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Long-term deepened snow promotes tundra evergreen shrub growth and summertime ecosystem net CO_2 gain but reduces soil carbon and nutrient pools

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Abstract

Arctic climate warming will be primarily during winter, resulting in increased snowfall in many regions. Previous tundra research on the impacts of deepened snow has generally been of short duration. Here, we report relatively long-term (7–9 years) effects of experimentally deepened snow on plant community structure, net ecosystem CO_2 exchange (NEE), and soil biogeochemistry in Canadian Low Arctic mesic shrub tundra. The snowfence treatment enhanced snow depth from 0.3 to ~1 m, increasing winter soil temperatures by ~3°C, but with no effect on summer soil temperature, moisture, or thaw depth. Nevertheless, shoot biomass of the evergreen shrub *Rhododendron subarcticum* was near-doubled by the snowfences, leading to a 52% increase in aboveground vascular plant biomass. Additionally, summertime NEE rates, measured in collars containing similar plant biomass across treatments, were consistently reduced ~30% in the snowfenced plots due to decreased ecosystem respiration rather than increased gross photosynthesis. Phosphate in the organic soil layer (0–10 cm depth) and nitrate in the mineral soil layer (15–25 cm depth) were substantially reduced within the snowfences (47–70 and 43%–73% reductions, respectively, across sampling times). Finally, the snowfences tended ($p = .08$) to reduce mineral soil layer C% by 40%, but with considerable within- and among plot variation due to cryoturbation across the landscape. These results indicate that enhanced snow accumulation is likely to further increase dominance of *R. subarcticum* in its favored locations, and reduce summertime respiration and soil biogeochemical pools. Since evergreens are relatively slow growing and of low stature, their increased dominance may constrain vegetation-related feedbacks to climate change. We found no evidence that deepened snow promoted deciduous shrub growth in mesic tundra, and conclude that the relatively strong *R. subarcticum* response to snow accumulation may explain the extensive spatial variability in observed circumpolar patterns of evergreen and deciduous shrub growth over the past 30 years.

KEYWORDS
Arctic, carbon cycling, climate change, deciduous shrub, snowfence, soil microbes, vegetation changes, winter

1 | INTRODUCTION

Arctic regions warmed far more in autumn and winter than during the growing season over the past three decades (Hartmann et al., 2013; Screen & Simmonds, 2010; Serreze, Barrett, Stroeve, Kindig, & Holland, 2009). As a result, many circumpolar areas received more snowfall (Callaghan et al., 2011; Hartmann et al., 2013). Climate models project that this differential seasonal warming amplification continues throughout the rest of the century, with the extent of winter warming being at least four times greater than in summer (Bintanja & Van Der Linden, 2013), and with associated increases in peak-regional snowfall of more than 50% (Bintanja & Selten, 2014; Collins et al., 2013).

Permafrost-affected ecosystems are an important component of the global carbon (C) cycle as they contain a vast pool of old, thermally protected, soil organic matter (SOM) (Hugelius et al., 2014; Tarnocai et al., 2009). Warmer soils enhance microbial breakdown of SOM, and lead to increased emissions of greenhouse gases (e.g., CO_2, CH_4, and N_2O), as observed in many experimental open-top chamber (OTC) summer warming field studies across a range of pan-Arctic ecosystems (Dorrepaal et al., 2009; Natali, Schuur, Webb, Pries, & Crummer, 2014; Oberbauer et al., 2007; Voigt et al., 2016). These observations strongly suggest that the fate of tundra soil C will be a critical component of global climate change feedbacks associated with a warming climate (Chapin et al., 2000; Davidson & Janssens, 2006; Mcguire et al., 2009; Schuur et al., 2008, 2015).

Tundra ecosystem respiration rates are inherently much lower in winter than in summer. Nevertheless, soil microbes remain active down to at least −10°C (Elberling & Brandt, 2003; Mikan, Schimel, & Doyle, 2002), and because the full cold season (i.e., autumn + winter + early spring snowmelt period) lasts 4–5 times longer than the growing season, substantial cumulative CO_2 and CH_4 releases occur over the full cold season (Belshe, Schuur, & Bolker, 2013; Björkman et al., 2010; Oechel et al., 2000; Webb et al., 2016; Zona et al., 2016). Multiple snowfence studies have demonstrated that wintertime microbial breakdown of SOM is enhanced due to the greater thermal insulation provided by deeper snow, resulting in increased greenhouse gas emissions to the atmosphere and release of nutrients into the soil (Larsen, Grogan, Jonasson, & Michelsen, 2007; Natali et al., 2011, 2014; Nobrega & Grogan, 2007; Schimel, Bilbrough, & Welker, 2004; Semenchuk, Christiansen, Grogan, Elberling, & Cooper, 2016; Semenchuk et al., 2015; Webb et al., 2016).

Enhanced nutrient supply into soil microbes and the soil solution during the cold season may in-turn alleviate nutrient limitations on tundra plant growth during the growing season, thereby promoting C uptake from the atmosphere and increasing ecosystem C storage both aboveground (stems and leaves) and belowground (roots) (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Demarco, Mack, Bret-Harte, Burton, & Shaver, 2014; Elmendorf et al., 2012a; Iversen et al., 2015; Zamin, Bret-Harte, & Grogan, 2014). For example, warm winter periods during the 20th century correlate with enhanced shrub secondary growth (Hollesen et al., 2015), suggesting that winter climate could indeed be an important driver of deciduous shrub growth. Furthermore, deciduous shrubs can modify their local winter soil microclimate by trapping windblown snow, thereby enhancing snow depth and consequently soil organic matter decomposition and nutrient mobilization that is hypothesized to further promote shrub expansion (Sturm et al., 2005).

However, while warmer soils as a result of deepened snow may significantly affect soil microbes within days to weeks, it may take years to decades before significant changes in tundra plant cover become apparent (Shaver et al., 2000). Thus, depending on the timescale investigated, initial short-term conclusions of a changing winter climate on soil C respiratory losses may ultimately have to be modified due to enhanced growing season plant C uptake, and changing vegetation community structure (Elmendorf et al., 2012b), leading to net gains in ecosystem C storage in the longer term. How tundra plant communities respond to a changing winter climate will therefore be a key factor mediating the magnitude and direction by which tundra ecosystems act as net sinks or sources of atmospheric C in the future. Current estimates suggest that Arctic tundra is a CO_2 source on an annual basis, as winter emissions generally have exceeded summertime gains since the 1980s (Belshe et al., 2013). However, despite a growing consensus on the importance of winter processes on ecosystem function, considerable uncertainty is associated with these winter fluxes as most tundra ecosystem climate change research has focused on effects of summer warming on net carbon balance (decomposition and plant production). By contrast, Arctic winter climate change studies—especially those on the effects of deepened snow—are relatively rare and mostly short-term, leaving an urgent longer-term knowledge gap still to be filled (Brooks et al., 2011).

Snowfences are the most commonly used methodology to mimic winter climate change as they passively enhance snow depth, resulting in greater soil thermal insulation from severely cold air temperatures. Previous snowfence studies have generally found species-specific effects on plant growth and cover, without clear plant functional type response patterns within and across Arctic and alpine tundra sites (Natali et al., 2014; Rumpf, Semenchuk, Dullinger, & Cooper, 2014; Wipf & Rixen, 2010). Despite the proposed importance of winter climate on deciduous shrub growth (Sturm et al., 2005), very few snowfence studies have reported increased deciduous shrub growth (Wahren, Walker, & Bret-Harte, 2005), whereas several others have observed no effect (Natali et al., 2014; Zamin & Grogan, 2012). These different responses to deepened snow appear to be determined by the initial plant community structure, with deciduous shrubs responding most in moist sites where they are relatively abundant, and species of evergreens or sedges dominating growth responses in dry heath and mesic tundra vegetation types where deciduous shrubs are less common (Natali et al., 2014; Wahren et al., 2005). However, short-term functional type responses have been shown to change over a few years (Natali, Schuur, & Rubin, 2012; Natali et al., 2014), emphasizing the need for longer-term snowfence studies as critical to understand future plant responses to winter climate change.

Longer-term summer warming studies suggest that initial warming-induced increases in CO_2 release rates are not maintained and, ultimately, that similar or even reduced CO_2 efflux rates, compared to ambient conditions, occur after a couple of years (Melillo et al., 2002; Oechel et al., 2000; Rustad et al., 2001). Modeling (Eliasson et al., 2005; Kirschbaum, 2004; Knorr, Frey, & Curtis, 2005) and lab incubation studies (Craine, Fierer, Mclauchlan, & Elmore, 2013) suggest that depletion of easily decomposable SOM and/or reduced microbial C-use efficiency could be driving the observed declines in CO_2 efflux from warming treatments (Allison, Wallenstein, & Bradford, 2010; Bradford et al., 2008; Hartley & Ineson, 2008; Rousk, Frey, & Baath, 2012). This potential discrepancy between short- and longer-term impacts of climate change on soil C cycling is clearly important because climate change impacts on ecosystems need to be understood over a time course of at least decades to centuries. Yet, effects of longer term increased snowfall on tundra ecosystem C cycling remain largely unknown.

Similar to other snowfence studies (Morgner, Elberling, Strebel, & Cooper, 2010; Natali et al., 2011), experimentally deepened snow generally enhances cold season ecosystem respiration rates at the site used in the present study (Nobrega & Grogan, 2007) although inter-annual variation has been reported and attributed to particular fall climate conditions (Grogan, 2012). Trace gas release after snowmelt in early spring was not affected by the deepened snow treatment after 2 years (Buckeridge, Cen, Layzell, & Grogan, 2010). However, more recently, we observed that growing season ecosystem respiration rates were consistently and significantly reduced in our snowfence plots after 8–9 years of winter climate manipulation (Christiansen, 2016), suggesting that the initial ecosystem impact of deepened snow had changed, creating legacy effects in the process.

