

Divergent carbon cycle response of forest and grass-dominated northern temperate ecosystems to record winter warming

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Abstract

Northern temperate ecosystems are experiencing warmer and more variable winters, trends that are expected to continue into the foreseeable future. Despite this, most studies have focused on climate change impacts during the growing season, particularly when comparing responses across different vegetation cover types. Here we examined how a perennial grassland and adjacent mixed forest ecosystem in New Hampshire, United States, responded to a period of highly variable winters from 2014 through 2017 that included the warmest winter on record to date. In the grassland, record-breaking temperatures in the winter of 2015/2016 led to a February onset of plant growth and the ecosystem became a sustained carbon sink well before winter ended, taking up roughly 90 g/m² more carbon during the winter to spring transition than in other recorded years. The forest was an unusually large carbon source during the same period. While forest photosynthesis was restricted by leaf-out phenology, warm winter temperatures caused large pulses of ecosystem respiration that released nearly 230 g C/m² from February through April, more than double the carbon losses during that period in cooler years. These findings suggest that, as winters continue to warm, increases in ecosystem respiration outside the growing season could outpace increases in carbon uptake during a longer growing season, particularly in forests that depend on leaf-out timing to initiate carbon uptake. In ecosystems with a perennial leaf habit, warming winter temperatures are more likely to increase ecosystem carbon uptake through extension of the active growing season. Our results highlight the importance of understanding relationships among antecedent winter conditions and carbon exchange across land-cover types to understand how landscape carbon exchange will change under projected climate warming.

KEY WORDS

eddy covariance, grassland, land use, phenology, snow, temperate forest, vernal transition, winter climate change

1 | INTRODUCTION

Climate change in northern temperate regions has been most pronounced during the winter, a pattern that is expected to continue into

the future (Hayhoe et al., 2007; Notaro, Lorenz, Hoving, & Schummer, 2014; USGCRP, 2017). As winter temperatures rise and snow depth and duration decline (Burakowski, Wake, Braswell, & Brown, 2008; Choi, Robinson, & Kang, 2010; Contosta et al., 2019), the insulative

effect of consistent snowpack on soils is reduced, leading to greater winter soil temperature variability with consequences for ecosystem carbon (C) metabolism (Henry, 2008; Kreyling & Henry, 2011). Moreover, the timing of critical springtime transitions, such as snow melt, soil thaw, and leaf-out are altered (Contosta et al., 2017). The timing and order of these vernal transitions have substantial influence on interannual variability in productivity and C sequestration (Danielewska, Urbaniak, & Olejnik, 2015; Hufkens et al., 2016; Keenan et al., 2014; Ouimette et al., 2018; Richardson et al., 2013).

While there has been considerable interest in how earlier springs will affect annual C exchange through extended growing seasons, the directional effects of warm winters and early vernal transitions on C uptake and loss during the winter to spring transition have not been consistent across studies or vegetation types. Warm winters with early snowmelt often lead to longer growing seasons, which can enhance annual ecosystem C uptake (Danielewska et al., 2015; Delpierre et al., 2009; Galvagno et al., 2013; Keenan et al., 2014; Pulliainen et al., 2017; Wolf et al., 2016). However, the early loss of snow can also lead to photosynthesis occurring during unfavorable conditions (Winchell, Barnard, Monson, Burns, & Molotch, 2016), arrested physiological development of vegetation (Galvagno et al., 2013), or enhanced water stress (Arnone et al., 2008; Hu, Moore, Burns, & Monson, 2010) that offset C gains from the elongated growing season. The influence of winter and early spring conditions on ecosystem C losses has also been mixed. Increased winter soil temperature variability has been shown to suppress ecosystem C losses where absence of an insulative snow buffer causes cooler soils (Brooks, McKnight, & Elder, 2004; Monson et al., 2006; Muhr, Borken, & Matzner, 2009), but can stimulate soil respiration following soil freezing events (Maljanen, Alm, Martikainen, & Repo, 2010; Reinmann & Templer, 2018) or when early snow melt causes rapid soil warming (Guo et al., 2018; Welp, Randerson, & Liu, 2007). A generalized understanding of how the balance between ecosystem C uptake and C loss responds to warming winter and spring conditions remains elusive.

Due to recent and continuing forest conversion in northern temperate regions (Olofsson, Holden, Bullock, & Woodcock, 2016; Thompson, Plisinski, Olofsson, Holden, & Duveneck, 2017), there is a need to understand how winter climate change will affect C cycling in both forested and nonforested ecosystems across mixed-use landscapes. Differences among vegetation types in the physiological

mechanisms driving seasonal changes in C assimilation mean that contrasting land cover will likely express differential responses to warm antecedent winter conditions. In winter 2015/2016 (hereafter referred to as winter 2016), the northeastern United States experienced an extremely warm winter, with mean air temperatures that broke long-term records in all seven New England states (NCEI, 2017). At 4.3°C above the 20th century mean, winter 2016 was accompanied by very little snowfall or snowpack accumulation (NCEI, 2017). Because these conditions fall within the 3.1–5.3°C range of projected winter warming for the end of the 21st century in this region (Hayhoe et al., 2007; Notaro et al., 2014), the 2016 winter provides an opportunity to examine how ecosystems will respond to future winter climate. Here we used this natural experiment to evaluate how warm winters in northern temperate ecosystems affect ecosystem C cycling during the winter to spring transitional period across a mixed forest and a perennial grassland.

We examined eddy covariance carbon dioxide (CO_2) flux measurements during the winter to spring transitional period at a mature, mixed evergreen-deciduous temperate forest and a colocated managed perennial grassland near Durham, NH, for 4 years, including the period following the extreme winter of 2016. We present data from the winter to spring transitional period for 2014, 2016, and 2017 at the grassland and 2015, 2016, and 2017 at the forest. Data gaps prevented inclusion of all years at both sites, but similar conditions in 2014 and 2015 provide a meaningful comparison of ecosystem response to cold and snowy conditions versus record winter warming in 2016. We used a 15 year record of climate data available from the United States Climate Reference Network (USCRN; Bell et al., 2013; Diamond et al., 2013) and United States Historical Climate Network (USHCN; Williams, Jr., Menne, Vose, & Easterling, 2006) to characterize mean winter to spring conditions in Durham, NH, along with site-level meteorological and modeled (Flerchinger & Saxton, 1989a) snow depth data to describe the individual site conditions during years in our record.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted at two sites dominated by contrasting vegetation cover located within 8 km of one another in Durham, NH (Figure 1). Kingman Farm (43°10'19"N, 70°57'15"W; 34.5 m a.s.l.) is a

