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Declines in northern forest tree growth following snowpack decline and soil freezing

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Abstract

Changes in growing season climate are often the foci of research exploring forest response to climate change. By contrast, little is known about tree growth response to projected declines in winter snowpack and increases in soil freezing in seasonally snow-covered forest ecosystems, despite extensive documentation of the importance of winter climate in mediating ecological processes. We conducted a 5-year snow-removal experiment whereby snow was removed for the first 4–6 weeks of winter in a northern hardwood forest at the Hubbard Brook Experimental Forest in New Hampshire, USA. Our results indicate that adverse impacts of reduced snowpack and increased soil freezing on the physiology of *Acer saccharum* (sugar maple), a dominant species across northern temperate forests, are accompanied by a 40 ± 3% reduction in aboveground woody biomass increment, averaged across the 6 years following the start of the experiment. Further, we find no indication of growth recovery 1 year after cessation of the experiment. Based on these findings, we integrate spatial modeling of snowpack depth with forest inventory data to develop a spatially explicit, regional-scale assessment of the vulnerability of forest aboveground growth to projected declines in snowpack depth and increased soil frost. These analyses indicate that nearly 65% of sugar maple basal area in the northeastern United States resides in areas that typically experience insulating snowpack. However, under the RCP 4.5 and 8.5 emissions scenarios, we project a 49%–95% reduction in forest area experiencing insulating snowpack by the year 2099 in the northeastern United States, leaving large areas of northern forest vulnerable to these changes in winter climate, particularly along the northern edge of the region. Our study demonstrates that research focusing on growing season climate alone overestimates the stimulatory effect of warming temperatures on tree and forest growth in seasonally snow-covered forests.

KEYWORDS
snow depth, snowpack, soil freezing, soil frost, sugar maple, tree growth, winter climate change

1 | INTRODUCTION

Feedbacks between climate and the carbon (C) cycle remain a considerable source of uncertainty for both global climate projections and terrestrial net primary productivity (NPP; Heimann & Reichstein, 2008). Empirical studies and the C cycle-climate feedback models that rely on them for parameterization often use growing season climate conditions to explore relationships between climate and plant growth or ecosystem NPP (Friedlingstein et al., 2006; Sanders-

DeMott & Templer, 2017). However, winter climate conditions in seasonally snow-covered systems have direct effects on plant physiological processes (Campbell, Mitchell, Groffman, Christenson, & Hardy, 2005; Campbell, Socci, & Templer, 2014; Cleavitt et al., 2008; Comerford et al., 2013; Drescher & Thomas, 2013; Frey, 1983; Makoto et al., 2014; Tierney et al., 2003) that also play an important role in mediating NPP. Nearly half of the land area in the Northern Hemisphere is influenced by seasonal snow cover (Zhang, Heginbottom, Barry, & Brown, 2003), including northern forest ecosystems (i.e., north temperate and boreal forests), which collectively comprise a globally important C sink of ~0.6 Pg C/year (Goodale et al., 2002). Satellite data, model projections and in situ observations together show that rates of C uptake and NPP in these forest ecosystems have increased from winter warming that has lengthened the growing season in recent decades (Xia et al., 2014). However, the future response of northern forest C sequestration to continued warming remains uncertain due to confounding effects of reduced soil insulation associated with projected reductions in snowfall and snowpack depth and duration (Notaro, Lorenz, Hoving, & Schummer, 2014).

Over the past few decades, substantial progress has been made in our understanding of the important roles winter snowpack has in regulating soil frost severity (Hardy et al., 2001) and a range of ecosystem processes that affect plant growth including fine root dynamics (Comerford et al., 2013; Reinmann & Templer, 2016; Tierney et al., 2001), soil C and nitrogen (N) cycling (Blankinship & Hart, 2012), and sapling survival (Drescher & Thomas, 2013; Frey, 1983). It is well-documented that increased depth and duration of soil freezing caused by snowpack reductions adversely impacts root vitality (Comerford et al., 2013), shoot elongation (Comerford et al., 2013), N uptake by trees, and N retention by northern forests (Campbell et al., 2014), and leads to greater foliar Al:Ca ratios of hardwood trees (Comerford et al., 2013). However, the multiyear response of tree growth and aboveground C storage in seasonally snow-covered forest ecosystems is not yet known. Further, little is known about the spatial patterns and extent to which conditions induced at the plot scale in field experiments might exist under projected changes in winter climate.

The northern hardwood forest, which occupies the southern portion of the northern forest, comprises more than 22 million ha of North America and has historically been within the geographic extent of persistent and insulating winter snowpack (Estilow, Young, & Robinson, 2015). However, over the 21st century, these forests are projected to experience some of North America's largest declines in winter snowpack depth and duration (Demaria, Roundy, Wi, & Palmer, 2016; Estilow et al., 2015) and increases in soil frost severity (Brown & DeGaetano, 2011; Henry, 2008). Together, these changes will result in winter conditions rarely experienced by these forest ecosystems in the past. Under current snowpack conditions, the northern hardwood forest is a net C sink (Van Deusen & Heath, 2017) and is dominated by valuable timber species such as sugar maple (*Acer saccharum* Marsh.), which in addition to being a defining tree species of the northern hardwood forest also plays an economically vital role in the maple syrup and tourism industries (North East State Foresters Association, 2013). Previous research has shown that physiological processes of sugar maple trees growing in seasonally snow-covered regions are particularly vulnerable to declines in winter snowpack and increases in soil freezing (e.g., Campbell et al., 2014; Cleavitt et al., 2008; Comerford et al., 2013; Tierney et al., 2001). Consequently, the combination of declines in snowpack depth, a primary control of soil frost development, and relative abundance of sugar maple trees will likely be a key driver of spatial patterns in northern hardwood forest ecosystem response to winter climate change.

The northern hardwood forest is an ideal system to study the effects of winter climate changes on tree growth because these forests are likely to experience a profound shift in snowpack and soil frost dynamics over the next century. We conducted a 5-year snow-removal experiment in a seasonally snow-covered northern hardwood forest at Hubbard Brook Experimental Forest (HBEF) in New Hampshire, U.S.A., to quantify the response of tree growth to projected declines in insulating winter snowpack and increases in the depth and duration of soil freezing. We integrate spatial modeling of snowpack depth with U.S. Department of Agriculture Forest Inventory and Analysis data (FIA) to develop a spatially explicit, regional-scale assessment of vulnerability of forest growth to projected declines in snowpack depth and increases in soil freezing.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at Hubbard Brook Experimental Forest (HBEF), a long-term ecological research site (LTER) located in the White Mountains, NH (43°56′N, 71°45′W). Sugar maple, yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) are the dominant canopy tree species. HBEF has a continental climate with cold winters (mean January temperature is −9°C) and mild summers (mean July temperature is 18°C) and receives approximately 1,400 mm of precipitation evenly distributed throughout the year (Bailey, Hornbeck, Campbell, & Eagar, 2003) and a continuous snowpack (typical winter maximum depths of 72–106 cm across elevations) typically present from late-December to mid-April (Campbell et al., 2010). At HBEF, maximum soil frost depth is typically <10 cm, but rare occurrences of deeper soil frost have been observed (Bailey et al., 2003).