In this study, we investigated relatively long-term (7–9 years) impacts of experimentally deepened snow on growing season net ecosystem CO_2 exchange, aboveground plant cover and biomass pools, as well as organic (0–10 cm) and mineral (15–25 cm) soil layer carbon and nutrient pools in a mesic birch hummock tundra vegetation type that is widespread across the Arctic (Walker et al., 2005). Overall, our research objectives were to identify potential legacy effects of a changing winter climate on summertime ecosystem function by quantifying vegetation change, CO_2 fluxes, and changes in plant and soil carbon and nutrient pools. We structured this by investigating the following research questions:

- Does long-term deepened snow alter plant community structure in mesic birch hummock vegetation?
- Does the previously observed decrease in summertime ecosystem respiration, due to long-term deepened snow, significantly affect net ecosystem CO_2 exchange rates (NEE) across the growing season?
- Does long-term deepened snow significantly affect ecosystem net carbon balance by enhancing primary production and/or soil carbon losses?

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted near the Terrestrial Ecosystem Research Station (TERS) at Daring Lake (64°52′N, 111°34′W), 300 km NE of Yellowknife, Northwest Territories, Canada. The study area lies within the continuous permafrost zone in the central Canadian Low Arctic and has a continental climate with an annual mean temperature of −9°C (with mean diel temperatures ranging from −40°C in January to +20°C in July), annual rainfall of around 140 mm, and ~30–40 cm of snow accumulating during the winter in low-lying flat areas (all data are 1996–2013 averages; Bob Reid and Shawne Kokelj, unpublished). First snowfall is usually in mid-October with snow cover typically well below 10 cm depth through November, resulting in fully frozen surface soils at the time of bulk snow accumulation (December through May).

This study was focused on lowland mesic birch hummock tundra which occurs within a mosaic of tundra vegetation types in the middle of a gently sloping wide valley (~4 km^2) that is bordered by an esker and Canadian Shield bedrock outcrops. The soil in this area is well-drained, with no water table or evidence of permafrost degradation, and is classified as an orthic dystric turbic cryosoil (i.e., portions of the organic and mineral soil horizons are frequently intermixed due to cryoturbation). Birch hummock tundra vegetation is characterized by 10–30 cm tall hummocks, and the plant biomass is dominated by the evergreens *Rhododendron subarcticum* and *Vaccinium vitis-idaea* (totaling ~53 and ~27%, respectively, of aboveground vascular plant biomass) and mosses and lichens as well as some sedge (*Eriophorum vaginatum*) (Zamin et al., 2014). The deciduous shrub *Betula glandulosa* is consistently present, but at relatively low frequency and biomass (1–2 ramets/m^2; <30 cm tall; ~7% of aboveground vascular plant biomass). This vegetation type is a component of the low stature shrub tundra class that covers ~14% of the non-glaciated circumpolar Arctic (Walker et al., 2005).

2.2 | Experimental setup and design

Snowfences made of double-wrapped construction fencing (15 m long, 1.2 m high, $n = 5$) and unfenced control plots ($n = 5$) were established in similar patches of birch hummock tundra during summer 2004. The fences reduce wind speeds on their leeward sides, resulting in deepened snow patches reaching out ~20 m from both sides of each fence. Snow depth is uniformly enhanced to 90–100 cm within at least 3 meters perpendicular from each fence, corresponding to ~2.5 times the ambient snow depth (~30–40 cm) and snowmelt water equivalent (Christiansen, unpubl. data). Control plots are all situated at least 30 m from the nearest snowfence plot to ensure sufficient separation from deepened snow patches. Due to enhanced snow accumulation, complete snowmelt date is usually delayed 7–10 days each spring in the deepened snow plots relative to ambient conditions (Buckeridge & Grogan, 2008; Nobrega & Grogan, 2007), which is within ambient inter-annual snowmelt timing

variation. Surface water pooling (i.e., inundation) in the snowfence plots is confined to this short period in early spring, directly at/after bulk snowmelt where the soil profile is still frozen all the way to the surface (pers. obs.). Seasonal photographs of the experimental study area are shown in Figure S1.

2.3 | Soil microclimate

Soil temperature at 5 cm depth was measured hourly and logged as 4-hourly means continuously from September 2007 through May 2014 using thermocouple probes (n = 1 per treatment) connected to dataloggers (CR10X, Campbell Scientific, Logan, UT, USA). Volumetric soil moisture content (VWC) was recorded at the same frequency, using dielectric permittivity probes (CSC 16, Campbell Scientific, Logan, UT, USA) that measured soil moisture across the 0–5 cm depth interval (n = 2 per treatment). In addition, we measured soil thaw depth, soil temperatures at 5, 10, 15, and 20 cm depth as well as volumetric soil moisture in the top 12 cm bi-weekly (during the snow-free season), using a steel rod inserted into the ground, digital handheld thermometers (Spectrum Technologies, Aurora, IL, USA) and a handheld VWC probe (Hydrosense, Campbell Scientific, Logan, UT, USA), respectively. To account for within-plot heterogeneity, we divided each plot into a grid consisting of 39 subplots, and all 39 measurements per plot per date were then averaged into one datum in the statistical analyses. Last, to more confidently assess the snowfence treatment effects on seasonal temperatures and degree-days, we inserted multiple mini-temperature dataloggers (iButton, Maxim Integrated, San Jose, CA, USA) into the plots in autumn of 2013 (n = 10 and 12 per treatment at 5 and 30 cm soil depths, respectively).

2.4 | Plant cover and biomass

Permanent 1 × 1 meter vegetation monitoring subplots were established in each control and deepened snow plot in late-summer 2004. In these subplots, we determined vegetation composition using the point intercept method (Jonasson, 1988) during late-July/early-August of 2005 and 2011, measuring 100 intercepts per subplot using a pin (ø < 1 mm) and a 100 grid point frame, with all aboveground hits recorded on the way down. Percent cover of each species was calculated as the proportion of the 100 grid points containing at least one hit of that species. To convert point intercept hits to aboveground biomass estimations, we used separate regression parameters for each plant species, and moss and lichens obtained from previous studies conducted in the same valley (~300 m away) and in the same mesic birch hummock vegetation type as our study site (Zamin & Grogan, 2013; Zamin et al., 2014). Briefly, point intercept analysis was performed in unmanipulated 1 × 1 meter plots (n = 5), and subsequently a 0.4 × 0.4 m area was harvested within each of these point-framed plots. All harvested aboveground vascular plant species were sorted to species level and tissue type, whereas mosses and lichens were grouped separately. All biomass data were then extrapolated to 1 m^2 (for detailed methodology, see Zamin et al., 2014). For each deciduous and evergreen shrub species, aboveground biomass was modeled using separate regression parameters for leaf and stem tissue, while biomass estimations for all other plant species, and mosses and lichens, were performed with one set of parameters each (Table S1 shows regression parameters and their statistics). Subsequently, aboveground carbon, nitrogen, and phosphorus concentrations were obtained from Zamin (2013), and applied separately to the biomass estimations as described above. Finally, litter mass data were obtained from another previous study that sampled litter in 2008 after 4 years of deepened snow treatment (Vankoughnett & Grogan, 2014).

2.5 | Growing season ecosystem CO_2 fluxes

We measured net ecosystem CO_2 exchange (NEE) and ecosystem respiration (R_{eco}) using an infrared gas analyzer (IRGA) Li6400 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE, USA) in combination with custom-made polypropylene collars (10 cm length, 30 cm diameter). We inserted two collars (>1 m apart) ~6–7 cm into the ground in each plot in June 2012. The collars were placed in inter-hummock areas, situated approximately 1–2 m perpendicular to a snowfence and at least 1.5 m from the plot edges. The collars contained the most abundant vascular plant species in the study area, but *B. glandulosa* was not included due to its large stature. We estimated plant cover inside all collars in August 2012 using point framing (Jonasson, 1988), and a one-factor ANOVA showed no difference in vascular plant cover between treatments. Daytime flux measurements were performed weekly during the snow-free season (17 July–28 August 2012, and 9 June–9 July 2013) using a custom-made plastic chamber (total volume: ~20 L), which fitted into a water-filled groove on top of each collar, ensuring an airtight seal. To secure adequate headspace air mixing, the chamber was fitted with two small air circulation fans and a small pressure equilibration vent.

At each collar, a full measurement set consisted of an NEE measurement during ambient light conditions, followed by aeration of the chamber for 20–30 s to equilibrate gas concentrations and temperatures to ambient conditions before initiating an R_{eco} measurement with the chamber covered over with a dark cloth. Prior to each NEE and R_{eco} recording, but after placing the chamber in the collar, we allowed for 5–10 s equilibration before recording each individual flux measurement for 120 s, logging temporal changes in headspace CO_2 concentration every second. Additionally, during each gas flux measurement, four measurements of soil temperatures at 5, 10, 15, and 20 cm depth and soil moisture (as described above) were recorded adjacent to each collar, and the average was used in the statistical analyses. All flux data were visually inspected for consistency over time prior to analyses. Subsequently, to avoid underestimation of absolute flux rates, all fluxes were calculated using nonlinear regression using the HMR package (Pedersen, Petersen, & Schelde, 2010) in R v. 2.15.2 (R Development Core Team, 2012). Last, gross ecosystem production (GEP) was calculated as NEE − R_{eco}. Each control or snowfence treatment plot flux average (based on measurements from both collars) was used as a single datum in the statistical analyses. Q_{10}

values were calculated based on first-order exponential relationships between 5 cm soil temperature and R_{eco}.