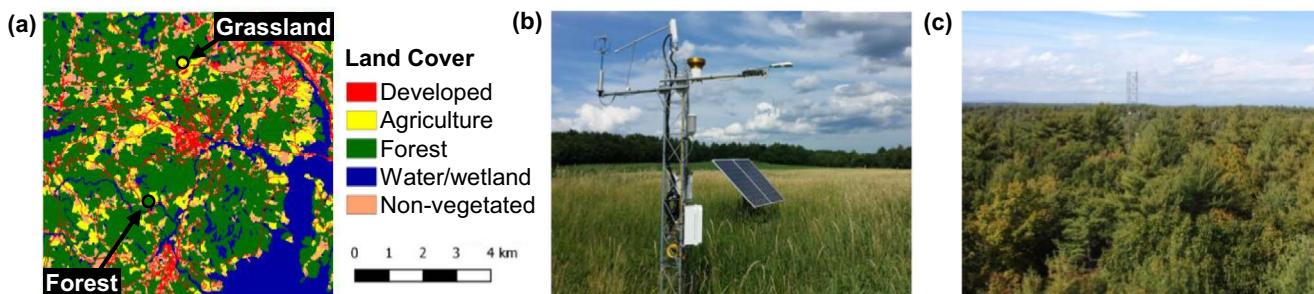


FIGURE 1 (a) Land-cover map of Durham, NH, and surrounding areas with location of two eddy covariance flux towers. (b) Photo of flux tower above grassland at Kingman Farm. (c) Photo of flux tower above mixed forest [Colour figure can be viewed at wileyonlinelibrary.com]

perennial grassland managed for hay production, and Thompson Farm ($43^{\circ}06'32''\text{N}$, $70^{\circ}57'03''\text{W}$; 23.3 m a.s.l.) is a mature, mixed deciduous temperate forest. The sites are characterized by a cool temperate climate with a mean annual air temperature of 8.9°C , mean winter air temperature of -3.0°C , mean annual precipitation of 1,170 mm, and annual snowfall of 114 cm from 1981 to 2010 (New Hampshire State Climate Office, 2014). The sites are located in a mixed landscape dominated by forest, developed, and agricultural land uses (Justice, Deely, & Rubin, 2002; Figure 1). The Kingman Farm grassland has been under agricultural management for research and crop production since the mid-1850s (Langley-Turnbaugh & Keirstead, 2005). During this study, the site was under management for C3 non-arctic grasses (*Panicum* sp., *Spartina* sp., *Medicago sativa*) harvested three to four times each year. The Thompson Farm mixed forest is approximately 100 years old. Basal area is 49% evergreen needle-leaf and 51% broadleaf deciduous composed primarily of red maple (*Acer rubrum*), red oak (*Quercus rubra*), and white pine (*Pinus strobus*) with a dense understory of other broadleaf deciduous species.

2.2 | Meteorological data

To characterize long-term average winter conditions during the winter to spring transition at the study sites, we acquired high-quality meteorological data from 2002 to 2017 from two USCRN stations colocated with the study sites (Bell et al., 2013; Diamond et al., 2013). The USCRN Durham 2N station is located 400 m west of the Kingman Farm grassland tower and the USCRN Durham 2SSW station is located in a grassland 400 m east of the Thompson Farm forest tower. Both stations record subhourly air temperature at 1.5 m, soil temperature at 5 cm depth, and precipitation. Daily snow depth data for Durham, NH, during the study period (2014–2017) were acquired from the USHCN station USC00272174 (Williams, Jr. et al., 2006) and used to characterize local winter snow conditions in each of the study years. Mean values and standard deviations of daily December–April air temperature, soil temperature, and snow depth were computed across both sites for the entire USCRN record (2002–2017 for air temperature and snow depth and 2010–2017 for soil temperature) and the time series were smoothed to a 14 day rolling mean. We also calculated the number of days in each winter with snow depth greater than 10 cm in Durham, NH, from the USHCN dataset to characterize snow cover in each study year. We used tower observations (see below) of air and soil temperature at each site in 2016 and 2017 (when we had daily paired measurements) to determine whether there were site differences in mean monthly air and soil temperatures during the winter to spring transition period (February–April).

2.3 | Estimated snow depth

Snow depth data from the single USHCN station were insufficient for comparing snow cover between study sites of differing land uses. Instead, daily snow depth was estimated for each site using the Simultaneous Heat and Water Flux (SHAW) model Version 3.0

(Flerchinger & Saxton, 1989a). SHAW uses an energy balance approach to calculate transfers of heat, liquid water, and water vapor that occur across ecosystem layers including the canopy, snowpack, and soil. Site-specific model parameters include vegetation and soil structural characteristics that allow for simulation of distinct patterns of snow accumulation and melt in an open field and beneath a forest canopy. The SHAW model's snow depth predictions have been successfully validated at both agricultural and forested sites (Campbell et al., 2010; Flerchinger & Saxton, 1989b). The model was driven for each site by hourly climate measurements from the respective towers (see below), including air temperature, wind-speed, relative humidity, precipitation, and solar radiation from 2013 to 2017. Daily snow depth measurements at Thompson Farm forest (below canopy) and in an open grassland adjacent to the forest from winter 2016/2017 were used to validate the modeled snow depth at forest and grassland cover types, respectively. The model slightly underpredicted snow depth (mean bias = -2 cm) at the forest and overpredicted snow depth at the grassland (mean bias = $+1.3\text{ cm}$; Figure S1). However, overall model error was low (root mean squared error [RMSE] = 6.5 cm at the forest and 9.8 cm at the grassland) and the relative magnitude of snow depth and timing of snowmelt across years was supported by USHCN snow data.

2.4 | Net ecosystem exchange

Tower-based sensors were installed at each site in early 2014 to sample fluxes of CO_2 via the eddy covariance technique. Each tower was equipped with a LI-COR 7200 enclosed path $\text{CO}_2/\text{H}_2\text{O}$ analyzer, Gill Windmaster 3D sonic anemometer, and a suite of meteorological sensors that include air and soil temperature/humidity probes and a net radiometer. Sensors were deployed at 3.6 m height at the grassland and at 32 m height at the forest. Eddy covariance data were collected at a frequency of 10 Hz and ancillary meteorological data every minute. Half-hourly fluxes of CO_2 were computed from the covariation of high frequency vertical wind direction and CO_2 concentration using the EddyPro software package (Version 6.2.1, LI-COR Biosciences). We report CO_2 fluxes as net ecosystem exchange (NEE), where negative values indicate net uptake of CO_2 by vegetated land surface and positive values indicate net loss of CO_2 to the atmosphere. Nighttime measurements of CO_2 fluxes made during low-turbulence conditions with potential advective losses of CO_2 (Aubinet, 2008) were identified and removed when friction velocity, u^* , was below a calculated site-specific threshold (Papale et al., 2006). To account for uncertainty in u^* threshold estimation, bootstrapping was applied to u^* threshold estimates and we report a range of cumulative fluxes calculated based on the 5% and 95% estimates (Papale et al., 2006; Wutzler, Reichstein, Moffat, & Migliavacca, 2018). Gapfilling of CO_2 fluxes was performed using the marginal distribution sampling methodology (Reichstein et al., 2005). All u^* estimation and CO_2 flux gapfilling were conducted with the R-based (R Core Team, 2016) eddy covariance processing tool, 'REddyProc' (Wutzler et al., 2018).