2.2 | Experimental design

Four reference and four snow-removal plots in pairs (each 169 m^2) were established in 2007 (see Templer et al., 2012 for details). Each plot was centered on three sugar maple trees (DBH ≥20 cm), with the exception of two reference plots, which both contained one red maple (*Acer rubrum* L.) and two sugar maple trees. Species abundance and composition in the eight plots were similar as indicated by leaf litterfall sorted to tree species. The first snowfall of each

winter was packed down to 3–5 cm to maintain the albedo of the forest floor and minimize disturbance to the litter layer during shoveling. Shoveling was used to remove snow from the four treatment plots from mid-December through mid-January during the winters of 2008/2009 through 2012/2013. Snow accumulated naturally in the four reference plots throughout winter and from mid-January onward in the four snow-removal plots.

We measured snow and soil frost depth every 7–10 days from late-October to early-May during the winters of 2008/2009 through 2012/2013. The depth and duration of soil frost were integrated into the parameter "area under the curve" (AUC; Duran et al., 2014; Reinmann & Templer, 2016) measured in "cm days", which increases with greater depth and/or duration of soil frost and is used here as a metric for quantifying cumulative exposure to soil frost. Volumetric soil moisture was measured hourly at soil depths of 15 and 30 cm in each of two locations in each plot using CS616 time domain reflectometers connected to CR1000 dataloggers (Campbell Scientific, Logan, UT, USA).

2.3 | Tree growth and productivity at HBEF

We collected two 5-mm-diameter increment cores (90° apart from one another) 1.3 m above the ground from each of the two to three sugar maple trees near the center of each plot prior to leaf-out in early-May of 2015. In total, 44 cores were collected, but because of four cores with rotten wood (one tree from each of two reference plots), a total of 40 cores were analyzed (n = 8 trees from reference plots, n = 12 tree from snow-removal plots). Dried, sanded and mounted tree cores were scanned using a high-resolution color scanner (Epson Perfection V700 Photo), and ring increments were measured to 0.001 mm using WinDENDRO 2012 (Regent Instruments, Inc., Sainte-Foy, QC, Canada) image analysis software. For quality control purposes, two researchers measured each tree core. The diffuse-porous nature of sugar maple trees can make accurate determination of tree rings difficult using WinDENDRO, particularly in years when growth is suppressed. Therefore, a Velmex measurement system (Velmex, East Bloomfield, NY, USA) and Measure J2X software (v.4.2, VoorTech Consulting, Holderness, NH, USA) were used to verify ring width measurements derived from WinDENDRO for tree cores exhibiting suppressed growth or when there were discrepancies in ring placement between the two researchers reading each core. Cross-dating was done visually with the assistance of COFECHA (Holmes, 1983).

To control for tree size effects on ring widths, raw tree ring measurements were converted to basal area increment (BAI) following:

$$BAI = (R_n^2 \pi) - (R_{n-1}^2 \pi), \tag{1}$$

where R_n = the radius of the tree at the end of year n and R_{n-1} is the radius of the tree at the end of the previous year. Tree-level BAI was calculated by averaging each year's BAI across the two cores collected from each tree. Plot-level mean BAI was calculated from the chronologies of the trees cored within each plot. Rates of tree growth, defined here as woody biomass increment, were

calculated at the tree-level by converting BAI to biomass increment using allometric equations for sugar maple trees at HBEF (Whittaker, Bormann, & Likens, 1974). Tree growth indices were used to quantify tree-level changes in growth relative to mean tree growth during the 10 years prior to the start of the experiment (1999–2008). Plot-level tree growth indices were calculated by averaging the tree-level growth indices across the trees within each plot.

The effects of reduced snowpack and increased soil freezing on tree growth indices for sugar maples at the plot level (described above) were scaled up to estimate the impacts of these changes in winter climate on forest growth at HBEF using past measurements of tree growth and sugar maple relative basal area at HBEF (mean of 1991–2001; Siccama et al., 2007). We made the conservative assumption that sugar maple is the only tree species in this forest whose growth is impacted by soil freezing. For example, if in year one of the snow-removal experiment sugar maple growth in our plots declined to 85% of pre-experiment growth rates, HBEF forest growth would be calculated as the sum of (a) forest-scale sugar maple growth reported by Siccama et al. (2007) multiplied by 0.85 and (b) the forest-scale growth of the other tree species at HBEF also reported by Siccama et al. (2007).

2.4 | Statistical analyses

All statistical analyses were conducted in R version 3.0.2 (R Core Team). A linear mixed effects model (LMM; lme function; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) with plot as the random effect, to account for the lack of independence among repeated measures from each plot, was used to quantify the relationship between AUC for soil frost (described above) and sugar maple growth indices, and to detect significant increases or decreases in tree growth over time (i.e., a slope significantly different than zero). A LMM coefficient of determination for the fixed effects (i.e., marginal r^2; $R^2_{\text{LMM}(m)}$) proposed by Nakagawa and Schielzeth (2013) was used as an absolute estimator of model fit. We used analysis of covariance (ANCOVA) to examine potential differences in temporal trends in the slope of BAI between reference and snow-removal plots before (mean 1999–2008) and after the start of the experiment. Analysis of variance (ANOVA) was used to quantify differences between plot types for soil freezing, snowpack and soil water content. ANOVA was also used for our mesoscale analysis of HBEF forest growth projected from our plot-level data to quantify differences between snow-removal and reference conditions.

Assumptions of normality and constant variance were assessed by visual inspection of residuals and Shapiro–Wilk normality test and response variables were log-transformed as necessary. Unless otherwise noted, values presented are means and standard error.

2.5 | Vulnerability of forest aboveground growth to projected declines in winter snowpack

Our findings here, as well as those from previous studies, highlight sugar maple trees as being particularly sensitive to declines in winter