2.6 | Soil sampling

We randomly selected inter-hummock areas within 2 m perpendicular to each snowfence, and with at least 1.5 m to the edges of the plot and at least 1 m to a CO_2 flux collar (see below), that is, well within the uniform snowdrift area. We used a metal corer (4 cm diameter) to obtain 10 cm long soil cores from the upper organic horizon (0–10 cm) and the upper mineral horizon (15–25 cm depth interval) on 17 June 2013 (organic horizon only), 12 July 2012, and 11 August 2012. Sampling inter-hummock areas is a methodological standardization that is common practice in this type of ecosystem (Buckeridge & Grogan, 2008; Vankoughnett & Grogan, 2014; Zamin et al., 2014). All depths were measured from the green-brown moss transition layer, and if the organic soil horizon was <10 cm deep, the bottom mineral soil part of the core (no more than 1–2 cm) was carefully removed with a serrated knife, and conversely, in the rare occurrences where obvious organic soil was present at the top of the mineral soil cores, it was also removed. All cores were kept cool and brought back to the field lab where they were stored at 5°C and processed within 48 hr of sampling.

2.7 | Soil biogeochemistry

Aboveground vegetation and any surface litter was removed from the organic soil cores before picking out large roots (ø > 2 mm) and stones while homogenizing the soil samples. We used the chloroform-fumigation extraction methodology (Brookes, Landman, Pruden, & Jenkinson, 1985) with few modifications to determine microbial C, N, and P pools. Briefly, fresh soil subsamples (10 g) were extracted with (i) 0.5M K_2SO_4 to recover NH_4^+-N and total dissolved carbon and nitrogen pools (DOC and TDN, respectively); (ii) Bray-1 solution (Wu, He, Wei, O'donnell, & Syers, 2000) to recover PO_4^{3-}-P; and (iii) distilled water to recover NO_3^--N content and estimate specific UV absorbance (SUVA) of DOC (see below). Extractants were added in a 1:5 (soil fresh weight (g): extractant volume (ml)) ratio, except for Bray-1 which was added in a 1:4 ratio (Wu et al., 2000). Soil and extractant slurries were thoroughly shaken by hand for a minute four times over 1 h, and then allowed to settle for 30 min before vacuum-filtration through glass fiber filters (Fisher G4; 1.2 μm pore-size). Simultaneously, another set of fresh soil subsamples (10 g) was vacuum-incubated with ethanol-free chloroform ($CHCl_3$) for 24 hr at ~20°C, followed by extraction similar to nonfumigated samples with (i) 0.5 M K_2SO_4 to estimate microbial biomass pools of C and N (MBC and MBN, respectively); and (ii) Bray-1 solution to estimate microbial biomass pool of P (MBP), see further microbial biomass calculations below. During each run, duplicate blanks (without soil) were always included for all extractants to detect potential contamination during extraction and filtration. The extracted volume was immediately frozen at −20°C until further analyses in our Kingston-based lab.

DOC and TDN were determined in all K_2SO_4 extracts (fumigated and nonfumigated samples) by oxidative combustion and infrared DOC (Nelson & Sommers, 1996) or chemiluminescence (TDN) analysis, using a TOC-TN Auto-Analyzer (Shimadzu, Kyoto, Japan). Dissolved NH_4^+-N in K_2SO_4 extracts (nonfumigated), NO_3^--N in water extracts (nonfumigated), and PO_4^{3-}-P in Bray-1 extractions (fumigated and nonfumigated) were all determined colourimetrically using automated flow analysis on an Auto-Analyzer III (Bran-Leubbe, Norderstadt, Germany) with the salicylate (NH_4^+-N (Mulvaney, 1996)), sulphanilamide (NO_3^--N (Mulvaney, 1996)), and molybdate-ascorbic acid (PO_4^{3-}-P (Kuo, 1996)) methods, respectively. Microbial biomass C, N, and P (MBC, MBN, and MBP, respectively) were calculated as the difference between DOC, TDN, and PO_4^{3-}-P in fumigated and nonfumigated samples. No *K* correction factors for microbial extraction efficiency were applied to the fumigated samples. All extractions were corrected for dilution associated with gravimetric soil moisture content of each sample (see below).

To characterize the lability of the dissolved C fraction, we extracted water-soluble DOC from organic soils in winter (frozen soil, 16 May 2013) and spring (thawed soil, 16 June 2013), and mineral soils in summer (thawed soil, 8 July 2013). Single-point UV-Vis absorbance measurements (SUVA) in these water extracts were determined at 254 nm, which is the wavelength associated with absorbance by aromatic carbon compounds (Chin, Aiken, & Oloughlin, 1994), using an Aqualog spectrofluorometer (Horiba, Kyoto, Japan). For each sample and instrument blank (deionized water), the absorbance measurement was the average of 10 scans with the standard deviation of the UV measurement always being <0.0002 AU. The linearity of the absorbance over the observed range of DOC concentrations was verified using laboratory-prepared potassium hydrogen phthalate (KHP) solutions (r^2 = .999 for a six-point calibration, 0–100 ppm C; Potter & Wimsatt, 2005). SUVA of DOC (reported as L mg C^{-1} m^{-1}) was then calculated by dividing the UV-Vis absorbance at 254 nm by the DOC concentration of the sample.

Gravimetric soil moisture was estimated by oven-drying a third set of soil subsamples (10 g) at 60°C for 96 hr. The dried samples were then homogenized to a fine powder in a ball mill (Retsch, Haan, Germany) before total C and N were determined by combustion (HCl tests indicated that inorganic C contents were negligible), and infrared and thermal conductivity analysis, respectively (Elementar VARIO Micro Cube Analysensysteme, Hanau, Germany), and total P was determined by acid digestion (Parkinson & Allen, 1975) and subsequent flow-injection auto-analysis (Kuo, 1996). Soil pH was measured on samples (3 g) of the oven-dried soil (1:10 dried soil to deionized water ratio) using an Accumet AccupHast-R probe (Fisher Scientific, Ottawa, ON, Canada).

Soil layer specific C, N, and P pools in the measured depth intervals of the organic and mineral soil layers (0–10 and 15–25 cm, respectively) were calculated using the fixed soil depth standard methodology.

2.8 | Statistical analyses

Prior to each analysis, we visually inspected data distributions and either log or square-root transformations were applied as necessary to achieve variance homogeneity. Plant cover data were always arcsine square-root transformed. After each analysis, we tested model validity by visual inspection of the distribution of residuals, as well as residuals plotted against predicted values, and concluded that there were no obvious outliers or deviations from the assumptions of normality. All statistical analyses were performed using SAS 9.2 (SAS Institute, Cary, NC, USA), and all statistically significant main effects and interactions are reported. We tested for snowfence effects on soil biogeochemical pools, ecosystem gas fluxes, and plant cover and biomass pools using repeated measures linear mixed-effects models (PROC MIXED in SAS).

For all models, *plot* and *sampling date* were specified as separate random factors with *sampling date* also set as repeated factor within *plot*, and the deepened snow *treatment* was always specified as a fixed main effect. In the statistical models of ecosystem gas fluxes, we also included the handheld probe measures of *soil moisture* and *temperature* as linear covariates with fixed effect interactions. For the soil biogeochemical pools and plant cover models, we used *treatment* and *sampling date* (labeled *time* or *year*, respectively) as fixed main effects, including their interaction term, but with no covariates. The plant biomass and multiple probe temperature (iButton) data models consisted of *treatment* as the only fixed effect, and with no covariates. All full models were step-wise simplified using the AIC output, and covariance structure was determined by the two-model fit criteria AIC-output from PROC MIXED (Littell, Milliken, Stroup, & Wolfinger, 1996). Note that due to logistical constraints, mid-July through August soil sample and ecosystem CO_2 flux data were collected in 2012, while June to early-July measurements were obtained in 2013. We compared diel air temperature and precipitation data between the 2012 and 2013 growing seasons (June, July, and August; JJA), and found broadly similar weather patterns in both years (Figure S2). Accordingly, we report these measurements as if they were obtained over a single June through August growing season. In any event, this approach to reporting the data should have no bias effect in terms of the central focus of the study which is testing for statistical differences between the experimental snowfence treatment relative to controls.

Due to substantial spatial variability, we extended our mineral soil sampling to contain a total of 18 and 19 samples across all five snowfence and control plots, respectively. From these, we eliminated a total of six outlier mineral soil samples prior to statistical analysis on the basis that they contained carbon concentrations of at least 23% and therefore represent samples from tongues of organic C-rich soil that had been moved down into the mineral soil layer by cryoturbation. Thus, 2–4 samples were used for each plot mean composite prior to statistical analysis ($n = 5$ per treatment). The mineral soil C data are presented as a box and dot-density plot in accordance with recent recommendations aimed at enabling the reader to see critical patterns in raw data (Krzywinski & Altman, 2014; Weissgerber, Milic, Winham, & Garovic, 2015).

3 | RESULTS

3.1 | Effects of the snowfence treatment on soil microclimate in cold and growing seasons

Our continuous soil temperature 2007–2014 single-probe data, and highly replicated mini-datalogger 2013–2014 data, and handheld probe 2012–2013 data, together indicate warmer mean deep winter (1 January through 30 April) soil temperatures by up to ~6.5°C (range between years: 1.1–6.6°C) in both the organic and mineral soil layers of the snowfence plots (with some inter-annual variation; Figures 1 and S3, and Table S2), and no treatment effects on either growing season soil temperature, moisture, or full active layer depth (except for a very short period (1 week) just after snowmelt; Figures 1, S3–S6).