To determine how both C assimilation and ecosystem respiration responded to variation in winter to spring conditions at each site,

we examined the timing of net daytime and net daily C uptake initiation and the temperature sensitivity of nighttime NEE as a proxy for ecosystem respiration. We restricted our analyses to NEE data (not partitioned into gross primary production and ecosystem respiration) because the error associated with partitioning is large relative to measured NEE during the winter to spring transition. We identified the initiation of C assimilation as the start of daytime net C uptake, defined as the day of year when mean daytime (incoming solar radiation $>20 \text{ W/m}^2$) NEE reached 5% of its maximum annual value ($-0.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at both sites) based on a 5 day running mean (Ouimette et al., 2018). Similarly, the day of the year when C uptake began to exceed C losses and the ecosystem became a net C sink was identified as the start of daily net C uptake, and defined as the day when mean daily NEE (averaged over day and night) exceeded 5% of its annual maximum ($-0.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at both sites) based on a 5 day running mean. Varying u^* threshold selection did not affect estimation of these transition dates (data not shown). Due to the mixed deciduous and evergreen makeup of the forest canopy, we also quantified the timing of deciduous canopy leaf-out phenology in order to determine whether early season C uptake was driven primarily by evergreen species or by a combination of evergreen and deciduous species. We calculated a mean daily ratio of half-hourly incoming photosynthetically active radiation (PAR) simultaneously measured above and below the forest canopy (LI-COR 190-R Quantum Sensor) during peak daylight (above canopy PAR $> 1,000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The ratio declines precipitously as deciduous leaves emerge and intercept incoming radiation and provides an index for the timing of deciduous canopy development (Breda, 2003).

To examine the dependence of winter to spring ecosystem respiration on soil temperature, a Q_{10} response function (Black et al., 1996; Equation 1) was fit to half-hourly, u^* filtered, nongapfilled data restricted to nighttime conditions (defined as incoming radiation $<10 \text{ W/m}^2$ and used as a proxy for ecosystem respiration).

$$R_T = R_{T_{\text{ref}}} \times Q_{10}^{(T-T_{\text{ref}})/10} \quad (1)$$

Data were limited to February through April and soil temperatures during this period ranged from 0 to 15°C . In Equation (1), R_T is the ecosystem respiration (nighttime NEE) at a given soil temperature, T is the soil temperature in $^\circ\text{C}$, T_{ref} is a reference soil temperature of 5°C , and Q_{10} and $R_{T_{\text{ref}}}$ are fitted parameters representing the temperature sensitivity of respiration to a 10°C increase in soil temperature and rate of respiration at the reference soil temperature, respectively. We report the fitted parameters with a 95% confidence interval and the RMSE of the model fit for each year at each site.

The cumulative sum of NEE was calculated for an 86 day period from February (DOY 34) to April (DOY 120) in each year to capture the variation and magnitude of fluxes during the vernal transition period. Within this February through April period, original or high-quality gapfilled half-hourly data (Wutzler et al., 2018) comprise 93% of data points at Kingman Farm grassland and 92% of data points at Thompson Farm forest. We also compared the annual course of 14 day smoothed NEE across the study years to assess how the

magnitude of NEE during the winter to spring transition compares to the year as whole. In order to calculate an annual NEE estimate for each year despite data gaps (~2–4 weeks) during 2015 at the forest and 2016 at the grassland, we used multiple imputation (Hui et al., 2004) based on predictive mean matching using the ‘mice’ package for R (Version 3.5, Buuren & Groothuis-Oudshoorn, 2011).

3 | RESULTS

Similar to the region overall (NCEI 2017), mean air temperatures during meteorological winter (December, January, February) of 2016 were the warmest on record at -0.2°C , well above the 15 year mean across sites of $-3.3 \pm 1.7^\circ\text{C}$ for Durham, NH. Mean air temperatures across sites remained warmer than average through the winter to spring transition

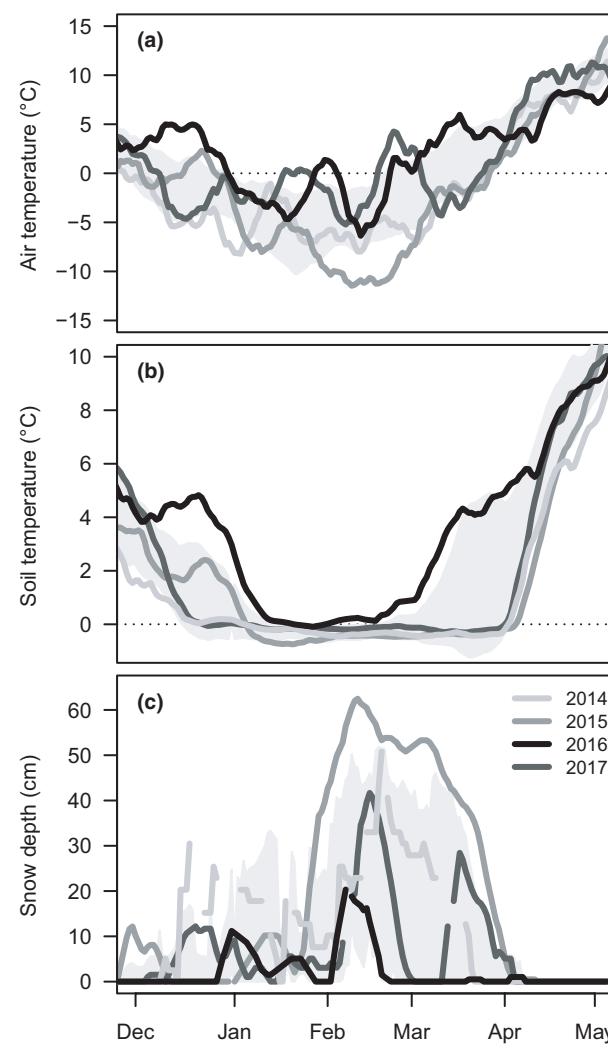


FIGURE 2 Meteorological conditions from the beginning of winter (DJF) through the winter to spring transition (FMA) in Durham, NH, from 2014 to 2017, including (a) air temperature, (b) soil temperature, and (c) snow depth along with the standard deviation about the Durham site record mean represented by the gray shaded regions. Air and soil temperature data represent the mean values across both sites derived from USCRN and snow depth data is derived from USHCN