snowpack in regions where an insulating winter snowpack is common. As such, the extent to which forest growth in forests of the Northeastern United States will be vulnerable to future changes in winter climate will, in part, hinge upon a forest's relative abundance of sugar maple trees and declines in winter snowpack. We developed a "Forest Vulnerability to Soil Frost Index" to assess spatial patterns in the degree of vulnerability to declines in forest growth (as mediated by sugar maple trees) to projected declines in midwinter (i.e., January and February) insulating snowpack and increases in soil freezing in the Northeastern United States (Connecticut, Maine, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont). Snow depth projections for the region were obtained with the variable infiltration capacity (VIC) hydrologic model for the period 1950–2099 (Demaria et al., 2016). VIC was forced with precipitation and temperature projections from ten general circulation models (GCMs) from the World Climate Research Project (WCRP) CMIP5 (Supporting Information Table S1). The GCMs were selected for the region using a modified version of the reliability ensemble average (REA) method, which measures the skill of each individual model representing the historical climate and the convergence of future climate to the ensemble mean. The projections include a medium representative concentration pathway (RCP 4.5) and a high concentration trajectory (RCP 8.5; Knutti & Sedláček, 2013). For each GCM and each 0.125° grid cell, the likelihood of mean midwinter (i.e., January–February) snow depth equal or larger than 20 cm was computed as the number of years with midwinters that met that criteria divided by the number of years in the 1951–2005 (55 years) and 2051–2099 records (50 years). The likelihood ensemble mean was computed for the ten GCMs. A snow depth threshold of 20 cm was used because previous snowpack manipulation work suggests that snow depths greater than 20 cm are sufficient to buffer against deep soil frost formation in the northeastern United States (Hardy et al., 2001). Values for likelihood of the presence of insulating snow range between 0% (i.e., no years with insulating snowpack) and 100% (i.e., all years have an insulating snowpack). Projected changes in the likelihood of a midwinter insulating snowpack were calculated as the difference between the historical likelihood (1951–2005) and projected (2051–2099) likelihood. Further, variations in topography, snow water equivalence, species composition, and forest structure can influence snowpack and soil frost dynamics, but exploring these microscale variations was beyond the scope of these projections. Forest area throughout the region and within zones that are likely (>50% probability) to experience midwinter insulating snowpack was calculated in ArcGIS version 10.5.1 (ESRI Redlands, CA, USA) using the spatially resolved historical and projected snow depths and the forest land cover categories from the 2011 National Land Cover Database (Homer et al., 2015). Forest species composition and relative basal area and biomass of sugar maple were calculated using data from the most recently completed 5-year FIA plot-level survey (as of April 2017; data available at www.fia.fs.fed.us) for the same spatial resolution as the VIC model by average data across FIA plots within each grid cell.

The Forest Vulnerability to Soil Frost Index is a unitless value bounded by 0 and 1 calculated at a 0.125° grid cell resolution by multiplying projected changes in the proportional likelihood (i.e., values range from 0 to 1) of an insulating snowpack by sugar maple relative basal area (i.e., current proportion of total forest basal). Higher values indicate both a large decline in the likelihood of an insulating snowpack and high sugar maple relative basal area. For example, a 75% decline in the likelihood of an insulating snowpack where sugar maple comprises 50% of forest basal area results in a Vulnerability Index of 0.375 (i.e., 0.75×0.5). Statistics on forest basal area derived from live trees were calculated from FIA plot data ($n = 9{,}101$ plots; Supporting Information Figure S1) using data from the most recently completed 5-year survey as of April 2017. FIA plot-level values were aggregated to the 0.125° native grid cell resolution of our VIC model using the Fishnet tool in ArcGIS and then averaging FIA basal area data within each grid cell.

3 | RESULTS

Sugar maple DBH averaged 28.8 ± 3.9 cm in the reference plots and 32.0 ± 1.7 cm in the snow-removal plots, and these differences were not statistically significant ($p = 0.4$). Prior to the start of the snow-removal treatments (1999–2008; hereafter "pre-experiment"), sugar maple growth (BAI) declined over time in both the reference ($p = 0.03$) and snow-removal plots ($p < 0.01$), but the rates of growth decline were not significantly different between plot types ($p = 0.13$; Supporting Information Figure S2). Snow removal during the first 5 weeks of winter reduced snowpack depth and duration and exposed sugar maple trees in the treatment plots to greater depth and duration of soil freezing compared to the reference plots ($p < 0.05$; Supporting Information Table S2) without altering soil bulk density (Campbell et al., 2014) or soil water content during the growing season ($p > 0.05$ across reference and snow-removal plots; data not shown). In contrast to the pre-experiment period, the rate of sugar maple growth decline in the snow-removal plots was significantly higher than for the reference plots during the period including five treatment years plus one "recovery" year ($p < 0.01$). We find that by the second year of snow removal and exposure to soil freezing, sugar maple growth declined by 48 ± 4.2% ($p = 0.02$) relative to pre-experiment (1999–2008) means. These growth declines persisted through the following three treatment years as well as the growing season following a winter with a return to ambient snowpack conditions. Collectively, during the 6-year period encompassing the five treatment years and the postexperiment recovery year, tree growth in the treatment plots averaged 40 ± 3% below pretreatment means (Figure 1). By comparison, growth of sugar maple trees exposed to ambient winter snowpack conditions during the same 6-year period did not vary significantly from the pre-experiment period (2.7 ± 15% increase; $p = 0.16$). We observed little synchrony in interannual patterns in tree growth of the sugar maple trees in our plots (Figure 1b), but most of the trees exhibited a decline in growth following a late-spring frost event in 2010 that defoliated sugar maple trees throughout the northeastern United States (Hufkens et al., 2012). While the growth rates for seven of the eight sugar maple trees measured in our reference plots rebounded between 2011 and 2014, the growth
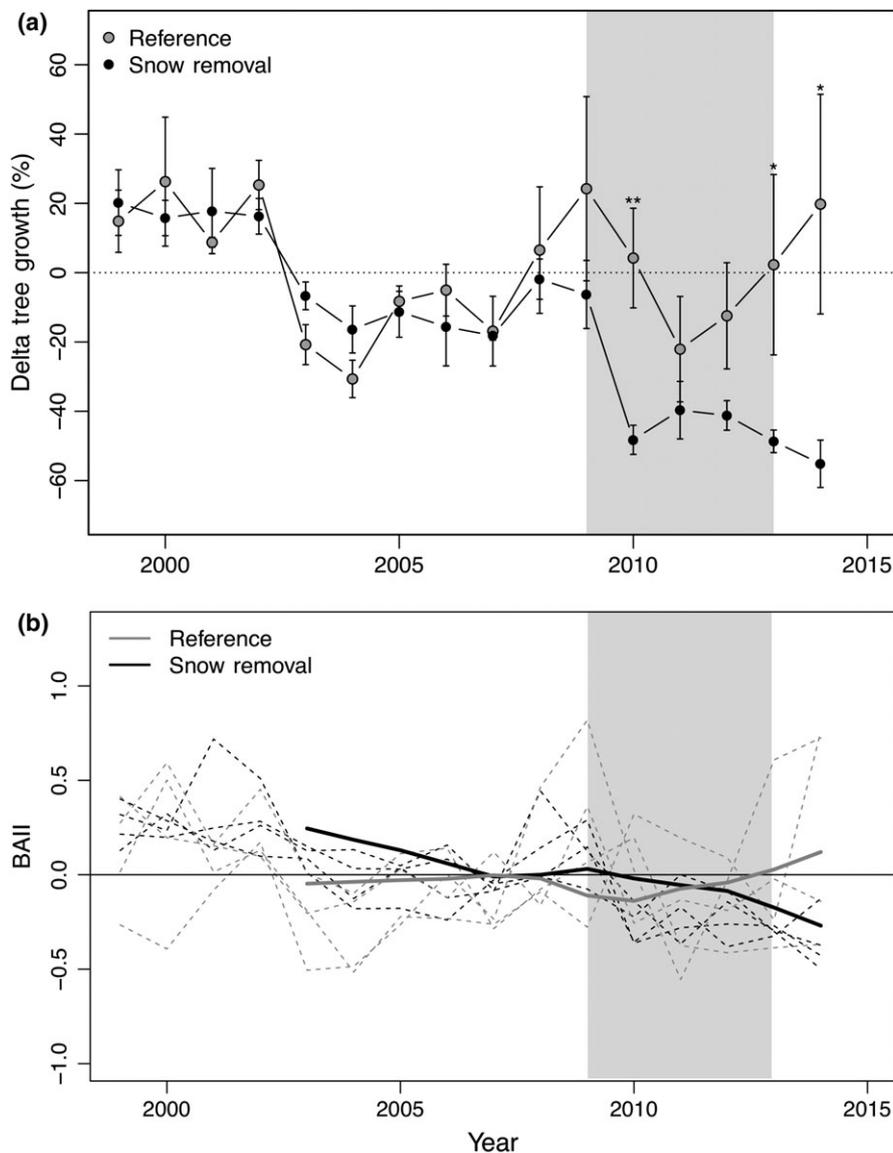
FIGURE 1 Temporal patterns in growth of sugar maple trees in reference and snow-removal plots. (a) Delta annual aboveground growth of sugar maple trees in our experimental plots, calculated as the relative difference between tree growth of reference or snow-removal plots and the 10-year mean tree growth prior to the start of the experiment (i.e., 1999–2008) for each plot type. Values are means and standard error and the comparatively small error bars in the snow-removal plots highlight the consistency of the magnitude of growth response to soil freezing across snow-removal plots within each year of study. For the period of time including the treatments years (2009–2013) and the "recovery" year (2014), delta tree growth of the snow-removal plots was significantly lower than the reference plots ($p < 0.01$). Asterisks indicate statistically significant differences between reference and snow-removal plots at $p = 0.05$ (**) and $p = 0.10$ (*) for individual years, based on ANCOVA. (b) Annual basal area increment index (BAII; i.e., BAI relative to 1999–2008 mean) for each plot (gray and black dashed lines for reference and snow-removal plots, respectively) and the 5-year running mean BAII for each plot type (solid lines). Plot-level values represent the mean BAII of the sugar maple trees in each plot. The gray shaded areas in each panel indicate the 5-year period when was removed for the first 4–5 weeks of each winter