The deepened snow treatment generally enhanced soil temperatures from December onwards (Figures 1 and S3), reducing the soil freezing degree days by ~100–700 annually over the 2007–2013 period, and resulting in a mean overall increase of ~40% in annual cumulative degree days (single-probe data; Table S2). Although these multi-year data were compiled using only one temperature probe per treatment, and therefore do not take into account spatial heterogeneity in soil temperature due to variation in soil heat capacity, conductivity, and moisture/ice content, the observed snow treatment pattern is very similar to the 42% increase in degree days recorded in the snowfence plots during 2013–14 using highly replicated mini-datalogger data (*Treatment:* $F_{1,16} = 162.88$; $p < .0001$; Figure 1, Table S2).

The date of complete snowmelt was delayed in the deepened snow treatment by ~7 days in 2013 (control and snowfence plots were snow-free on 27 May and 3 June, respectively; no data for 2012), which is similar to previous years (see Materials and Methods). This short delay in complete snowmelt due to the snowfences likely led to the transient differences observed in soil thaw depth, moisture, temperatures in early-June (Figures 1, S3–S6).

3.2 | Effects of the snow treatment on plant cover and biomass

The deepened snow treatment significantly altered plant community structure (Table 1). Between 2005 and 2011, the snowfence treatment increased percent cover of the abundant evergreen shrub *Rhododendron subarcticum* (*Treatment:* $F_{1,8} = 26.2$; $p < .001$) and the graminoid *Eriophorum vaginatum* (*Treatment:* $F_{1,8} = 6.5$; $p = .03$) by 96 and 285%, respectively, and tended to increase cover of *Rubus chamaemorus* (*Treatment:* $F_{1,8} = 4.1$; $p = .08$). These main effects of deepened snow were each associated with significant interaction terms between *Year* and *Treatment* (see Table 1 for details), indicating that plant cover of each of these species was similar between snowfenced and control plots in 2005 (considered the baseline year

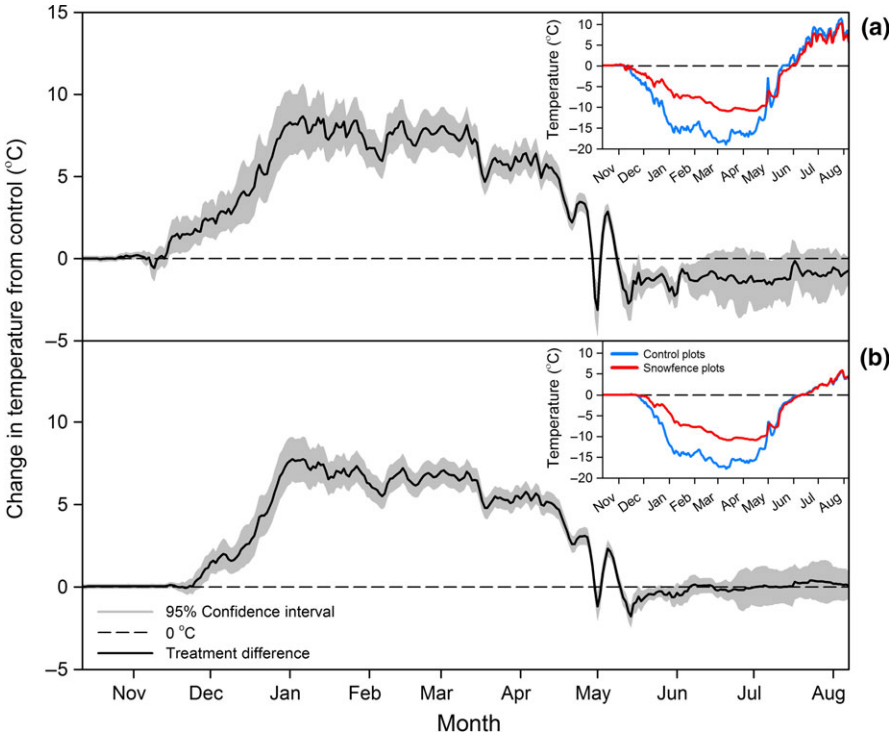

FIGURE 1 Diel soil temperature differences (black lines) between annually deepened snow (snowfences) and ambient snow (controls) treatments at 5 (a) and 30 (b) cm depth from 12 October 2013 (early cold season) to 7 August 2014 (late-summer). Data are from mini-temperature dataloggers (iButton; n = 10–12 per treatment at each soil depth) installed in August 2013, that is, after the 2012–2013 CO_2 flux measurement period reported in this study (see Table S2 for additional soil temperature data spanning 2007–2014). Positive values (i.e. above the zero line) indicate warmer soils in the annually deepened snow treatment, and the grey fills indicate 95% confidence interval limits. Inserts show diel soil temperatures of the corresponding control (blue lines) and snowfence (red lines) plot temperatures [Colour figure can be viewed at wileyonlinelibrary.com]

prior to any treatment effect), and that the treatment differences developed over the period from 2005 to 2011. By contrast, deciduous shrub species cover was unaffected by the deepened snow treatment or across the 7 year dataset (within control plots). Finally, although there were no snowfence effects, the combination of standing dead vascular plant and dead moss cover increased over the study period, and lichen biomass tended to decline (*Year*: $F_{1,8}$ = 11.4, p = .01; and $F_{1,16}$ = 4.2, p = .06, respectively; Table 1).

Our aboveground biomass calculations from the 2011 percent cover data for each species indicated a similar pattern of treatment effects as described above (Tables 2 and S3). At the growth-form level, the snowfences increased evergreen shrub biomass and total vascular plant biomass by 91% and 52%, respectively. Furthermore, and primarily as a result of increased C and N contents in *R. subarcticum* (Table S3), total vascular plant carbon and nitrogen accumulation increased in the snowfences (*Treatment:* $F_{1,8}$ = 18.7, p < .01; and $F_{1,8}$ = 19.5, p < .01, respectively). Nevertheless, total aboveground biomass (including moss and lichen) was not significantly affected (*Treatment:* $F_{1,8}$ = 3.3; p = .11; Table 2), likely due to the large components of lichen and moss biomass within this pool.

3.3 | Effects of the snowfence treatment on growing season ecosystem CO_2 exchange fluxes

Following 8–9 years of the annually deepened snow treatment, daytime net ecosystem CO_2 exchange (NEE) rates were significantly reduced throughout the growing season in the snowfence plots (*Treatment:* $F_{1,9.6}$ = 5.7; p = .04; Figure 2a and Table S4). In other words, although the NEE rates were often positive, indicating net CO_2 release from the ecosystem to the atmosphere, the snowfence treatment reduced the magnitude of this C release (i.e., it promoted greater ecosystem net C gain) by ~30% across the entire growing season. Overall, NEE CO_2 source rates were positively correlated with soil temperature at 5 cm depth (*Soil temperature*: $F_{1,23.9}$ = 144.8; p < .01), but the magnitude of this effect varied during the growing season (*Treatment* × *Soil Temperature:* $F_{1,23.8}$ = 11.7; p < .01).

Gross ecosystem photosynthesis (GEP) rates were generally unaffected by the deepened snow treatment (Figure 2b; Table S4). However, early season GEP rates on 9 and 13 June were lower in the deepened snow plots relative to controls, likely due to delayed leaf phenology, leading to greater NEE rates in the deepened snow plots on 9 June (the only measurement date where NEE was not lower in the deepened snow treatment relative to controls). *Betula glandulosa* leaf-out was delayed ~1 week in the deepened snow treatment (Casper Christiansen, *pers. obs.*).

Ecosystem respiration (R_{eco}) rates were consistently reduced (by 20% on average) in the deepened snow plots from snowmelt onwards (*Treatment:* $F_{1,20}$ = 11.9; p < .01; Figure 2c). Similar to NEE, soil temperature at 5 cm depth was positively correlated with R_{eco} across treatments and sampling dates (*Soil temperature:* $F_{1,27}$ = 211.2; p < .01), but the magnitude of this effect varied during the growing season (*Treatment* × *Soil Temperature:* $F_{1,10.3}$ = 6.6; p = .03). Nevertheless, Q_{10} values based on a first-order relationship between 5 cm soil temperature and R_{eco} were similar across treatments (3.0 ± 0.2 and 2.6 ± 0.2 for controls and snowfence plots, respectively).

3.4 | Effects of the snow treatment on soil biogeochemistry

Eight years of experimentally deepened snow tended to lower total organic carbon concentrations in the mineral soil layer (15–25 cm

TABLE 1 Effects of annually deepened snow on percent cover of vascular plants, lichen, moss, litter, and combined dead plant and moss cover after 1 and 7 years of the snowfence treatment (measured in 2005 and 2011, respectively. Values are means ± 1 *SE* (n = 5), and statistical results are shown in bold as *$p \leq .1$; **$p \leq .05$, and ***$p \leq .001$