period (Figure 2a). Mean winter soil temperatures across sites were generally more stable than air temperatures both across and within years (Figure 2b). However, in 2016 soil temperatures warmed early in the year resulting in a mean soil temperature of 3.7°C during the winter to spring transition period of February through April, well above the mean of $2.4 \pm 1.2^{\circ}\text{C}$ for this period of the year (Figure 2b). Although total winter precipitation was similar across years (ranging from a winter total of 299.9–303.7 mm for December through February), snow accumulation varied widely. The total number of days with at least 10 cm of snow cover ranged from a low of 11 days in 2016 to a record high of 58 days in 2015 (Figure 2c). Overall, the winters in this study can be characterized as follows: winters 2014 and 2015 were relatively cold and with intermediate to high snow, winter 2016 was extremely warm with very little snow and warm soils, and winter 2017 was moderately warm with intermediate snow cover.

There were measurable differences between sites in environmental conditions measured at the flux towers during the winter to spring transition. During the 2 years with tower data available for both sites (2016 and 2017), the monthly air temperatures in February, March, and April were on average $0.63 \pm 0.09^{\circ}\text{C}$ cooler at the grassland than

the forest ($p < .001$ for all months, Figure S2). However, in February 2016 and 2017 soil temperatures at the grassland were significantly cooler by $0.83 \pm 0.22^{\circ}\text{C}$ ($p < .0001$) and in April, significantly warmer than the forest by $1.86 \pm 0.39^{\circ}\text{C}$ ($p < .0001$; Figure S2). Modeled snowpack closely agreed with the USHCN Durham observations (Figure S1), although there were subtle differences between sites in maximum snow depth and snow melt timing (Figure 3). Following the cold and snowy winters of 2014 and 2015 at the grassland and forest sites, warming air temperatures led to a single snow melt event in early April (DOY 94 at the grassland in 2014 and DOY 91 at the forest in 2015) that coincided with a rapid increase in soil temperature, whereas in both 2016 and 2017 there were multiple snow melt events (Figure 3).

Fluxes of CO_2 responded strongly to snow melt in most winters. Both sites experienced an abrupt transition (<5 days) from a stable winter state of near-zero NEE to a more dynamic daily flux following the completion of snow melt. During the extremely warm winter of 2016, the ground became consistently snow-free in mid-February (DOY 51 at the grassland and DOY 53 at the forest), approximately 5 weeks early relative to other years in the

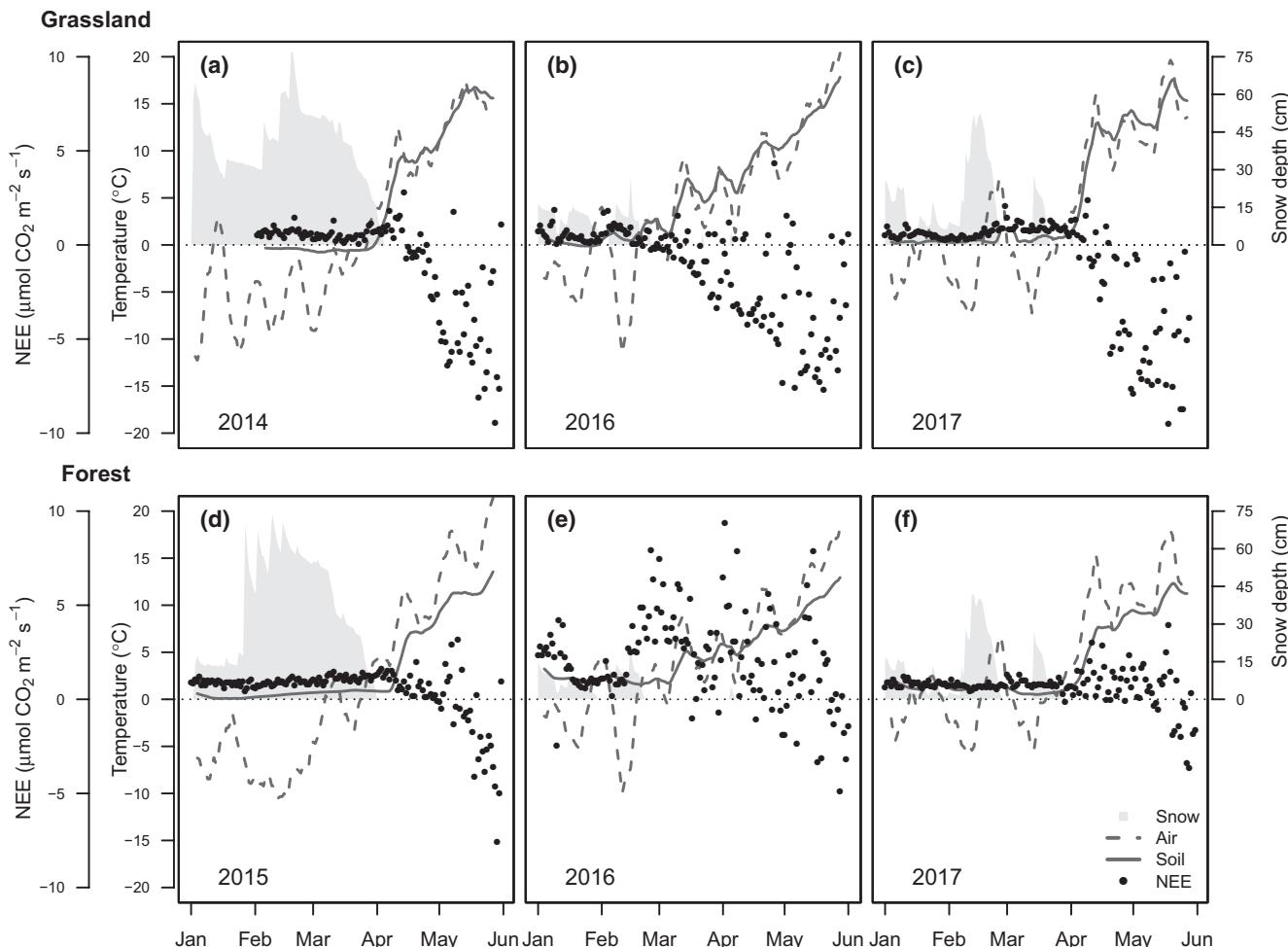


FIGURE 3 Time series of modeled snow depth (right axis), air and soil temperature (left inner axis), and mean daily net ecosystem exchange (NEE; left outer axis) from January through May in 2014, 2016, and 2017 at the grassland (a–c) and 2015, 2016, and 2017 at the forest (d–f). Data gaps prevented inclusion of all years for both sites

record, and the stable winter condition of near-zero NEE ended much earlier at both sites. In 2016, net C uptake at the grassland began 2 days before the early snow melt in February. In contrast, the forest experienced large C losses during the same period, with pulses of ecosystem respiration coinciding with periods of warm soil and air temperatures occurring before leaf-out and consequently there was a long lag (over 90 days) between snow melt and the time at which the forest eventually became a consistent C sink. Although air temperatures in winter 2017 were above average (Figure 2), snow melt timing differed by only 4–8 days from the cooler winters of 2014 and 2015, but was nearly 5 weeks later (DOY 86 at the grassland and DOY 87 at the forest) than in the record warm winter of 2016. Vernal transitions of snow, soil, and air temperatures, and NEE were near simultaneous in 2017, similar to the cold snowy winters of 2014 at the grassland and 2015 at the forest (Figure 3).