for 10 of the 12 trees in the snow-removal plots remained suppressed (Figure 1b).

Previously reported forest composition and tree growth analyses indicate that sugar maple comprised one-third of the aboveground biomass and 55% of the woody biomass increment at HBEF between 1991 and 2001 (Siccama et al., 2007). Using these statistics and our plot-level data, we estimate that from 2009 (start of experiment) through 2014 (1 year after end of snow removal), the effects

of reduced snowpack and increased soil freezing on sugar maple growth translates to reductions in rates of aboveground forest C storage by 20 ± 6.8% (Figure 2) or 0.3 ± 0.1 Mg C ha^{-1} year^{-1} across northern hardwood forests at HBEF.

There was no rebound in tree growth in treatment plots during the recovery year, but further research is needed to determine the time scale for the recovery of tree growth and physiology to soil freezing. Indeed, we find that cumulative exposure to soil freezing
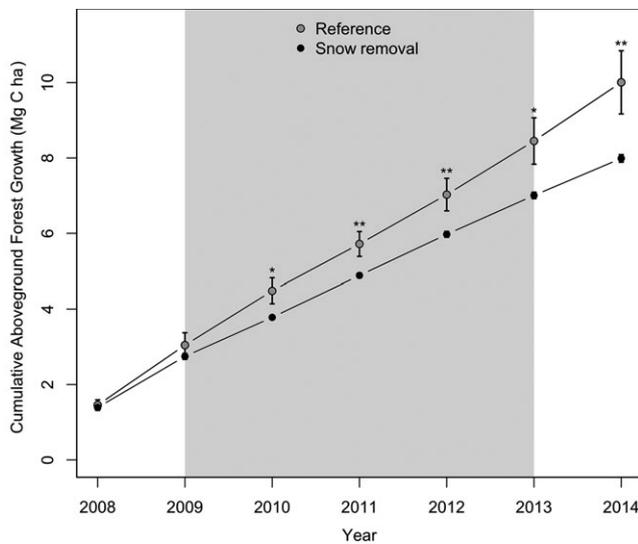
FIGURE 2 Cumulative aboveground forest growth (includes all species) scaled from plot-level sugar maple growth data in this study and tree species composition and growth data from northern hardwood forests at HBEF (from Siccama et al., 2007; see Section 2). Gray shaded area indicates the 5-year period when snow was removed for the first 4–5 weeks of each winter. Values are means and *SE*. The small error bars associated with the snow-removal plots reflect the largely consistent sugar maple growth response to reduced snow pack and increased soil freezing across plots. Asterisks indicate statistically significant differences between reference and snow-removal plots at $p = 0.05$ (**) and $p = 0.10$ (*)

FIGURE 3 Relationship between delta annual sugar maple tree growth and cumulative exposure to soil freezing (i.e., "area under the curve", AUC). Delta tree growth was calculated as the relative difference between annual tree growth and the 10-year mean tree growth prior to the start of the experiment (i.e., 1999–2008) for each tree. AUC for soil frost (described in "Section 2") is measured in "cm days" and increases with greater depth and/or duration of soil frost. Note that each experimental plot is represented by six points characterizing cumulative AUC for soil frost and delta tree growth annually between 2009 and 2014

(i.e., cumulative AUC) during previous years plays an important role in driving sugar maple growth. Examining all 20 trees in this study together to capture a wide range of soil frost conditions, we find that sugar maple growth declined exponentially with cumulative exposure to soil freezing between 2009 and 2013 ($p = 0.005$; Figure 3). This pattern suggests that cumulative exposure to soil freezing is an important driver of the response of tree growth to reductions in snowpack during the first few years, but the marginal impact of additional exposure to soil freezing declines thereafter.