Functional group	Plant species (% cover)	2005		2011		Year	Treatment	Year × Treatment
		Controls	Snowfences	Controls	Snowfences			
Deciduous	*Betula glandulosa*	7.8 (2.1)	6.6 (2.5)	9.4 (3.4)	6.4 (2.9)	NS	NS	NS
	Vaccinium uliginosum	9.6 (4.7)	4 (2.2)	9.8 (4.8)	5.4 (3)	NS	NS	NS
	Total	17.4 (5.3)	10.6 (3.9)	19.2 (5.9)	11.8 (4.5)	NS	NS	NS
Evergreen	*Rhododendron subarcticum*	37.2 (7.2)	40.6 (8.6)	**28.2 (4.7)**	**55.4 (8.3)*** **	NS	$F_{1,8}$ = 26.2, p < .001	$F_{1,8}$ = 26.3, p < .001
	Vaccinium vitis-idaea	29.2 (4.9)	33.4 (4.7)	31.6 (5.8)	40.2 (7.4)	NS	NS	NS
	Andromeda polaris	6.6 (3.7)	4 (2)	7.4 (5.56)	2.6 (1.3)	NS	NS	NS
	Total	73 (5.4)	78.0 (7.2)	**67.2 (5.8)**	**98.2 (7.3)****	NS	$F_{1,8}$ = 7.8, p = .02	$F_{1,8}$ = 7.8, p = .02
Graminoid	*Eriophorum vaginatum*	3.4 (1.9)	5.0 (4)	**4.0 (1.92)**	**15.4 (7.1)****	$F_{1,8}$ = 8.2, p = .02	$F_{1,8}$ = 6.5, p = .03	$F_{1,8}$ = 6.6, p = .03
	Total	3.4 (1.9)	5.0 (4)	**5.8 (1.8)**	**15.6 (7.1)***	$F_{1,8}$ = 10.9, p = .01	$F_{1,8}$ = 4.4, p = .07	$F_{1,8}$ = 4.4, p = .07
Forb	*Rubus chamaemorus*	0.6 (0.6)	0.2 (0.2)	**0.4 (0.24)**	**1.4 (0.4)***	NS	$F_{1,8}$ = 4.1, p = .08	$F_{1,8}$ = 4.1, p = .08
Lichens		**86.6 (6.4)**	**68.2 (6.4)**	**57.6 (4.2)**	**52.4 (6.5)**	$F_{1,16}$ = 4.2, p = .06	NS	NS
Mosses		14.4 (3.1)	17.2 (4.8)	26.6 (4.3)	30.0 (9.6)	NS	NS	NS
Litter		64.6 (1.6)	65.8 (4.1)	78.4 (3.5)	81.8 (10.3)	NS	NS	NS
Standing dead plant and dead moss combined		**25.8 (5.5)**	**34.2 (8.4)**	**42.8 (9.4)**	**67.8 (22.1)**	$F_{1,8}$ = 11.4, p = .01	NS	NS

depth; *Treatment:* $F_{1,8}$ = 3.98; p = .08) despite substantial sample variability among and within plots (Table 3, Figure 3; mean reduction ~40%). By contrast, there were no snowfence effects on total organic carbon or nitrogen concentrations or pools in the overlying organic soil layer (0–10 cm depth; Table 3).

Additionally, mineral soil layer NO_3^- pools in both July and August were reduced by up to 73% in the deepened snow plots relative to controls (*Treatment:* $F_{1,16}$ = 5.5, p = .03), whereas the mineral soil layer DOC, DON, NH_4^+, and PO_4^{3-} pools were unaffected (Table 4). The snowfences had no effect on microbial biomass C and N in either soil layer. However, microbial biomass P and soluble phosphate in the organic soil layer were reduced by ~47% or more (*Treatment:* $F_{1,28}$ = 3.8, p = .06; and $F_{1,28}$ = 7.5, p = .01, respectively) in each of the three growing season sampling months (the overall reduction in microbial biomass P being at least a factor 10 greater in magnitude), and mineral soil layer microbial biomass P was reduced by ~60% in August (*Treatment* × *Time*: $F_{1,7.6}$ = 8.4; p = .02; Table 4).

As expected, comparison of the organic and mineral soils 1–2 weeks after thaw (i.e., spring and mid-summer, respectively) indicated higher SUVA (i.e., more aromatic/recalcitrant compounds) in the mineral soil layer relative to the organic soil layer (Table 4). However, the snowfences did not alter growing season organic or mineral soil dissolved organic carbon chemical quality as represented by the DOC SUVA values (Table 4).

4 | DISCUSSION

To the best of our knowledge, this is the first study to demonstrate that persistent changes in tundra winter climate may strongly promote evergreen shrub growth and reduce soil nutrient and carbon contents, with at least one legacy effect being a reduction in growing season net ecosystem CO_2 loss to the atmosphere. Our results for mesic birch hummock tundra contrast with those from other analogous snowfence experiments that span a broad range of tundra vegetation types, suggesting diverse ecosystem responses to a changing winter climate across the Arctic.

4.1 | Effects of the snowfence treatment on plant cover and biomass

The deepened snow treatment almost doubled cover of the evergreen shrub *R. subarcticum* (96% increase) after 7 years. This species was already abundant in our control plots (28% cover), and its treatment response resulted in significant increases in the total vascular plant aboveground biomass and C pool (by ~33 g C/m^2). Why would growth of this evergreen shrub species be promoted by the deepened snow treatment? Evergreen shrubs are particularly well adapted to the stresses of low-nutrient tundra environments (Aerts & Chapin, 2000), while deciduous shrubs generally are more

TABLE 2 Effects of annually deepened snow on estimated vascular plant, lichen, and moss biomass pools after 7 years of treatment. Values are based on plant species percent cover data measured in 2011 (Table 1), converted to biomass using linear regression with parameters estimated separately for leaf and stem components of each individual plant species (Zamin et al., 2014), see Materials and Methods for details. Carbon and nutrient contents were estimated using species-specific nutrient concentrations for each vascular species, and as functional groups for lichens and mosses (Zamin & Grogan, 2013). [a]Litter mass was sampled in 2008 after 4 years of deepened snow treatment (Vankoughnett & Grogan, 2014). Values are means ± 1 *SE* (n = 5), and statistical results are shown in bold as *$p \leq .1$; **$p \leq .01$, and ***$p \leq .001$

Plant biomass pools (g dry weight/m^2)	Controls	Snowfences	Treatment effect
Vascular plant aboveground biomass			
Deciduous shrubs	35.7 (8.9)	22.2 (8.7)	NS
Evergreen shrubs	**76.6 (9)**	**146.2 (10)*** **	$F_{1,8}$ = 26.6, $p < .001$
Graminoids	6.4 (1.4)	10.9 (3.2)	NS
Forbs	0.5 (0.3)	1.5 (0.4)	NS
Total	**119.2 (12.9)**	**180.7 (7)****	$F_{1,8}$ = 17.8, $p < .01$
Lichens	157.9 (6)	149.9 (9.1)	NS
Mosses	97.5 (10.6)	102 (21)	NS
Littermass[a]	1122 (413.7)	825.4 (294)	NS
Total aboveground pools (including mosses and lichens)			
Biomass	374.6 (16.3)	432.6 (27.9)	NS (p = .11)
Carbon	**170.2 (8)**	**201.5 (12.4)***	$F_{1,8}$ = 4.6, p = .06
Nitrogen	**2.4 (0.1)**	**2.9 (0.2)***	$F_{1,8}$ = 4, p = .08
Phosphorus	0.4 (0.1)	0.4 (0.2)	NS

abundant in relatively fertile soils, and certainly rise to dominance in response to persistent high-level nutrient additions (Chapin et al., 1995). However, unlike deciduous shrubs, evergreens can photosynthesize under snow (Starr & Oberbauer, 2003) and can take up and store available soil nutrients and water during the winter-spring transition when soils are just starting to thaw (Larsen, Michelsen, Jonasson, Beier, & Grogan, 2012; Mckane et al., 2002; Moser et al., 2016). Therefore, evergreens should theoretically be favored when climate-warming leads to increases in spring soil nutrient pools, even if complete snowmelt is delayed by ~1 week. While we observed reduced or similar growing season nutrient pools in our treatment plots, previous research at our site has demonstrated that soil nutrient pools are significantly enhanced in the snowfence plots during the snowmelt period (Buckeridge & Grogan, 2010), and therefore we attribute the evergreen treatment response to greater nutrient availability at that time.

Consistent with the longer-term vegetation responses observed in our study, the only other snowfence study of comparable duration (8 years), where changes in vegetation composition and/or cover are reported, found increased evergreen shrub growth in a dry heath site that, like ours, was not dominated by deciduous shrubs (Wahren et al., 2005). In contrast, evergreen and sedge cover declined after 8 years of deepened snow treatment in a nearby moist acidic tussock tundra site. This differential effect was attributed to shading by increased deciduous shrub cover (Wahren et al., 2005), and was sustained even after 20 years of snow manipulation (Leffler, Klein, Oberbauer, & Welker, 2016). However, snow depth in those sites was increased up to 3 m, whereas our increase was from ~0.3 (ambient) up to a maximum of 1 m, suggesting that our conclusions are likely more realistic in terms of both inter-annual and landscape-scale spatial variation in low Arctic tundra snow depths, as well as climate predictions (Bintanja & Van Der Linden, 2013).

Positive evergreen shrub biomass responses have been observed in unmanipulated long-term monitoring plots that have undergone ambient climate warming over 30 years (Elmendorf et al., 2012b), and in experimental summer warming studies across numerous circumpolar tundra ecosystems (Elmendorf et al., 2012a), including *R. subarcticum* at our study site (Zamin et al., 2014). Furthermore, in the large parts of the primarily continental Arctic that are currently covered by low stature mesic evergreen-shrub dominated tundra, and where no or relatively small changes in climate have been observed so far (Hartmann et al., 2013), deciduous shrubs do not seem to be expanding as fast as observed in, for example, Alaska (Jia, Epstein, & Walker, 2006) and Eastern Canada (Tremblay, Levesque, & Boudreau, 2012). Continued or increased dominance by evergreen shrubs in these Arctic regions is important because their low stature, relatively slow growth rates and recalcitrant litter all tend to impede the impact of future warming on SOM decomposition and nutrient mobilization rates, potentially further favoring evergreens and restricting or delaying expansion of deciduous shrubs.