We used the start of daytime net C uptake as a proxy for the initiation of gross primary production, or C assimilation, defined as the date when sustained negative NEE during the daytime (defined by incoming radiation $>20 \text{ W/m}^2$) began. The start of daily net C uptake was identified to determine when the ecosystem switched from a C source to a net C sink, defined by the date when sustained negative daily (including both day and night) averaged NEE began. Using a 5 day running mean, we determined that both daytime net C uptake and daily net C uptake started earlier in spring at the grassland than the forest throughout the period of record. Following the warm winter of 2016, daytime net C uptake began early relative to the other years measured at both sites (Figure 4). At the grassland, daytime net C uptake began on February 18, 2016 (DOY 49), a time that normally represents the peak period of winter in New Hampshire. This was 56 days earlier than in 2014 (DOY 105) and 48 days earlier than in 2017 (DOY 97). At the forest, daytime net C uptake began on March 14, 2016 (DOY 74), 42 days earlier than in 2015 (DOY 116) and 36 days earlier than in 2017 (DOY 110).

In contrast to the onset of net daytime C uptake, the start of the net daily C sink period was slower to respond to warm conditions at both sites. While the grassland became a net daily C sink much earlier in 2016 relative to other years, the forest did not. The grassland switched from a C source to a C sink on March 14, 2016 (DOY 74), 34 days earlier than in 2014 (DOY 108) and 31 days earlier than in 2017 (DOY 105). The forest did not become a net C sink until May 24, 2016 (DOY 145), which was 11 days later than in 2015 (DOY 134) and 4 days later than in 2017 (DOY 141). As a result, the lag between the start of net daytime C uptake and the day the ecosystem became a net C sink was expanded in 2016 at both sites (Figure 4). At the grassland, this lag was 3 days in 2014, 8 days in 2017, and 25 days in 2016. The interval between the start of net daytime C uptake and the beginning of the net daily C sink was longer at the forest site, particularly in 2016. It was 18 days in 2015, 31 days in 2017, and 71 days in 2016. The deciduous canopy did not develop until after May 1 (DOY 121) in any study year, as indicated by the ratio of below to above canopy PAR (Figure 5).

Estimated Q_{10} values for nighttime NEE during the February–April winter to spring transition period ranged from 4.35 to 4.47 at

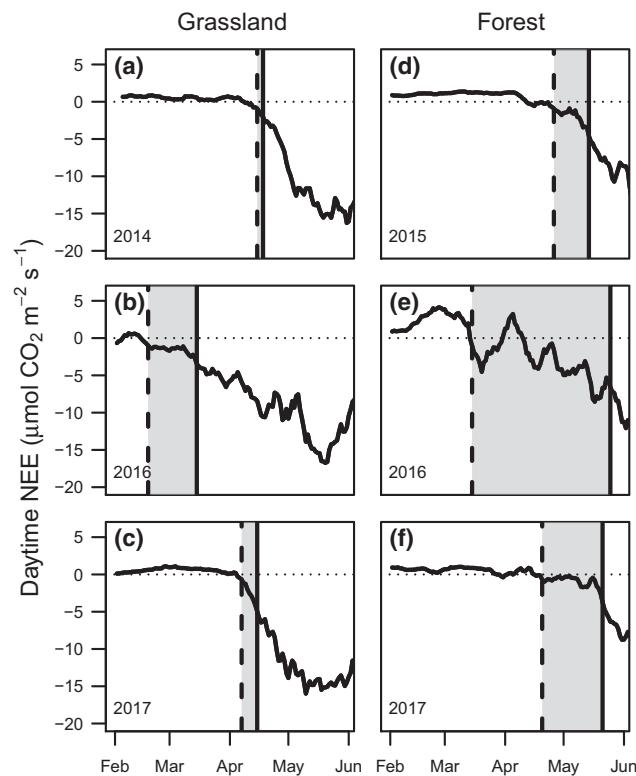


FIGURE 4 Mean daytime net ecosystem exchange (NEE) plotted as 5 day running mean from February through May at the grassland (a–c) in 2014, 2016, and 2017 and forest (d–f) in 2015, 2016, and 2017. Dashed vertical lines represent the start of daytime net carbon uptake and solid vertical lines represent the day ecosystem switched to a daily carbon sink with shaded area representing the lag time between the start of daytime and daily net carbon uptake

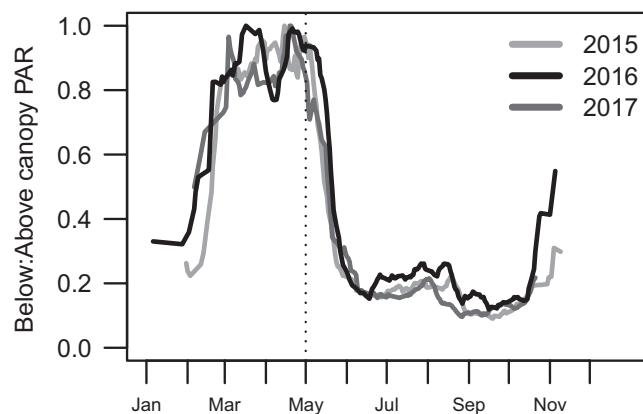


FIGURE 5 Timing of deciduous forest canopy development indicated through the normalized ratio of incoming photosynthetically active radiation (PAR) measured below and above the forest canopy. The dotted vertical line serves as a visual aid to demonstrate that this decline occurred after May 1 in each year

the grassland and from 3.61 to 4.65 at the forest site. Parameter estimates along with their associated uncertainties are presented in Table 1. Estimated Q_{10} was slightly lower at the grassland and

TABLE 1 Soil temperature response of February–April ecosystem respiration at the grassland and forest

	Grassland			Forest		
	Q_{10}	R_0	RMSE	Q_{10}	R_0	RMSE
2014	4.47 (4.13–4.81)	1.74 (1.68–1.80)	1.11	—	—	—
2015	—	—	—	4.44 (4.28–4.60)	1.62 (1.58–1.66)	1.15
2016	4.35 (4.08–4.62)	2.22 (2.18–2.26)	1.13	3.61 (3.39–3.83)	4.99 (4.84–5.14)	4.53
2017	4.39 (4.26–4.52)	2.07 (2.03–2.11)	0.93	4.65 (4.49–4.81)	1.55 (1.52–1.58)	0.96

Note: Estimated parameters with 95% CI presented in parentheses.

