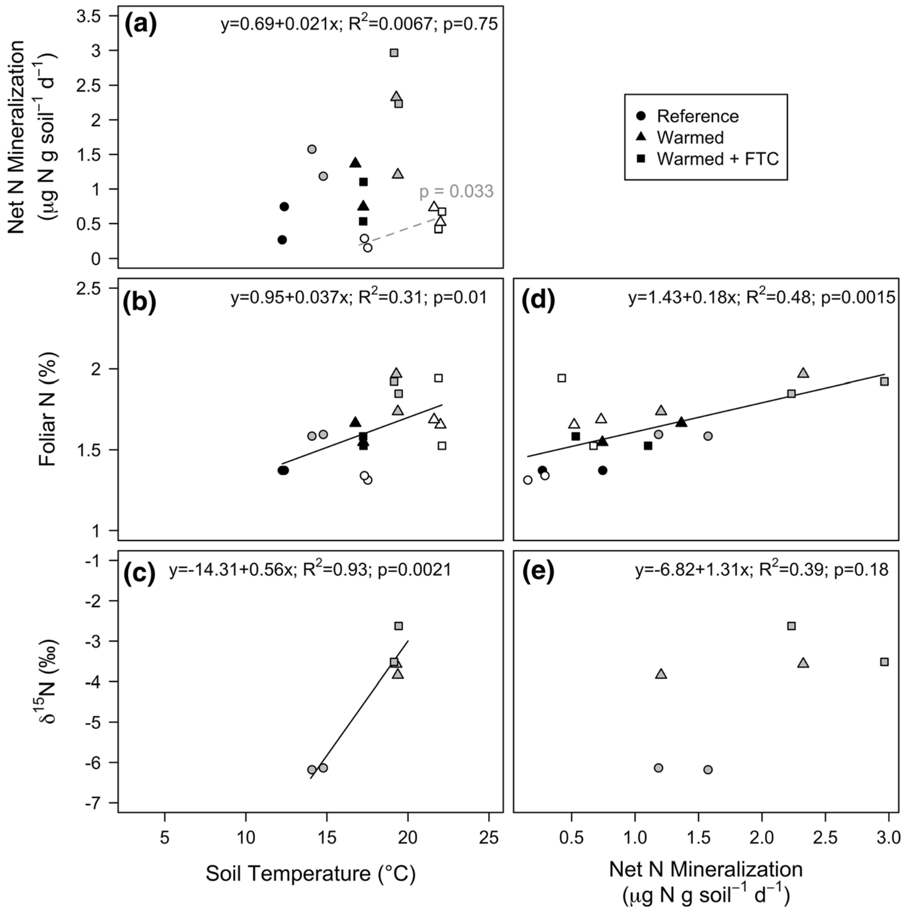

Fig. 2 Relationships between soil temperature (5 cm depth) and net nitrogen mineralization (Panel a), foliar nitrogen (Panel b), and foliar $\delta^{15}N$ (Panel c) and relationships between net nitrogen mineralization and foliar nitrogen (Panel d) and foliar $\delta^{15}N$ (Panel e) throughout the 2017 growing season. Statistical results are the same when examining the relationship between net ammonification and net nitrogen mineralization and other variables. Different symbols represent the three treatments. The grayscale of the symbol distinguishes between times in the growing season; the early growing season (mid-May) symbols are black, the peak growing season (mid-July) symbols are gray, and the late growing season (mid-September) symbols are white. R^2, equations, and p-values are for the best fit line, with grey line and *p*-value for the peak growing season only. Note: foliar samples only analyzed for $\delta^{15}N$ in the peak growing season

thaw cycles in the previous winter. It is possible that it took longer for net N mineralization to respond to increases in soil temperature and therefore while we observed these increases in 2017 (this study), we did not observe similar increases in soils collected in 2014 (as reported in Sorensen et al. 2018). It is also worth noting that Sorensen et al. (2018) incubated field soils from all plots in the laboratory at the same temperature and therefore did not observe the immediate effects of in situ temperature manipulations. Similar to our results, in a study at Harvard Forest, MA, researchers observed significant increases in net N mineralization after just one year of warming (Butler et al. 2012), and those rates persisted for an additional seven years of treatment. However, those researchers did not examine the combined effects of winter and growing season changes in soil temperatures. Our results indicate that N responses to growing season soil warming were maintained in plots also experiencing winter soil freeze/thaw cycles (Campbell et al. 2014; Durán et al. 2014; Sorensen et al. 2016), indicating that warmer growing season temperatures lead to greater N availability for plants that is not offset by winter freeze/thaw cycles. Greater N availability may counteract other factors leading to lower N availability in