4.2 | Effects of the snowfence treatment on growing season ecosystem CO_2 exchange fluxes

The ~30% decline in growing season daytime NEE (i.e., reduced ecosystem net CO_2 release to the atmosphere) was almost entirely driven by consistently decreased R_{eco} rates (Figure 2). Ecosystem respiration is the sum of autotrophic (aboveground shoots and leaves, and belowground roots) and heterotrophic (microbial decomposition) sources. The absence of a snowfence effect on GEP rates suggests that the reduction in CO_2 emissions was primarily due to decreases in heterotrophic respiration derived from bulk soil carbon sources. In support of this conclusion, previous winter climate change manipulations have had either no effect (Pries et al., 2015), or have reduced (Nowinski, Taneva, Trumbore, & Welker, 2010) the relative contribution from autotrophic sources on summertime R_{eco}. Furthermore, the collars used for gas flux-measurements were installed in 2012 in such a way that they contained similar plant species and aboveground plant cover across treatments (see Materials and Methods). Therefore, in contrast to vascular plant biomass differences observed in our permanent vegetation subplots, plant biomass inside the collars was likely similar across all treatment plots,

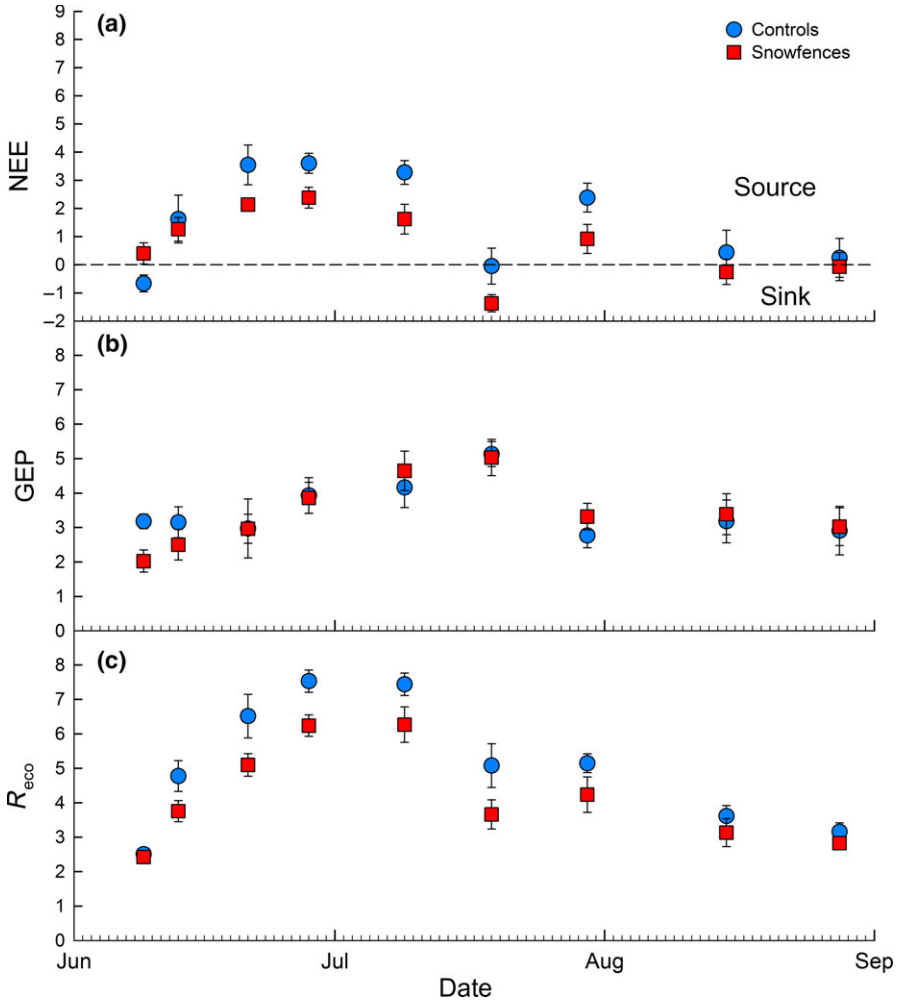

FIGURE 2 Effects of 8–9 years of annually deepened snow on daytime rates of net ecosystem exchange (NEE) (a), gross ecosystem production (GEP) (b), and ecosystem respiration (R_{eco}) (c) during the growing season (data are μmol CO_2 m^{-2} s^{-1}). Blue circles and red squares indicate control (ambient snow regime) and snowfence plots (deepened snow treatment), respectively (n = 5, ± 1 *SE*). Positive NEE rates indicate net loss of carbon to the atmosphere (ecosystem source), whereas negative NEE rates indicate net uptake of atmospheric carbon (ecosystem sink). Note that plant biomass inside the gas flux collars was likely similar across all treatment plots as the collars were installed in 2012 in such a way that they contained similar plant species and aboveground plant cover across treatments. Furthermore, note that June and early-July measurements were performed in 2013 and mid-July to late-August measurements were performed in 2012. See Materials and Methods for details [Colour figure can be viewed at wileyonlinelibrary.com]

suggesting that changes in R_{eco} were primarily from other (heterotrophic) sources.

Other Arctic snowfence studies have reported contrasting effects of deepened snow on growing season CO_2 exchange (Lupascu, Welker, Xu, & Czimczik, 2014; Natali et al., 2014; Rogers, Sullivan, & Welker, 2011; Semenchuk et al., 2016). Overall, studies reporting enhanced summertime R_{eco} generally also observed increased plant productivity and soil temperature, moisture, and/or thaw depth, indicating that a combination of enhanced autotrophic and heterotrophic respiration rates contributed to R_{eco} (Natali et al., 2014; Rogers et al., 2011). By contrast, studies reporting declines in summertime R_{eco} rates had negligible treatment effects on GEP and microclimate (this study; Semenchuk et al., 2016). One potential explanation for the reduction in R_{eco} in these latter studies is prolonged depletion in the labile soil C pool following multiple years of enhanced wintertime CO_2 release under deepened snow, as hypothesized by Semenchuk et al. (2016) and also observed in experimental summer-warming studies (Melillo et al., 2002). We partially tested that hypothesis by analyzing DOC-SUVA in both soil layers, but found no snowfence effects (Table 4) indicating similar quality of soluble C pools across treatments. Nevertheless, mineral soil layer (15–25 cm depth) C% tended (p = .08) to be reduced by 40% in our deepened snow plots, and overall summertime Q_{10}-values (i.e., temperature response of respiration rates) were similar across treatments, making us speculate that wintertime soil organic matter depletion in the uppermost mineral layer may have been at least partially responsible for the decrease in growing season ecosystem respiration in the snowfence plots (see full discussion on soil biogeochemistry below).

4.3 | Effects of the snowfence treatment on soil nutrients and microbial biomass

In organic soil horizons, short-term studies indicate that deepened snow increases cold season nitrogen mineralization (Schimel et al., 2004; but see Myers-Smith & Hik, 2013), leading to greater spring nutrient pulses (Buckeridge & Grogan, 2010). However, although some studies have reported increases in summer soil nitrogen availability (Demarco, Mack, & Bret-Harte, 2011; Semenchuk et al., 2015), we observed no effects on growing season inorganic (NH_4^+, NO_3^-) and organic N compounds (DON, including amino acids), or microbial biomass C and N in the organic soil layer after 9 years of deepened snow. Moreover, organic soil PO_4^{3-} and microbial biomass P pools were reduced by 47–70% in the deepened snow plots. What could be responsible for this large decline in soil and microbial P pools? The

TABLE 3 Effects of annually deepened snow (snowfences) on soil geochemical properties in organic (0–10 cm) and mineral (15–25 cm) soil layers after 8 years (values are means ± 1 *SE*; $n = 5$ per treatment in each soil layer). All soil pools were calculated using the fixed depth method, and those that differ between treatments are highlighted in bold as $*p \leq .1$. Note that six outlier samples with carbon concentrations of at least 23% were eliminated from the statistical analysis of the mineral soil layer data on the basis that they represent samples from tongues of organic C-rich soil that had been moved down into the mineral soil layer by cryoturbation (see Materials and Methods and Figure 3)

	Organic soil layer (0–10 cm)			Mineral soil layer (15–25 cm)		
Soil geochemistry	Controls	Snowfences	Treatment effect	Controls	Snowfences	Treatment effect
% Soil C	44.8 (0.5)	42.9 (1.0)	NS	**6.5 (1.0)**	**3.9 (0.8)** *	$F_{1,8} = 3.98$; $p = .08$
% Soil N	1.36 (0.09)	1.39 (0.07)	NS	**0.28 (0.04)**	**0.17 (0.03)** *	$F_{1,8} = 3.97$; $p = .08$
% Soil P	0.09 (0.01)	0.1 (0.01)	NS	0.05 (0.01)	0.06 (0.01)	NS
Soil C:N ratio	34.1 (3.2)	31.4 (2.2)	NS	23.0 (1.3)	22.8 (0.39)	NS
Soil sample layer carbon pool (g C/m^2)	7106 (640)	7,076 (595)	NS	7,123 (1194)	4,748 (964)	NS
Soil sample layer nitrogen pool (g N/m^2)	218 (29.6)	232 (31.2)	NS	310 (50.7)	210 (42.7)	NS
Soil sample layer phosphorus pool (g P/m^2)	13.1 (2.1)	14.5 (1.4)	NS	52.9 (6.3)	69.6 (14.7)	NS
Soil pH	3.32 (0.04)	3.32 (0.02)	NS	4.46 (0.08)	4.59 (0.06)	NS
Bulk density (g/cm^3)	0.15 (0.01)	0.15 (0.01)	NS	1.09 (0.02)	1.12 (0.1)	NS
Soil sample depth (cm)	0–10	0–10		15–25	15–25	
Full extent of thawed active layer (by mid-August 2013)	10.8 (2.3)	10.9 (0.9)	NS	58.9 (8.0)	57.3 (4.1)	NS