Abbreviation: RMSE, root mean squared error.

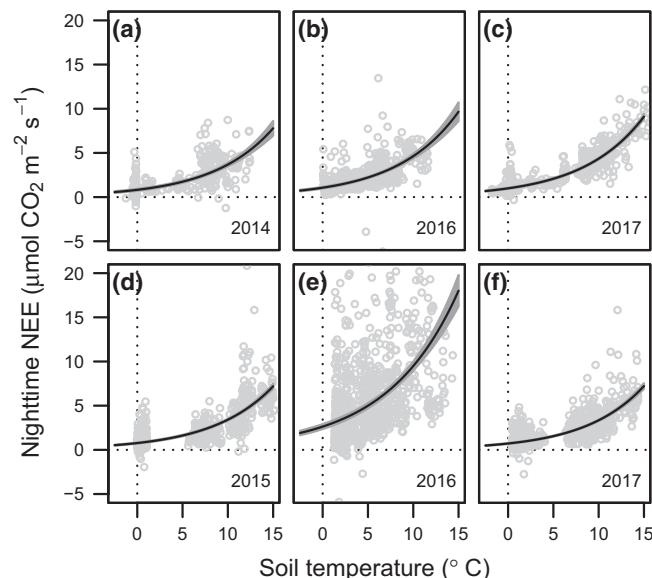


FIGURE 6 Temperature response curves of half-hourly nighttime net ecosystem exchange (a proxy for ecosystem respiration) to soil temperature during the winter to spring transition period (February, March, April) in 2014, 2016, and 2017 at the grassland (a–c) and 2015, 2016, and 2017 at the forest (d–f). Shaded regions represent the 95% confidence interval of the model (Equation 1) and gray points represent individual half-hourly measurements

significantly lower at the forest site during the warm winter to spring of 2016 (Table 1, Figure 6). At the grassland, basal ecosystem respiration at 5°C ranged from 1.74 to 2.22 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with a slight increase during 2016. However, estimated basal respiration at the forest in 2016 was 4.99 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, exceeding estimates for 2015 and 2017 (1.62 and 1.55, respectively; Table 1). The Q_{10} model fit also displayed a relatively high RMSE at the forest site in 2016. Notably, the presence of an insulating snowpack at the forest in 2015 and 2017 kept winter soil temperature stable and near freezing during winter with very rapid warming following snow melt. Due to these dynamics, there was a gap in nighttime soil temperatures observed approximately between 0 and 5°C during the transition from winter to spring during winters with ample snowpack (2015 and 2017; Figure 6).

The variable responses of C uptake timing across sites led to large differences in NEE during the winter to spring transition, which

TABLE 2 Cumulative winter to spring (February through April) and annual net ecosystem exchange (NEE) from 2014 to 2017

	Grassland		Forest	
	Winter to spring	Annual	Winter to spring	Annual
2014	37.3 (−37.6, −35.0)	−126.7 (−124.6, −137.4)	—	—
2015	—	—	87.0 (−82.5, −89.3)	−490.8 (−520.7, −479.7)
2016	−61.6 (61.6, 66.0)	−60.6 (−59.4, −81.9)	227.4 (−224.1, −284.2)	−238.1 (−255.7, −182.7)
2017	33.4 (−37.0, −31.8)	−11.4 (−1.5, −27.2)	85.5 (−82.3, −87.0)	−445.7 (−448.9, −440.1)

Note: Values are reported in g C/m² for either the 3 month period in each year or the entire year. Uncertainty is based on bootstrapping of u^* threshold estimation (5%, 95%).

dramatically altered cumulative C exchange during this period of the year (Table 2, Figure 7). In 2016, the grassland took up roughly twice the amount of C that it lost to the atmosphere during the same period in 2014 and 2017, an approximately 90 g C/m² increase in cumulative C uptake for this 3 month period (Figure 7c, Table 2). In contrast, the forest was a net C source during the winter to spring transition in all years, but the warm, snow-free winter of 2016 led to approximately 140 g C/m² additional C loss to the atmosphere relative to 2015 and 2017 (Figure 7d, Table 2). Despite variation in winter air temperatures between all measured years (Figure 2), C losses from both the grassland and the forest during the winter to spring transition was remarkably consistent across 2014 and 2017 for the grassland and 2015 and 2017 for the forest, with large differences observed only in the record warm winter of 2016.

The response of C cycling to the warm conditions in 2016 was important relative to the annual C uptake estimates for both sites. At the grassland, the total C uptake during the 2016 winter to spring transition was roughly equal to the total annual C uptake for that year (Table 2). Interannual comparisons in annual C uptake at the grassland, however, are confounded by the strong effect of management (especially in mid-growing season 2017) on annual C fluxes.