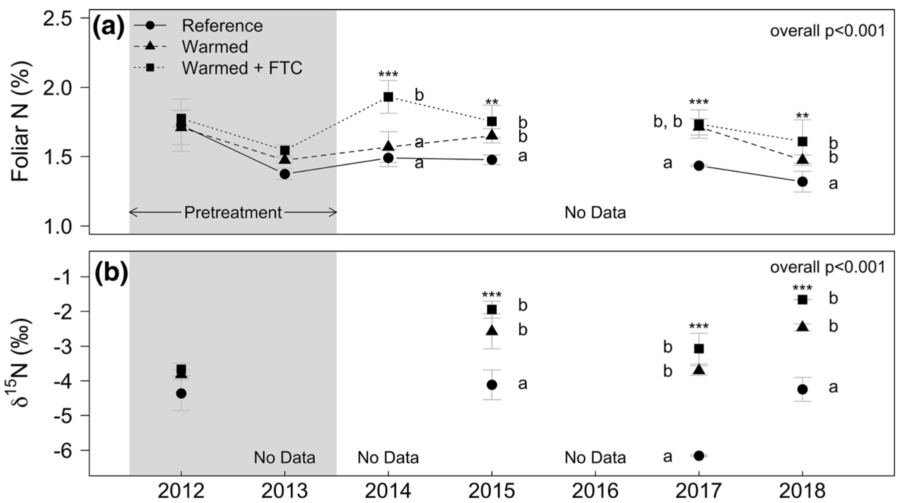

Fig. 3 Foliar nitrogen concentration (Panel a) and $\delta^{15}N$ (Panel b) from 2012 and 2013 (pre-treatment years) to 2018 across treatments. Error bars represent standard error of the means, with means calculated across the entire growing season. Statistics are shown for models with tree nested within plot within each year. The shaded region represents the two pre-treatment years. Different letters within a year represent statistically significant differences among treatments for a given year. Overall p-value representing LME analysis across all post-treatment years provided and asterisks describe p-values with "**"$p = 0.001$ and "***"$p < 0.001$ during specific years. Note: no foliar N data were collected in 2016; no foliar $\delta^{15}N$ data were collected in 2013, 2014, and 2016

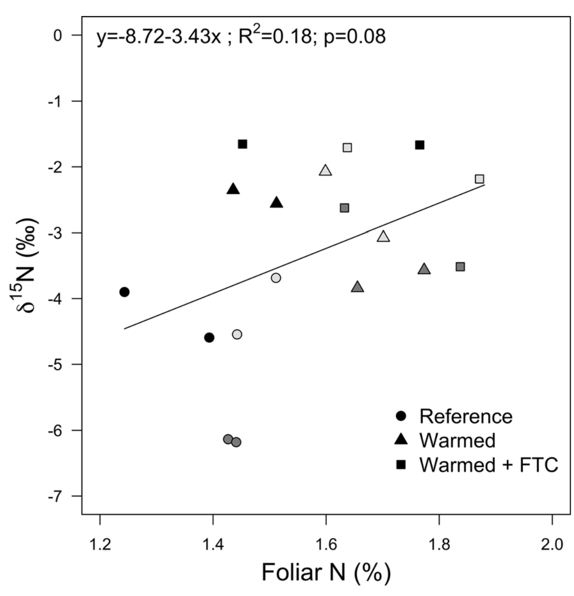

Fig. 4 Relationship between foliar nitrogen concentration and $\delta^{15}N$. Different symbols represent the three treatment. The grayscale of the symbol distinguishes between post-treatment years; data from 2015 are light gray, data from 2017 are dark gray, and data from 2018 are black. R^2, equation, and p-value are for the best fit line. Note: foliar samples only analyzed for $\delta^{15}N$ in the peak growing season

northern hardwood forests, and possibly in other N-limited forests.

Plant nitrogen

The enhanced foliar N that we observed in plots warmed in the growing season are consistent with past studies that showed greater N uptake with greater N availability (Bassirirad 2000) and positive relationships between foliar N and soil temperatures (Van Cleve et al. 1990; Butler et al. 2012; Bai et al. 2013). Higher foliar N concentrations with greater N availability due to soil warming are not surprising because N is an essential, but often limiting nutrient in northern hardwoods (Vadeboncoeur 2010). However, our results do not show decreases in foliar N after the addition of soil freeze/thaw cycles in winter that examine the effect of changes in winter alone (Li et al. 2016), likely due to the positive effects of soil warming on foliar N. Our results demonstrate that foliar N in northern hardwood forests may continue to increase with the projected rise in air temperatures over the next century for this region, and might not decrease even with greater frequency of soil freeze/thaw cycles in winter.

Winter freeze/thaw cycles damage roots and reduce their capacity to take up N per root biomass in the following early growing season, as demonstrated in this CCASE experiment (Sanders-DeMott et al. 2018) and in a past snow-removal experiment (Campbell et al. 2014) at the HBEF. Yet, winter soil freeze/thaw cycles in this study did not lessen the positive effects of soil warming in the growing season on foliar N. Our observation of increased foliar N with growing season soil warming indicates that potential reductions in N uptake by roots due to soil freezing in winter may be offset when combined with the positive effects of soil warming in the growing season that increase N uptake by trees. We therefore conclude that foliar N concentrations are more responsive to growing season soil warming than to winter soil freeze/thaw cycles.