The vulnerability of forest growth across the northeastern United States to future declines in snowpack depends, at least in part, on the relative of abundance of sugar maple in the region's forests, given their high sensitivity to snowpack depth and duration. Integrating historical (1950–2005) snow cover data collected here with 2011 National Land Cover Database data (Homer et al., 2015) indicate that 8.6 million ha out of 17.9 million ha of total forestland in the seven states comprising the northeastern United States typically (i.e., >50% of years) experience an insulating snowpack of at least 20 cm deep during midwinter (January and February; Figure 4). Our analysis of FIA tree species composition and basal area data indicates that nearly 65% of the sugar maple basal area in the northeastern United States resides in areas that typically experience insulating snowpack. The VIC model we used to estimate future snow depth under the RCP 4.5 and 8.5 emissions scenarios suggests that the northeastern United States will experience a 49% to 94% reduction in the forest area and up to a 96% reduction in sugar maple basal area that will
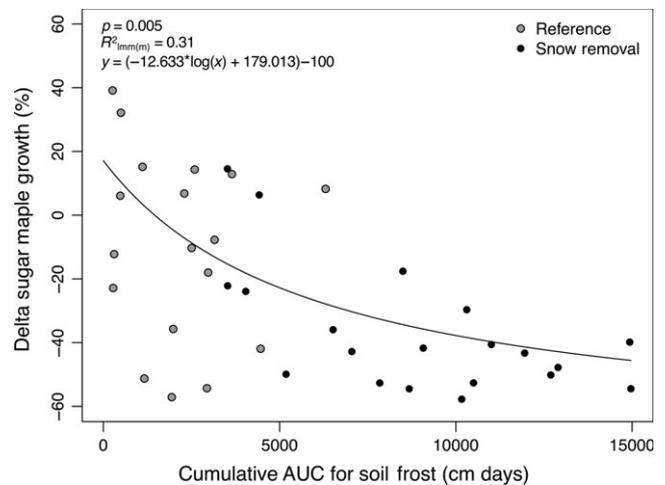
typically experience an insulating snowpack by the year 2099 (Figure 4b–e; Supporting Information Figure S3).

As a visual tool for assessing the spatial patterns in the magnitude of risk of forest growth in response to a shrinking snowpack in the northeastern United States, we integrated our projected changes in the likelihood of insulating snowpack with the current relative basal area of sugar maple (i.e., proportion of total forest basal area; Figure 4d). The combination of high sugar maple basal area and large projected declines in snowpack depth makes forest growth in the deciduous forests of the northeastern United States along the Canadian border particularly vulnerable to the negative effects of a reduced snowpack (Figure 4e). For example, the mean Forest Vulnerability to Soil Frost Index for a northern state such as Vermont, which is 76% forested, is 0.15, which is nearly four times higher than the northeastern United States as a whole (average Vulnerability Index for the entire northeastern United States equal to 0.04).

4 | DISCUSSION

In seasonally snow-covered ecosystems, winter climate plays an important role in mediating a range of ecological processes during the growing season (Campbell et al., 2005), yet these dynamics are often overlooked when considering the future impacts of climate change on ecosystem function. To simulate the effects of projected changes in winter snowpack on forest growth in the northeastern United States during the growing season we reduced early-winter snowpack depth, which significantly increased the depth and duration of soil freezing during each of five consecutive treatment years.
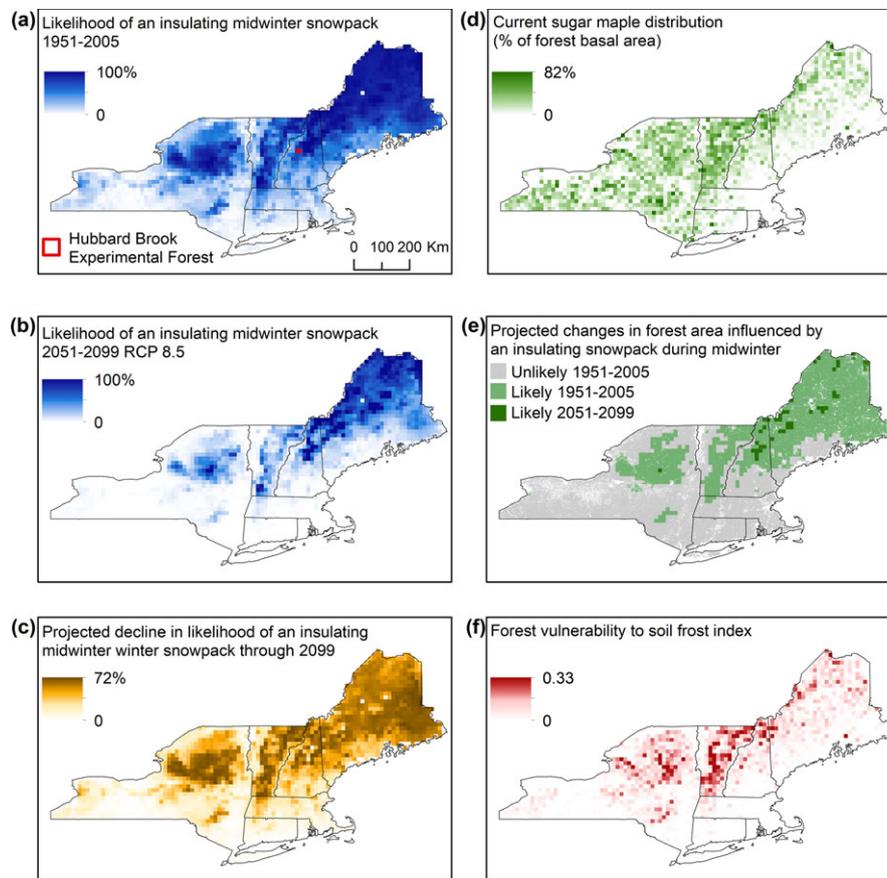
FIGURE 4 Spatial patterns in the vulnerability of forest growth to changes in winter climate as a function of projected declines in insulating winter snowpack and the current relative basal area of sugar maple trees. Mean historical (1951–2005) (a) and projected (2051–2099 under RCP 8.5) (b) likelihood of an insulating snowpack (>20 cm deep) being present during midwinter (January and February). (c) Projected decline in likelihood of an insulating snowpack during midwinter between the historical (1951–2005) and projected time periods (2051–2099). (d) Current sugar maple contribution to total forest basal area (from FIA data). (e) Historic and RCP 8.5 projected changes in the area of forest influenced by an insulating midwinter snowpack. Data from the 2011 National Land Cover Database (NLCD) were used to determine forest area. Changes in forest area influenced by an insulating snowpack were calculated using a combination of the spatially explicit NLCD forest cover data and the snowpack data used for panels "a" and "c" derived from the VIC model described in the methods. "Unlikely" indicates that the probability of an insulating snowpack in any year is <50%, while "Likely" indicates the probability in any year is >50%. (f) Forest aboveground growth vulnerability to projected declines in midwinter snowpack and increases in soil freezing during 2051–2099 relative to the period 1951–2005. The Forest Vulnerability to Soil Frost Index is a unitless value that increases with forest vulnerability (i.e., potential for reduced forest productivity) and is calculated by multiplying the values in panels C and E (see Section 2 for details). We highlight RCP 8.5 projections here because it is currently the most likely scenario (Sanford, Frumhoff, Luers, & Gulledge, 2014); see Supporting Information Figure S3 for RCP 4.5 projections [Colour figure can be viewed at wileyonlinelibrary.com]

Previously published data from the sugar maple trees in this experiment indicate that these changes in winter climate reduce tree root vitality by 37% (as determined by relative electrolyte leakage; Comerford et al., 2013) and shoot elongation by 46% (similar to the delta tree growth observed here; Comerford et al., 2013), while resulting in a net efflux of ammonium from roots during the early-growing season (Campbell et al., 2014); similar impacts have also been observed in other northern forest ecosystems (e.g., Cleavitt et al., 2008; Gaul, Hertel, & Leuschner, 2008; Tierney et al., 2001). Here, we show that large declines in sugar maple tree growth and northern hardwood forest C sequestration co-occur with these adverse impacts of reduced snowpack and increased soil freezing on tree physiology. Further, we find that tree growth declines

exponentially with cumulative exposure to soil freezing and that tree growth in the treatment plots did not rebound 1 year following cessation of our 5-year manipulation. However, the amount of time necessary for tree growth to rebound from this external stressor remains uncertain.