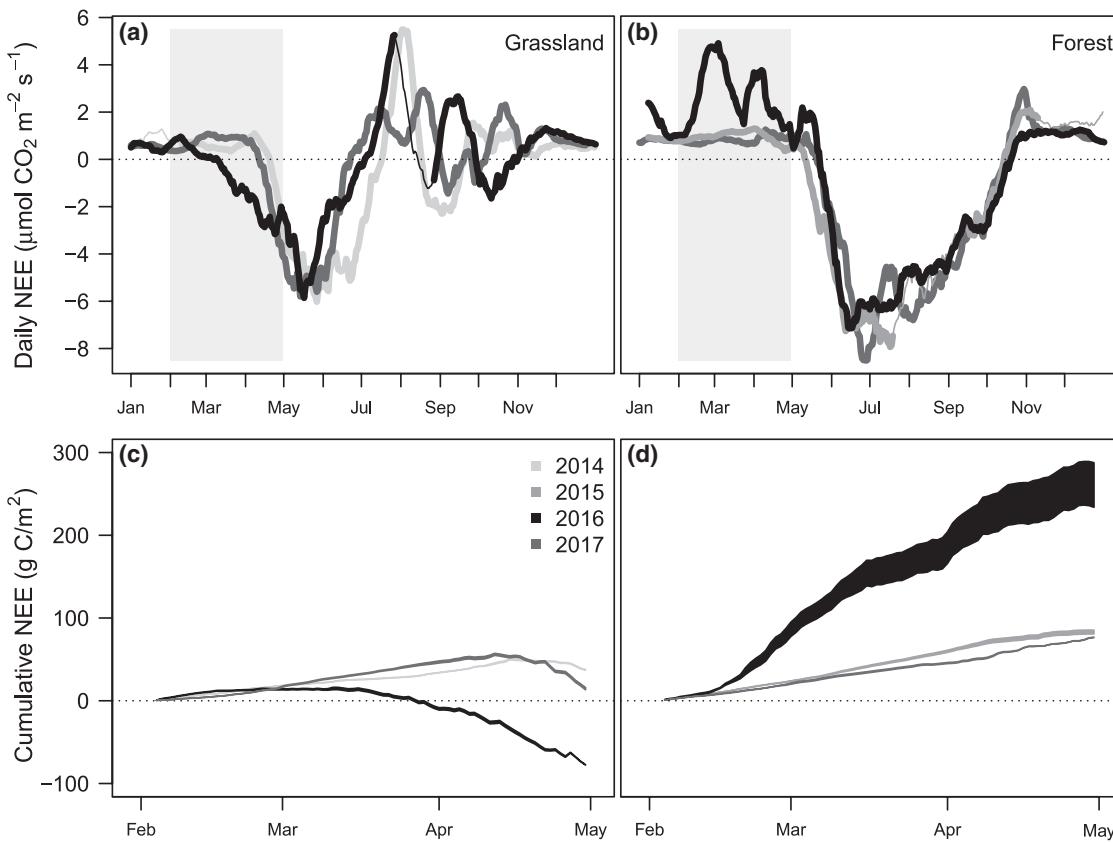


FIGURE 7 Mean daily net ecosystem exchange (NEE) across the year for (a) 2014, 2016, and 2017 at the grassland and (b) 2015, 2016, and 2017 at the forest. The dashed lines represent large gaps filled by multiple imputation for annual estimates. The gray shaded region marks the winter to spring transition period of February through April for which cumulative fluxes are shown in the lower panels for (c) the grassland and (d) the forest. The range of error for the cumulative fluxes associated with the 5% and 95% bootstrapped u^* estimates for data filtering prior to gapfilling is represented by the width of the colored areas for each year

In contrast, the large C losses at the forest during the 2016 winter to spring transition caused a ~50% reduction in total annual C uptake relative to 2015 and 2017.

4 | DISCUSSION

Warm winter air and soil temperatures in early 2016 led the grassland to become a cumulative sink for C early in the winter to spring transition. In contrast, the forest was a large source of C to the atmosphere during the same period. The strong, but divergent, C cycle responses observed across sites in 2016 are substantial relative to annual C exchange and appear to be driven by a combination of vegetation-specific limitations to leaf-out timing and interrelated anomalies in air temperature, snow cover, and soil temperature, rather than air temperature alone. Although winter temperatures in 2016 were record-breaking relative to recent history, these conditions are expected to be common by the end of the century when mean winter temperatures are projected to be 3.1–5.3°C warmer than the present (Hayhoe et al., 2007; Notaro et al., 2014). To our knowledge, this is the first report of how naturally occurring warm winter conditions affect C dynamics in paired temperate ecosystems of contrasting vegetation cover. These

observations provide novel insight into how C cycling will respond to winter climate warming across the landscape and suggest that early growing season carbon uptake and loss have important implications for net carbon exchange at both a seasonal and annual scale.

4.1 | Advanced C uptake in grasslands

Significant C uptake by the grassland during the 2016 winter to spring transition was likely driven by a combination of warm air temperatures and very little snow that enhanced winter light availability to vegetation. Perennial temperate grasses can photosynthesize at air temperatures as low as -4°C if suitable light is available (Skinner, 2007) and periods of mid-winter light enhance biomass accumulation of grasses in the early growing season (Vankoughnett, Way, & Henry, 2016). Although sustained net C uptake by the grasses only began after the final snow of the season had melted, daytime C assimilation was observed during transient snow-free periods as early as January 2016 (Figure S3). Grasses are particularly sensitive to pulses of warm temperature during the winter and early spring relative to the peak growing season (Nagelmüller, Kirchgessner, Yates, Hiltbold, & Walter, 2016; Wingler & Hennessy, 2016), and therefore can respond rapidly to advantageous conditions during periods of anomalous winter

warmth. The early C uptake in 2016 substantially altered the annual timing of C uptake at the grassland site. The cumulative net C uptake during February through April 2016 of -61.6 g C/m^2 is twice the magnitude of C loss during the same period in 2014 and 2017 and on par with the total C uptake during that year.

While this early C uptake was substantial in 2016, an advanced start to the growing season in grasslands does not necessarily imply greater NEE at an annual scale. Early C uptake during warm winters and/or early snow melt can be offset by sluggish gains in photosynthetic capacity (Galvagno et al., 2013), late-season frost damage (Henry, Hutchison, Kim, & McWhirter, 2014; Liu et al., 2018), increased winter respiration (Schuerings et al., 2013), and/or midsummer moisture stress (Ganjurjav et al., 2016). Our dataset is insufficient for testing how early C assimilation influenced interannual variation in cumulative annual NEE at this site due to changes in growing season management activities in 2017. However, despite differences in timing of management activities across the years there were no clear differences in broad patterns of peak NEE during the growing seasons following the winters of interest (Figure 7a). Productivity in temperate agricultural systems tends to be strong in years with mild winters across Europe (Bjerke, Tømmervik, Zielke, & Jørgensen, 2015) and models project that elongated growing seasons will enhance grassland NEE across the Midwestern United States, despite increased moisture stress (Hufkens et al., 2016; Wolf et al., 2016). Our results indicate a significant shift in seasonality with winter warming and the potential for a longer growing season for grasses in the northeast region. Whatever changes take place during other times of year, the rapid changes taking place during the winter to spring period will make this period increasingly important to annual C budgets and worthy of more careful scrutiny.