The enriched foliar $\delta^{15}N$ values in the *warmed* and *warmed + FTC* plots relative to *reference* plots across three post-treatment years (2015, 2017, and 2018) are not surprising given the greater rates of net mineralization (Fig. 1) and amount of N in soil solution (Sanders-DeMott et al. 2018) in the *warmed* and *warmed + FTC* plots. The higher amounts of N available in the four warmed plots (*warmed* and *warmed + FTC* plots; Figs. 1 and 2) may have been associated with greater N losses via denitrification or leaching that led to ^{15}N enrichment of soil N pools in those plots relative to the *reference* plots, thereby enriching the N available for plant uptake and $\delta^{15}N$ observed in foliage (Fig. 3).

There are other mechanisms that could lead to higher $\delta^{15}N$ values in the *warmed* and *warmed + FTC* compared to reference plots. For example, a change in the relative contribution of ammonium and nitrate to plant N uptake and change in reliance on arbuscular mycorrhizal N could lead to higher foliar $\delta^{15}N$ values in the warmed compared to reference plots. Specifically, studies have demonstrated lower $\delta^{15}N$ values in soil nitrate compared to ammonium due to isotopic fractionation during nitrification (Miller and Bowman 2002; Koba et al. 2003). However, our past work shows that the red maple trees in the CCASE plots take up more than 95% of their N as ammonium and the ratio of ammonium to nitrate uptake does not change with growing season warming or winter soil freeze/thaw cycles (Sanders-DeMott et al. 2018). Our past results from the CCASE experiment also demonstrate a decrease in arbuscular mycorrhizal abundance, the mycorrhizal type associated with red maple trees (Klingeman et al. 2002), in roots in the warmed plots, but no change in abundance with the combination of growing season soil warming and winter soil freeze/thaw cycles (Garcia et al. 2020). However, because we did not explicitly measure the linkage between mycorrhizal abundance and N uptake, we cannot say whether the change in fungal abundance on roots affected foliar $\delta^{15}N$ values. Thus, although we do not know the exact mechanism(s) that caused higher foliar $\delta^{15}N$ values in the warmed plots, we know that soil warming increased soil N availability (this study) and soil solution N (Sanders-DeMott et al. 2018), which possibly increased N losses through denitrification and/or leaching. Regardless of the mechanisms, the higher $\delta^{15}N$ values in red maple foliage of the *warmed* and *warmed + FTC* plots compared to the *reference* plots shows that projected increases in growing season soil temperatures may counteract other factors contributing to N oligotrophication in northern hardwood forests by further increasing N availability and perhaps N uptake by trees.

The positive relationship between $\delta^{15}N$ and N in foliage we observed across all plots has been well-documented in temperate forests (Martinelli et al. 1999; Pardo et al. 2006) and globally (Hobbie et al. 2000; Craine et al. 2009, 2015). While we acknowledge that the positive relationship between $\delta^{15}N$ values and N concentrations in foliage is somewhat low ($R^2 = 0.18$), we believe this result is ecologically significant and shows that N uptake by trees likely increases with soil N availability in this forest, especially in soils warmed in the growing season.

Conclusions

As air temperatures rise (Hayhoe et al. 2007; IPCC 2014; Lynch et al. 2016), the snowpack shrinks (Estilow et al. 2012; Demaria et al. 2016; Reinmann et al. 2019), and the frequency of winter soil freeze/thaw cycle events increases (Henry 2008; Campbell et al. 2010; Brown and DeGaetano 2011) over the next century in the northeastern U.S., N cycling patterns in northern hardwood forest ecosystems are likely to change. Our results indicate that examining in situ rates of net N mineralization, foliar N, and natural abundance foliar $\delta^{15}N$ values in response to projected changes in temperatures in both the growing season and winter reveal responses that would not otherwise be evident either through lab incubations of soils or roots, or by examining individual seasons alone. Based on the results from this study, we conclude that warmer soils in the growing season, despite increased frequency of soil freeze/thaw cycles in winter, will increase soil N availability to northern hardwood trees through enhanced rates of net N mineralization. The stimulatory effects of increased soil temperatures on net N mineralization will likely increase N uptake by trees, outweighing detrimental effects of soil freeze/thaw cycles on plant N uptake. Our findings demonstrate that the projected increase in soil temperatures in hardwood forests over the next century may lessen other factors that lead to N oligotrophication if rates of soil net N mineralization continue to increase and keep pace with N demand by trees, and depending on how rates of atmospheric N deposition change in the future.

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Author's contributions PHT and RSD conceived and designed the experiment. JLH, KS, MB, and RSD collected the data. JLH analyzed the data. PHT and JLH led the writing of the manuscript. All authors contributed to writing and editing of the manuscript.

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Data availability The data in this paper are publicly available through the Hubbard Brook Experimental Forest data archives (Templer et al. 2020a, b).

Code availability R code is available upon request.

Compliance with ethical standards

Conflict of interest The authors confirm they do not have any conflict of interest.

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