To the extent that the response of sugar maple trees to a loss of an insulating snowpack in this experiment is representative of the sugar maple population across the northeastern United States, our findings suggest that in the absence of compensatory growth response from acclimation and/or longer and warmer growing seasons (see Discussion below), such changes in winter climate will reduce sugar maple tree growth by up to 40%. Assuming sugar maple contribution to forest productivity is proportional to its

relative biomass (i.e., 22%; derived from data compiled for Figure 4), we anticipate these declines in sugar maple growth to reduce rates of forest C sequestration by 8.8 ± 0.3% across the 3.3 million ha of deciduous forest in the northeastern United States that historically experience insulating snowpack. Further, because soil microbial biomass and rates of soil C mineralization and heterotrophic soil respiration in northern hardwood forests do not appear to be altered by reductions in snowpack and increases in soil freezing (Sorensen, Templer, & Finzi, 2016; Steinweg, Fisk, McAlexander, Groffman, & Hardy, 2008), the response of C sequestration in this forest type to these changes in winter climate will likely be mediated by changes in tree growth. By contrast, Reinmann and Templer (2016) found that reduced winter snowpack and increased soil freezing has either no effect or a small stimulatory effect on tree growth in a red oak (*Quercus rubra*)-red maple (*A. rubrum*) forest in Massachusetts, U.S.A.; however, that study was conducted in a region that does not typically experience a persistent insulating snowpack and the study involved only 1 year of reduced snowpack and increased soil freezing (we did not observe a significant decline in tree growth until after the second year of snow removal in this current study). Additionally, findings from a sapling experiment indicate that roots of sugar maple trees are more sensitive to soil freezing than those of red maple trees (Sanders-DeMott, McNellis, Jabouri, & Templer, 2018). The different findings between these studies could also point to distinct acclimation responses of trees to soil freezing based on the typical snow and soil freezing environments where they grow. It is possible that trees shift root biomass to deeper soil to avoid soil freezing; however, intraspecific adaptive responses of trees to cope with soil freezing is poorly understood.

The decreased growth response of sugar maple trees to reduced insulating snowpack could be transient in nature. While variations in sugar maple rooting behavior and morphology across gradients in soil freezing is unknown, sugar maple trees exhibit different physiological characteristics such as photosynthetic capacity and specific leaf area along climate gradients (Ledig & Korbobo, 1983), which likely contributes to the species' ability to be competitive across a broad geographic area. However, the extent to which genotypes currently growing in regions with an insulating snowpack have the plasticity to acclimate to increased soil freezing and temper the duration of the growth response observed here remains to be seen; we found no indication of acclimation of sugar maple trees from the 6 years of growth data that we analyzed following the start of our experiment.

To our knowledge, little is known about the extent to which southern and northern populations of sugar maple trees have different capacities to cope with or acclimate to soil freezing. While understanding these dynamics was beyond the scope of our work, such insights would make important contributions to our understanding of ecosystem response to climate change in seasonally snow-covered regions. In addition to changes in snowpack and soil freezing conditions, climate change is projected to result in longer and warmer growing seasons. While a longer and warmer growing season will likely stimulate tree growth in the north temperate region (Melillo et al., 2011), experiments exploring the interactive

effects of these changes in climate across seasons (i.e., increased winter soil freezing coupled with a longer, warmer growing season) have only recently been implemented (Sanders-DeMott, Sorensen, Reinmann, & Templer, 2018; Templer et al., 2017) and there are currently no published data on tree growth response.

Soil freezing in sugar maple stands at HBEF has been estimated to increase fine root mortality by 0.3 Mg C/ha (Tierney et al., 2001), which is comparable in magnitude to what we find for reductions in tree growth. While we did not explicitly quantify rates of root turnover in our experiment, Comerford et al. (2013) found root electrolyte leakage in our snow-removal plots to be 37% higher than in our reference plots, indicating elevated rates of root damage. These findings may suggest a shift in tree C allocation away from long-lived C pools in aboveground woody biomass and toward short-lived pools belowground to regrow fine roots, which is consistent with studies showing increases in compensatory root growth following soil freezing (Sorensen, Templer, Christenson et al., 2016; Tierney et al., 2001). Increased root damage and mortality are commonly observed responses to soil freezing, and our findings of reduced tree growth and forest C uptake may therefore extend to other systems where root damage is observed, such as Norway spruce (*Picea abies* (L.) H. Karst) forests in Germany (Gaul et al., 2008).

We find that locations within the northeastern United States that are expected to experience the largest declines in winter snowpack by the end of the 21st century also have some of the highest sugar maple relative basal area in the region. In particular, our Vulnerability Index suggests that growth and C sequestration in the deciduous forests along the U.S.–Canada border might be most adversely impacted by projected changes in winter climate. Our estimate of the importance of projected declines in winter snowpack depth as a driver of forest growth response to climate change is likely conservative because we only consider the response of sugar maple and not other tree species such as yellow birch (*Betula alleghaniensis* Britton), which has also been shown to incur root damage in response to soil freezing (Tierney et al., 2001). The collective growth response of communities of tree species to changes in winter climate (e.g., is one species' misfortune another species' opportunity?) remains uncertain. Certainly, projected warming and lengthening of the growing season could ameliorate some of the adverse impacts of reduced snowpack and increased soil freezing and these changes in winter climate will likely interact with changes in growing season climate to influence tree growth and forest NPP (Sanders-DeMott & Templer, 2017; Templer et al., 2017). Soil characteristics and nutrient availability play an important role in mediating sugar maple growth response to environmental stressors such as acid rain (Long, Horsley, Hallett, & Bailey, 2009), and spatial variation in soil characteristics might also mediate sugar maple growth response to soil freezing, but these relationships have yet to be evaluated. Here, we intentionally focus on projected changes in winter snowpack and soil frost conditions because the importance of these changes in climate as a mediator of tree growth and C sequestration response to climate change has been largely overlooked.