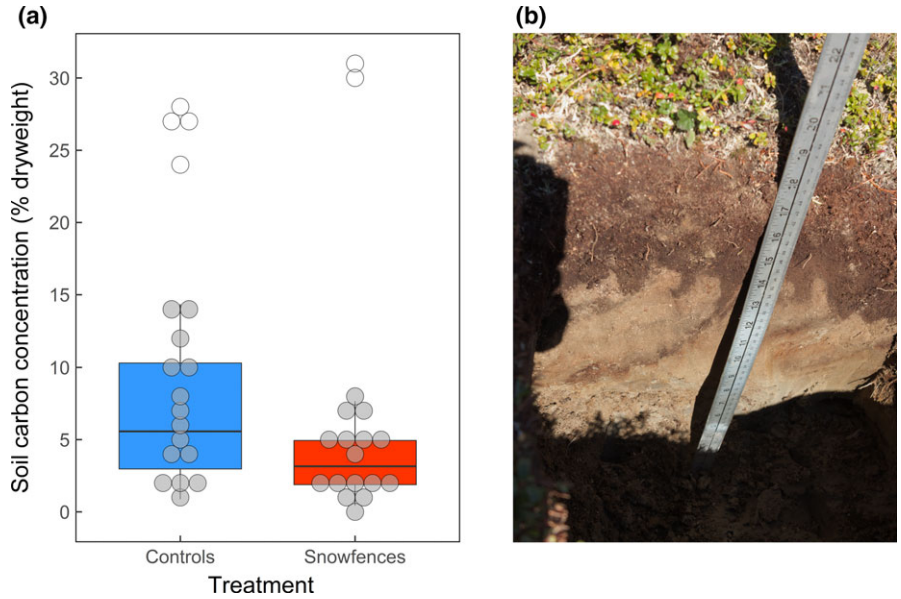

FIGURE 3 Total organic carbon concentrations in the mineral soil samples (gray filled circles) that were used in the statistical comparison of control (blue box, left; $n = 15$) and snowfence (red box, right; $n = 16$) plots after 8 years of treatment, visualized as a Tukey-style box and dot density plot (a). A small proportion of the total number of samples had unusually high carbon concentrations (>23% dry weight). Therefore, these six data points (open circles) were not included in the statistical analysis on the basis that they did not represent inherent mineral soil C, but were most likely from tongues of C-rich organic soil layer material moved down into the mineral soil layer by cryoturbation. The soil profile (b) from a pit dug ~5 m adjacent to a control plot in August 2012 illustrates several tongues of organic layer soil penetrating down into the mineral soil layer. For the statistical analysis, 2–4 separate soil samples within each plot were averaged into a single plot datum point ($n = 5$ per treatment; Table 3). For each treatment, the box bounds the interquartile range (IQR; Tukey, 1977), and includes the median (bold horizontal line) and Tukey-style whiskers (extended to a maximum of 1.5 × IQR). For the dot density overlay, data points within one unit on the *Y*-axis were binned together and stacked along the *X*-axis [Colour figure can be viewed at wileyonlinelibrary.com]

microbial community immobilizes P during the cold season and reaches peak annual MBP in late-winter (Buckeridge, Banerjee, Siciliano, & Grogan, 2013). At snowmelt, microbes are exposed to freeze-thaw stress and/or osmotic changes associated with the phase shift in water from frozen to liquid state (Jefferies, Walker, Edwards, & Dainty, 2010). Although soil microbial communities at our study site

TABLE 4 Effects of annually deepened snow (snowfences) on soil soluble carbon, nutrient, and microbial biomass pools in the sampled soil layers after 8–9 years. Values are means ± 1 *SE* (n = 5), and significant main factor effects of treatment (or its interaction with time) that differ significantly from each other within soil layers are shown in bold as *$p \leq .1$; **$p \leq .05$, and ***$p \leq .01$. For simplicity, we do not show main effects of time alone. Note that mineral soils were frozen in June and therefore were not sampled (- indicates no data)

		Organic soil (0–10 cm)			Mineral soil (15–25 cm)		
Soil biogeochemical variable	Month	Controls	Snowfences	Treatment effect	Controls	Snowfences	Treatment effect
Soluble organic carbon (DOC) pool (mg C/m^2)	June	12,128 (1,347)	11,367 (565.2)	NS	-	-	NS
	July	11,413 (1,106)	12,501 (2,828)		6,586 (928)	4,680 (496)	
	August	8,585 (458.6)	8,009 (617.6)		7,754 (1672)	7,134 (399.4)	
DOC-specific UV absorbance ($SUVA_{254}$) (L mg C^{-1} m^{-1})	June	3.04 (0.34)	2.95 (0.36)	NS	-	-	NS
	July	-	-		4.38 (0.3)	4.37 (0.24)	
	August	-	-		-	-	
Soluble organic nitrogen (DON) pool (mg N/m^2)	June	744.8 (47.7)	781.9 (43.5)	NS	-	-	NS
	July	718.5 (74.9)	751.3 (148)		567.8 (77.3)	429.4 (39.1)	
	August	513.8 (46.1)	474.6 (38.1)		708.4 (163.7)	718.5 (89.6)	
Soluble NH_4^+ pool (mg N/m^2)	June	42.1 (6.2)	45.5 (5.1)	NS	-	-	NS
	July	44.3 (5)	52.7 (14.2)		46.9 (12.4)	26 (6.5)	
	August	22.6 (2.1)	23.6 (3.1)		35.7 (3.4)	38.8 (5.5)	
Soluble NO_3^- pool (mg N/m^2)	June	7.9 (2.2)	7 (1.9)	NS	-	-	*Treatment:* $F_{1,16} = 5.49$; $p = .03$
	July	10.1 (2.2)	9.3 (1.6)		**32.3 (11.9)**	**8.8 (2)** *	
	August	3.1 (0.5)	1.9 (0.7)		**26.7 (6.6)**	**15.2 (4.3)** *	
Soluble PO_4^{3-} pool (mg P/m^2)	June	**109.3 (31.4)**	**41.8 (11.9)** ***	*Treatment:* $F_{1,28} = 7.47$; $p = .01$	-	-	NS
	July	**166.1 (69.1)**	**50 (17.1)** ***		658 (322)	608.4 (145.3)	
	August	**107.4 (34.5)**	**56.9 (24.5)** ***		912.8 (544.4)	299.7 (57.9)	
Microbial biomass carbon (MBC) pool (mg C/m^2)	June	58,770 (2,504)	61,937 (554.1)	NS	-	-	NS
	July	51,841 (5,608)	54,221 (7,351)		6,166 (1,709)	5,901 (2,899)	
	August	52,182 (5,230)	49,510 (4,243)		12,248 (2,188)	8,133 (1,770)	
Microbial biomass nitrogen (MBN) pool (mg N/m^2)	June	4,930 (385.5)	5,659 (159.5)	NS	-	-	NS
	July	4912 (540.4)	4657 (870.8)		525.2 (152)	346.7 (132.9)	
	August	5033 (1479)	3853 (384.3)		762 (292.7)	680.2 (184.7)	
Microbial biomass phosphorus (MBP) pool (mg P/m^2)	June	**868.2 (242.1)**	**390 (134)** *	*Treatment:* $F_{1,28} = 3.76$; $p = .06$	-	-	*Treatment:* $F_{1,7.8} = 7.78$; $p = .02$; *Treatment* × *Time:* $F_{1,7.6} = 8.36$; $p = .02$
	July	**1051 (323.5)**	**785 (362)** *		**96 (30)**	**145.3 (68.7)** **	
	August	**972 (248)**	**535 (188)** *		**210.4 (24.4)**	**82.4 (33.3)** **	

are relatively resistant to freeze-thaw stress (Kumar, Grogan, Chu, Christiansen, & Walker, 2013), substantial microbial N and P are clearly released into the soil solution at this time (Buckeridge & Grogan, 2010; Buckeridge et al., 2013), suggesting that osmotic pressure changes are primarily responsible. Soluble P pools decline to about one-third of the snowmelt peak in just a few days (Buckeridge et al., 2013), presumably due to surface run-off or downward leaching into the soil, similar to observed land-to-water lateral DOC fluxes (Finlay, Neff, Zimov, Davydova, & Davydov, 2006).

We speculate that the low soil pH at our study site (Table 3), in combination with acidic snowmelt water inputs (De Caritat et al., 2005), maintains an acidic soil environment during spring thaw where PO_4^{3-} occurs primarily in its most soluble form as $H_2PO_4^-$ (Chapin, Shaver, & Mooney, 2002). The substantially enhanced volume of snowmelt water in the deepened snow treatment plots may therefore have exacerbated P loss during each spring since the initiation of the snow treatment, leading to reduced organic soil MBP and PO_4^{3-} pools after 8 and 9 years. Mineral soil layer NO_3^- pools were