4.2 | Enhanced C loss in mixed forests

Although warm springs have been demonstrated to enhance annual gross C uptake of temperate forests by advancing leaf-out phenology (Keenan et al., 2014), our results suggest that extreme winter warming with reduced snowpack could lead to greater and earlier C losses that dominate the overall effect on net C balances. Although the temperature sensitivity of ecosystem respiration during the winter to spring period was generally similar between years, basal respiration throughout this period was elevated in 2016 indicating that the ecosystem was in a more active metabolic state. The early snow melt associated with shallow snowpack provided ample exposure of the forest floor to solar radiation beneath a relatively open canopy, warming soils, and stimulating respiration. This is reflected in the long delay in 2016 (over 10 weeks) between the beginning of net photosynthesis (as measured through net daytime C uptake) and the ecosystem switching to a daily C sink, with C uptake canceling out C loss. In contrast, the same window following the cold snowy winter of 2015 was just 2.5 weeks. Despite differences in the timing and magnitude of carbon fluxes during the winter to spring transition, patterns of NEE did not

differ dramatically during the remainder of the growing season across years, and therefore the early season C losses in 2016 were not offset by enhanced growing season C uptake. The 227.4 g C/m^2 cumulative C loss from the forested site in winter to spring of 2016 was nearly triple the C losses observed during the same period in other years of the study and caused a roughly 50% reduction in annual C sequestration. These findings suggest that predicting differences in the lag times for specific biotic processes such as ecosystem respiration, leaf expansion, and gross primary production is critical in understanding the long-term dynamics of C cycling in mixed temperate deciduous forests.

The length of time between initiation of daytime C assimilation and the system becoming a net daily C sink was moderated by the mixed evergreen-deciduous makeup of the canopy. Leaf-out of deciduous trees at the forest site did not occur until May in any of the study years (Figure 6), so all observed C uptake during the winter to spring transition quantified here is driven by evergreen species (mainly white pine), which comprised 49% of stand basal area. Although winter photosynthesis is limited by physiological factors beyond temperature and light availability in evergreen trees (Bowling et al., 2018), earlier snow melt and early season air warming often lead to advanced growing seasons that increase overall ecosystem C uptake in evergreen ecosystems (Barr et al., 2002; Pulliainen et al., 2017; Tanja et al., 2003). In contrast, the capacity of deciduous species to respond to warm winters and early season soil thaw is constrained by leaf-out timing, which is delayed substantially relative to activation of prior year evergreen needles (Hadley, O'Keefe, Munger, Hollinger, & Richardson, 2009). Increasing occurrence of favorable growing conditions in winter and early spring are therefore more likely to benefit C uptake by evergreen-dominated forest ecosystems (Novick et al., 2015).

While global observations indicate that the timing of leaf-out has been advancing at a rate of 3 days per decade (Parmesan, 2007), periods of unusual warmth in midwinter and very early spring are less effective at accelerating leaf-out than warm pulses that occur closer to the time that leaves emerge (Friedl et al., 2014). Furthermore, warm winters may partially counteract the accelerated bud burst and leaf-out that occur in a warm spring by delaying leaf-out due to insufficient winter chilling (Asse et al., 2018; Fu, Campioli, Deckmyn, & Janssens, 2012). Delayed leaf-out following warm winter and early spring conditions could extend the warm, but leafless period in deciduous forest ecosystems, leading to large C losses from the ecosystem before C uptake reaches full growing season capacity.

4.3 | Implications of winter to spring warming for broad-scale C cycling

There is compelling evidence that annual C fluxes from soils to the atmosphere are likely to increase with continued climate warming (Bond-Lamberty, Bailey, Chen, Gough, & Vargas, 2018; Crowther et al., 2016; Melillo et al., 2017). Yet, there is also substantial evidence to suggest that these increased C losses could be offset by elevated vegetation C uptake rates during

warmer growing seasons coupled with a lengthening of the C uptake period (Duvaneck & Thompson, 2017; Keenan et al., 2014; Richardson et al., 2018). Most studies exploring these contrasting C exchange dynamics focus on the period of C uptake activity, defined either directly through the onset of measured photosynthetic activity (e.g., gross primary production) or by proxies such as leaf-out or green up timing (Galvagno et al., 2013; Keenan et al., 2014). Our results suggest that, with rapid rates of warming in winter and early spring, the extension of the period of active ecosystem respiration could outpace the extension of the photosynthetically active growing season, particularly in deciduous forests where C uptake is strongly constrained by leaf-out phenology. Furthermore, the relatively high apparent temperature sensitivities that we observed ($Q_{10} \approx 3.6\text{--}4.6$) in the winter to spring period, which are in line with nongrowing season temperature sensitivities of nonfrozen soils documented in other studies in both grasslands (Tucker, 2014) and forests (Contosta, Frey, Ollinger, & Cooper, 2013), mean a greater potential amount of C loss for a given temperature increase as compared with the growing season. Failing to account for changes in C cycling that occur in the winter and early spring may substantially limit our understanding of how climate change will influence annual ecosystem C exchange.

Determining the overall effect of warmer winters on ecosystem C cycling requires careful consideration of the complex interplay among air temperature, soil temperature, and snow depth during winter (Groffman et al., 2001). Warmer winters with reduced snow depth and duration create more frequent bare ground conditions (Contosta et al., 2019), exposing soils and short stature vegetation to more dynamic winter weather. However, we observed high air and soil temperatures in the near snow-free record winter of 2016, winters with thin or intermittent snowpack that experience very cold and/or variable air temperatures can actually reduce soil temperatures and even induce deep soil freezing (Hardy et al., 2001). Experimental efforts to understand the effects of a shrinking snowpack on C fluxes in temperate ecosystems have often focused on the effects of these cooler soil temperatures and enhanced soil freezing conditions (Sanders-DeMott & Templer, 2017) with mixed results on the directional effect on C fluxes, especially in forests (Campbell & Laudon, 2019). While spells of below freezing winter air temperatures that cause soil freezing are expected to persist into the warming future (Cohen, 2016; Henry, 2008), the number of continuous days with frozen soil across temperate regions is expected to decline (Contosta et al., 2019; Henry, 2008). Snow-free conditions co-occurring with warm air temperatures, like those we observed in 2016, are likely to increase and are already becoming more common across many temperate regions (Contosta et al., 2019; Kreyling & Henry, 2011). While it is difficult to simulate both reduced snow and warmer temperatures in a controlled experiment under current climate conditions, the natural experiment afforded by the warm winter of 2016 provides insight into the large potential for C losses with warm winter soils and air.

4.4 | Conclusions

The effects of warmer winters on ecosystem C cycling will vary by vegetation type and the changing temporal dynamics of winter weather, moderated by snowpack and soil temperatures. Our observations from an extremely warm winter point to a longer period of favorable growing conditions for grasslands and an extended period of uncompensated ecosystem C losses early in the growing season for mixed and deciduous forests as winters warm. The cumulative changes to ecosystem C exchange during the winter to spring transition period have the potential to substantially alter net annual C uptake. The divergent carbon cycle responses from these two distinct northern temperate ecosystems provide important insights into how seasonal C cycles will respond to continued winter warming. These results highlight the value of understanding relationships among winter conditions and subsequent C exchange across land-cover types under the range of novel winter conditions expected with projected climate warming. Developing a better predictive understanding of the climatic controls on ecosystem C losses and uptake during winter and early spring is imperative for projecting how changing patterns of snow and temperatures will impact ecosystem function in northern temperate regions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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