Findings from this study in conjunction with previously reported findings from this experiment provide evidence that reduced rates of

tree growth occurs in parallel with impaired root vitality and reductions in shoot elongation, foliar Ca:Al ratios, and N uptake rates following reductions in winter snowpack and increased depth and duration of soil freezing (Campbell et al., 2014; Comerford et al., 2013). Taken together, these findings indicate that by damaging tree roots, changes in winter climate that increase soil frost severity initiate a cascade of physiological responses that result in overall declines in rates of aboveground tree growth and woody biomass C storage by northern forest ecosystems. For context, the magnitude of declines in sugar maple growth that we present here are comparable to those observed in response to a multiyear tent caterpillar (*Malacosoma disstria)* defoliation (Gross, 1991), but more than twice as large as declines observed in acid rain-affected forests of Canada (Duchesne, Ouimet, & Houle, 2002). Further, the large reductions in sugar maple growth in response to reduced snowpack and increased soil freezing shown here could offset more than half of the greater than 34% projected increase in woody biomass increment (derived from PnET-BGC model runs) for HBEF and similar forests in response to the combination of CO_2 fertilization and longer growing seasons (Campbell et al., 2009).

Sugar maple trees play an important role in mediating ecosystem C and N cycling and in the forestry, maple products, and tourism industries. However, declines in sugar maple growth have been observed throughout a large portion of the northern hardwood forest in recent decades (Bishop et al., 2015). Our findings demonstrate that by reducing multiyear tree growth by 40% (average decline over the 5 years of the experiment plus one "recovery" year), changes in winter climate that increase the occurrence of severe soil frost are likely to substantially accelerate the decline of this economically important and ecologically dominant species and reduce the strength of the forest C sink throughout much of the northeastern United States. Our regional extrapolations are derived from a relatively small dataset from one particular region of the northeastern United States, but provide an important starting point for understanding regional implications of projected declines in winter snowpack. We suggest that by not considering the response of tree growth to projected changes in winter climate in seasonally snow-covered forest ecosystems, current approaches characterizing the response of forest ecosystems to climate change likely overestimate forest growth and C sequestration in these ecosystems.

AUTHOR CONTRIBUTIONS

P.H.T. conceived of the experimental design. Both A.B.R. and P.H.T. conceived of the project, collected and analyzed data, and wrote the manuscript. J.R.S. collected and analyzed data and contributed to the writing of this manuscript. E.M.C.D. analyzed data and contributed to the writing of this manuscript.

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REFERENCES

Bailey, A. S., Hornbeck, J. W., Campbell, J. L., & Eagar, C. (2003). Hydrometeorological Database for Hubbard Brook Experimental Forest : 1955 – 2000. General Technical Report NE-305. 40 pp.

Bishop, D. A., Beier, C. M., Pederson, N., Lawrence, G. B., Stella, J. C., & Sullivan, T. J. (2015). Regional growth decline of sugar maple (Acer saccharum) and its potential causes. *Ecosphere*, *6*(10), art179. https://doi.org/10.1890/es15-00260.1

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), art1. https://doi.org/10.1890/es11-00225.1

Brown, P. J., & DeGaetano, A. T. (2011). A paradox of cooling winter soil surface temperatures in a warming northeastern United States. *Agricultural and Forest Meteorology*, *151*(7), 947–956. https://doi.org/10.1016/j.agrformet.2011.02.014

Campbell, J. L., Mitchell, M. J., Groffman, P. M., Christenson, L. M., & Hardy, J. P. (2005). Winter in northeastern North America: A critical period for ecological processes. *Frontiers in Ecology and the Environment*, *3*(6), 314–322. https://doi.org/10.1890/1540-9295(2005)003[0314:WINNAA]2.0.CO;2

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. *Hydrological Processes*, 2465–2480. https://doi.org/10.1002/hyp.7666

Campbell, J. L., Rustad, L. E., Boyer, E. W., Christopher, S. F., Driscoll, C. T., Fernandez, I. J., … Ollinger, S. V. (2009). Consequences of climate change for biogeochemical cycling in forests of northeastern North America. This article is one of a selection of papers from NE Forests 2100: A Synthesis of Climate Change Impacts on Forests of the Northeastern US and Eastern Canada. *Canadian Journal of Forest Research*, *39*(2), 264–284. https://doi.org/10.1139/X08-104

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. *Global Change Biology*, *20*(8), 2663–2673. https://doi.org/10.1111/gcb.12532

Cleavitt, N. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Henry, K. S., & Driscoll, C. T. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research*, 38(1), 82–91. https://doi.org/10.1139/X07-133

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(1), 261–269. https://doi.org/10.1007/s00442-012-2393-x

Demaria, E. M., Roundy, J. K., Wi, S., & Palmer, R. (2016). The effects of climate change on seasonal snowpack and the hydrology of the Northeastern and Upper Midwest United States. *Journal of Climate*, 29, 6527–6541. https://doi.org/10.1175/JCLI-D-15-0632.1

Drescher, M., & Thomas, S. C. (2013). Snow cover manipulations alter survival of early life stages of cold-temperate tree species. *Oikos*, 122 (4), 541–554. https://doi.org/10.1111/j.1600-0706.2012.20642.x

Duchesne, L., Ouimet, R., & Houle, D. (2002). Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. *Journal of Environmental Quality*, 31(5), 1676–1683. https://doi.org/10.2134/jeq2002.1676

Duran, J., Morse, J. L., Groffman, P. M., Campbell, J. L., Christenson, L. M., Driscoll, C. T., … Templer, P. H. (2014). Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. *Global Change Biology*, 20(11), 3568–3577. https://doi.org/10.1111/gcb.12624

Estilow, T. W., Young, A. H., & Robinson, D. A. (2015). A long-term Northern Hemisphere snow cover extent data record for climate studies and monitoring. *Earth System Science Data*, 7(1), 137–142. https://doi.org/10.5194/essd-7-137-2015

Frey, W. (1983). The influence of snow on growth and survival of planted trees. *Arctic and Alpine Research*, 15(2), 241–251. https://doi.org/10.2307/1550925

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., … Zeng, N. (2006). Climate-carbon cycle feedback analysis: Results from the C 4 MIP model intercomparison. *Journal of Climate*, 19(14), 3337–3353. https://doi.org/10.1175/JCLI3800.1

Gaul, D., Hertel, D., & Leuschner, C. (2008). Effects of experimental soil frost on the fine-root system of mature Norway spruce. *Journal of Plant Nutrition and Soil Science*, 171(5), 690–698. https://doi.org/10.1002/jpln.200700284

Goodale, C. L., Apps, M. J., Birdsey, R. A., Field, C. B., Heath, L. S., Houghton, R. A., … Shvidenko, A. (2002). Forest carbon sinks in the northern hemisphere. *Ecological Applications*, 12(3), 891–899. https://doi.org/10.1890/1051-0761(2002)012[0891:FCSITN]2.0.CO;2

Gross, H. L. (1991). Dieback and growth loss of sugar maple associated with defoliation by the forest tent caterpillar. *The Forestry Chronicle*, 67(1), 33–42. https://doi.org/10.5558/tfc67033-1

Hardy, J. P., Groffman, P. M., Fitzhugh, R. D., Henry, K. S., Welman, A. T., Demers, J. D., … Nolan, S. (2001). Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry*, 56, 151–174. https://doi.org/10.1023/A:1013036803050

Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451(7176), 289–292. https://doi.org/10.1038/nature06591

Henry, H. A. L. (2008). Climate change and soil freezing dynamics: Historical trends and projected changes. *Climatic Change*, 87(3–4), 421–434. https://doi.org/10.1007/s10584-007-9322-8

Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69–78.