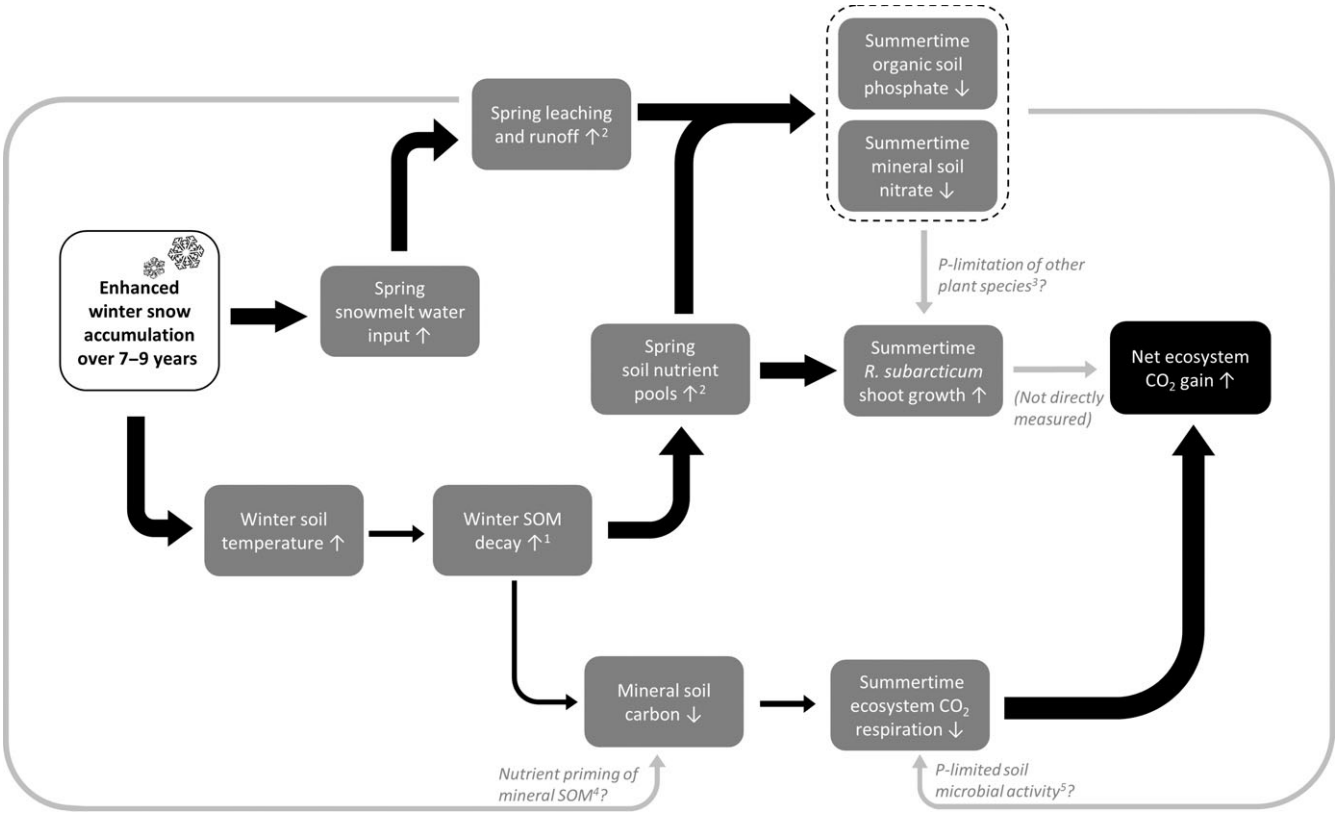

FIGURE 4 Conceptual diagram illustrating ecosystem feedbacks associated with deepened snow over 7–9 years in mesic low stature birch hummock tundra. The feedbacks included as black arrows are based exclusively on observed treatment effects in the present study, except for [1]Nobrega and Grogan (2007), and [2]Buckeridge and Grogan (2010), both of which used the same experimental plots as this study. Gray arrows indicate other potential feedbacks that are not directly supported by the observations in this study, but in [3]Zamin et al. (2014), [4]Mack et al. (2004), and [5]Manzoni et al. (2012). Note that additional possible impacts and feedbacks not included here (e.g., shifts in soil microbial community structure and physiology) may likely also be important, and that other tundra vegetation types could respond differently to deepened snow. Arrow sizes indicate the relative magnitude of the mechanistic effects between linked factors. See text for Discussion

also reduced (by 43–73%) in the snowfences, further suggesting that highly mobile nutrients such as nitrate may have been leached downwards in the soil profile. By contrast, PO_4^{3-} often binds to mineral surfaces and forms insoluble precipitates through anion exchange (Chapin et al., 2002), which may explain why mineral soil layer PO_4^{3-} was unaffected by deepened snow.

To the best of our knowledge, our study is the first to investigate soluble PO_4^{3-} dynamics following experimentally deepened snow. MBP generally accounts for ~30% of tundra soil organic P (Jonasson, Michelsen, & Schmidt, 1999), making MBP an essential ecosystem pool of potentially available P (i.e., phosphorus protected from mineral complex-interactions). Therefore, the observed dramatic reductions in P availability (and potential availability, MBP) may have strong effects on both plant production and microbial activities throughout the year, including subsoil mineral C storage (Mack, Schuur, Bret-Harte, Shaver, & Chapin, 2004; Nowinski, Trumbore, Schuur, Mack, & Shaver, 2008). For example, P co-limits plant growth together with N in most terrestrial ecosystems (Harpole et al., 2011), and this is also the case for the deciduous shrub *Betula* and the sedge *Eriophorum* at our study site (Zamin & Grogan, 2012; Zamin et al., 2014). More than 90% of the roots in this tundra ecosystem occur within the upper 10 cm (Churchland, Mayo-Bruinsma, Ronson, & Grogan, 2010), and decreased organic soil PO_4^{3-}, due to downward leaching and/or surface runoff, is very likely to influence plant productivity, and potentially community structure, as well as stoichiometric regulation of microbial decomposition activities and C-use efficiency (Manzoni, Taylor, Richter, Porporato, & Ågren, 2012).

4.4 | Effects of the snowfence treatment on soil carbon

Despite substantial intra- and inter-plot variation (Figure 3a), we observed a marginally significant statistical trend for reduced mineral soil layer %C in our deepened snow plots ($p = .08$; Table 3). It is well known that warmer winter soils under deepened snow enhance wintertime CO_2 efflux (up to a factor of 2.5; Larsen et al., 2007; Morgner et al., 2010; Natali et al., 2014; Schimel et al., 2004), including at our study site (Nobrega & Grogan, 2007). Microbial decomposition of recalcitrant as compared to labile SOM compounds is more sensitive to warming, due to greater activation energies required for enzymes to degrade lower quality SOM (Ågren &

Wetterstedt, 2007; Davidson & Janssens, 2006), and higher liquid water retention (Drotz, Sparrman, Schleucher, Nilsson, & Oquist, 2010) which drives microbial decomposition in frozen soils (Davidson & Janssens, 2006; Tilston, Sparrman, & Oquist, 2010). The snowfences increased winter soil temperatures similarly in both organic and mineral soil layers (up to 6°, Figure 1 and Table S2), and mineral soil C/N ratios and DOC-SUVA both suggest lower quality C substrate relative to the organic soil layer, indicating that the relative treatment effect (i.e., warmer winter soils) on CO_2 production should be greater at depth. Nevertheless, increased cold season CO_2 efflux in the deepened snow plots clearly cannot explain the full magnitude of mineral soil C loss (2375 g C/m^2, Table 3). We estimated that enhanced winter respiration from the mineral soil layer after 9 years of snow treatment could result in losses ranging from 227 to 518 g C/m^2 (as CO_2) using two completely separate calculation approaches (See Supplementary Information). Therefore, other processes must have contributed to the observed decline in mineral soil C%.

Stimulation of subsoil greenhouse gas production from downward leaching of solutes has recently been reported following experimental summer-warming (using OTCs) in sub-Arctic tundra (Voigt et al., 2016). Soil dendritic channels and pore spaces allow for downward transport of soluble nutrients to deeper soil layers at snowmelt (Jefferies et al., 2010), and priming of microbial decomposition of mineral soil layer OM by enhanced snowmelt water fluxes of N, P, and/or other unmeasured C and nutrient components from above may have contributed significantly to the observed reductions in mineral soil C (Mack et al., 2004; Nowinski et al., 2008; Wild et al., 2014). In addition, the heterogeneity in C concentrations across all our soil samples clearly indicates that physical mixing of organic and mineral soil layers is common at our site (Figure 3b). Cryoturbation stimulates C mineralization by enriching mineral soil with organic matter (Davidson & Janssens, 2006; Klaminder, Giesler, & Makoto, 2013; Michaelson & Ping, 2003). The greater snowmelt water input in the deepened snow plots may have enhanced cryoturbation and the consequent decomposition of SOM in the mineral layer. Alternatively, enhanced cryoturbation may have moved C-poor mineral soil from the base of the active layer upwards, potentially "diluting" the C concentration of the upper mineral soil layer that we sampled, and explaining some of the observed "depletion" as simply a redistribution of C within the soil profile.

Arctic soil C content is notoriously heterogeneous across small and large scales along both vertical and lateral dimensions. Natural landscape variability in snow cover and accumulation, driven by topography, has been found to correlate inversely with soil C storage patterns (Borner, Kielland, & Walker, 2008), but whether this is due to direct abiotic effects of deepened snow or rather plant–soil interactions (or both) is not currently well understood as tundra vegetation changes can promote soil C loss (Hartley et al., 2012; Parker, Subke, & Wookey, 2015; Wilmking, Harden, & Tape, 2006). Nevertheless, our study illustrates a trend toward reduced upper mineral layer soil C concentrations across replicate snowfence plots, and we hope our data here will prompt future research on effects of deepened snow on soil profile C storage.

Overall, there is now mounting evidence that changes in winter climate have sufficient potential to significantly affect summertime tundra plant and soil processes, and thereby to change ecosystem carbon balance (Figure 4). Our relatively long-term results, together with snowfence studies in other tundra vegetation types, suggest that future species' response patterns to deepened snow will vary depending on initial vegetation type and edaphic properties. In addition, deciduous shrub growth in particular appears more likely to respond to growing season lengthening and summer warming rather than deepened snow alone.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTION

C.T.C. and P.G. conceived the scientific objectives, analyzed the data, and wrote the paper. P.G. and G.H.R.H. established the experimental plots, and C.T.C. collected all field and lab data, except plant cover data (G.H.R.H.) and DOC-SUVA analyses (M.J.L.).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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