Homer, C. G., Dewitz, J. A., Yang, L., Jin, S., Danielson, P., Xian, G., … Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, 81(5), 345–354. https://doi.org/10.14358/PERS.81.5.345

Hufkens, K., Friedl, M. A., Keenan, T. F., Sonnentag, O., Bailey, A., O'Keefe, J., & Richardson, A. D. (2012). Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology*, 18(7), 2365–2377. https://doi.org/10.1111/j.1365-2486.2012.02712.x

Knutti, R., & Sedláček, J. (2013). Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, 3(4), 369–373. https://doi.org/10.1038/nclimate1716

Ledig, F. T., & Korbobo, D. R. (1983). Adaption of sugar maple populations along altitudinal agradients: Photosynthesis, respiration, and specific leaf weight. *American Journal of Botany*, 70(2), 256–265. https://doi.org/10.1002/j.1537-2197.1983.tb07866.x

Long, R. P., Horsley, S. B., Hallett, R. A., & Bailey, S. W. (2009). Sugar maple growth in relation to nutrition and stress in the northeastern United States. *Ecological Applications*, 19(6), 1454–1466. https://doi.org/10.1890/08-1535.1

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. *Ecological Research*, 29(4), 593–606. https://doi.org/10.1007/s11284-013-1115-0

Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., … Tang, J. (2011). Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, 108(23), 9508–9512. https://doi.org/10.1073/pnas.1018189108

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

North East State Foresters Association. (2013). The Economic Importance of New York's Forest-Based Economy. 20 pp.

Notaro, M., Lorenz, D., Hoving, C., & Schummer, M. (2014). Twenty-first-century projections of snowfall and winter severity across central-eastern North America. *Journal of Climate*, 27(17), 6526–6550. https://doi.org/10.1175/JCLI-D-13-00520.1

Pinheiro, J., Bates, D., DebRoy, S., Sarker, D., & R Core Team. (2017). nlme: Linear and nonlinear mixed effects models. Retrieved from http://CRAN.R-project. org/package=nlme. (Accessed 1 September 2017).

Reinmann, A. B., & Templer, P. H. (2016). Reduced winter snowpack and greater soil frost reduce live root biomass and stimulate radial growth and stem respiration of red maple (*Acer rubrum*) trees in a mixed-hardwood forest. *Ecosystems*, 19(1), 129–141. https://doi.org/10.1007/s10021-015-9923-4

Sanders-DeMott, R., McNellis, R., Jabouri, M., & Templer, P. H. (2018). Snow depth, soil temperature and plant-herbivore interactions mediate plant response to climate change. *Journal of Ecology*, 106, 1508–1519. https://doi.org/10.1111/1365-2745.12912

Sanders-DeMott, R., Sorensen, P. O., Reinmann, A. B., & Templer, P. H. (2018). 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. https://doi.org/10.1007/s10533-018-0422-5

Sanders-DeMott, R., & Templer, P. H. (2017). What about winter? Integrating the missing season into climate change experiments in seasonally snow covered ecosystems. *Methods in Ecology and Evolution*, 8, 1183–1191. https://doi.org/10.1111/2041-210X.12780

Sanford, T., Frumhoff, P. C., Luers, A., & Gulledge, J. (2014). The climate policy narrative for a dangerously warming world. *Nature Climate Change*, 4(3), 164–166. https://doi.org/10.1038/nclimate2148

Siccama, T. G., Fahey, T. J., Johnson, C. E., Sherry, T. W., Denny, E. G., Girdler, E. B., … Schwarz, P. A. (2007). Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook. *Canadian Journal of Forest Research*, 37, 737–749. https://doi.org/10.1139/X06-261

Sorensen, P. O., Templer, P. H., Christenson, L., Duran, J., Fahey, T., Fisk, M. C., … Finzi, A. C. (2016). Reduced snow cover alters root-microbe interactions and decreases nitrification rates in a northern hardwood forest. *Ecology*, *97*(12), 3359–3367. https://doi.org/10.1002/ecy.1599

Sorensen, P. O., Templer, P. H., & Finzi, A. C. (2016). Contrasting effects of winter snowpack and soil frost on growing season microbial biomass and enzyme activity in two mixed-hardwood forests. *Biogeochemistry*, *128*(1–2), 141–154. https://doi.org/10.1007/s10533-016-0199-3

Steinweg, J. M., Fisk, M. C., McAlexander, B., Groffman, P. M., & Hardy, J. P. (2008). Experimental snowpack reduction alters organic matter and net N mineralization potential of soil macroaggregates in a northern hardwood forest. *Biology and Fertility of Soils*, *45*(1), 1–10. https://doi.org/10.1007/s00374-008-0305-3

Templer, P. H., Reinmann, A. B., Sanders-Demott, R., Sorensen, P. O., Juice, S. M., Bowles, F., … Grant, N. (2017). Climate Change Across Seasons Experiment (CCASE): A New method for simulating future Climate in seasonally snow-covered ecosystems. *PLoS ONE*, *12*(2), e0171928. https://doi.org/10.1371/journal.pone.0171928

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. *Biology and Fertility of Soils*, *48*(4), 413–424. https://doi.org/10.1007/s00374-011-0636-3

Tierney, G. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Fitzhugh, R. D., Driscoll, C. T., & Yavitt, J. B. (2003). Environmental control of fine root dynamics in a northern hardwood forest. *Global Change Biology*, *9*(5), 670–679. https://doi.org/10.1046/j.1365-2486.2003.00622.x

Tierney, G. L., Fahey, T. J., Peter, 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. https://doi.org/10.1023/A:1013072519889

Van Deusen, P., & Heath, L. S. (2017). COLE web application suite. NCASI and USDA Forest Service, Northern Research Station. Retrieved from http://www.ncasi2.org/COLE/ (Accessed 15 January 2017).

Whittaker, R. H., Bormann, F. H., & Likens, G. E. (1974). The Hubbard Brook ecosystem study: Forest biomass and production. *Ecological Monographs*, *44*(2), 233–254. https://doi.org/10.2307/1942313

Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., & Wan, S. (2014). Terrestrial carbon cycle affected by non-uniform climate warming. *Nature Geoscience*, *7*(3), 173–180. https://doi.org/10.1038/ngeo2093

Zhang, T., Heginbottom, J. A., Barry, R., & Brown,, J. (2003). Distribution of seasonally and perennially frozen ground in the Northern Hemisphere. In M. Phillips, S. M. Springman, & L. U. Arenson (Eds.), *Proceedings of the 8th international conference on permafrost, 21–25 July 2003*, Zurich, Switzerland (pp. 1284–1289).

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