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REVIEW

Carbon response to changing winter conditions in northern regions: current understanding and emerging research needs

John L. Campbell and Hjalmar Laudon

Abstract: Winter is an important period for ecological processes in northern regions; however, compared to other seasons, the impacts of winter climate on ecosystems are poorly understood. In this review we evaluate the influence of winter climate on carbon dynamics based on the current state of knowledge and highlight emerging topics and future research challenges. Studies that have addressed this topic include plot-scale snow cover manipulation experiments that alter soil temperatures, empirical investigations along natural climatic gradients, laboratory temperature incubation experiments aimed at isolating influential factors in controlled environments, and time series of climate and carbon data that evaluate long-term natural variation and trends. Combined, these studies have demonstrated how winter climate can influence carbon in complex ways that in some cases are consistent across studies and in other cases are difficult to predict. Despite advances in our understanding, there is a great need for studies that further explore: (*i*) carry-over effects from one season to another, (*ii*) ecosystem processes in the fall–winter and winter–spring shoulder seasons, (*iii*) the impacts of extreme events, (*iv*) novel experimental approaches, and (*v*) improvements to models to include ecological effects of winter climate. We also call for the establishment of an international winter climate change research network that enhances collaboration and coordination among studies, which could provide a more thorough understanding of how the snow-covered period influences carbon cycling, thereby improving our ability to predict future responses to climate change.

Key words: carbon, climate change, cold season, snow, soil frost, winter.

Résumé : L'hiver est une période importante pour les processus écologiques dans les régions nordiques; cependant, comparativement aux autres saisons, les répercussions du climat hivernal sur les écosystèmes sont mal comprises. Dans le cadre de cet examen, nous évaluons les effets du climat hivernal sur la dynamique du carbone en fonction de l'état actuel des connaissances et signalons les nouveaux sujets et les défis futurs de la recherche. Les études abordant ce sujet comprennent des expériences qui modifient la température du sol par la manipulation de la couverture de neige sur des parcelles, des études empiriques suivant des gradients climatiques naturels, des expériences d'incubation à température de laboratoire visant à isoler les facteurs influents dans des environnements contrôlés et des séries chronologiques de données sur le climat et le carbone qui évaluent les variations naturelles et les tendances à long terme. Mises ensemble, ces études ont démontré comment le climat hivernal peut influer sur le carbone de façon complexe qui, dans certains cas, sont uniformes d'une étude à l'autre et, dans d'autres cas, sont difficiles à prévoir. Bien que notre compréhension ait progressé, il existe un grand besoin d'études qui explorent davantage : (*i*) les effets résiduels d'une saison à l'autre; (*ii*) les processus écosystémiques pendant les saisons intermédiaires automne–hiver et hiver–printemps; (*iii*) les répercussions d'événements extrêmes; (*iv*) les nouvelles approches expérimentales; (*v*) les améliorations apportées aux modèles pour inclure les effets écologiques du climat hivernal. Nous demandons également la création d'un réseau international de recherche sur les changements du climat hivernal afin d'améliorer la collaboration et la coordination entre les études, ce qui pourrait permettre de mieux comprendre comment la période de couverture de neige influe sur le cycle de carbone, nous permettant d'améliorer notre capacité de prévoir les réactions futures aux changements climatiques. [Traduit par la Rédaction]

Mots-clés : carbone, changement climatique, saison froide, neige, gel du sol, hiver.

Introduction

Much of the Northern Hemisphere has characteristically cold winters, with regions above ~30°N experiencing air temperatures below freezing, at least occasionally (Frauenfeld et al. 2007). These northern regions also typically have snow cover for at least part of the year, ranging from an average maximum of 50% of the land surface of the Northern Hemisphere in January to a minimum of 3% in August (Estilow et al. 2015). Both freezing air temperatures and snow cover regulate soil temperatures, affecting the depth, duration, and areal extent of frozen ground. Approximately 26% of the land mass in the Northern Hemisphere is comprised of permanently frozen ground (including ice sheets and glaciers), 51% is seasonally frozen, and 7% is intermittently frozen in the coldest month of the year (Fig. 1; Zhang et al. 2003).

Many areas in the northern hemisphere that experience cold temperatures also have large stocks of carbon. While polar and tundra ecosystems contain about 7% of the world's terrestrial organic carbon (~1900 Pg in global vegetation and soil carbon pools), moist boreal and cool temperate forests are among the most carbon-rich ecosystems (20% and 18%, respectively), even surpassing wet and moist tropical forests (14% and 16%, respectively; Scharlemann et al. 2014). Unlike tropical forests, where slightly more than half of the carbon is stored in above- and belowground phytomass, most of the carbon in polar (96%), boreal (93%–94%), and temperate forest (88%–92%) ecosystems is stored in

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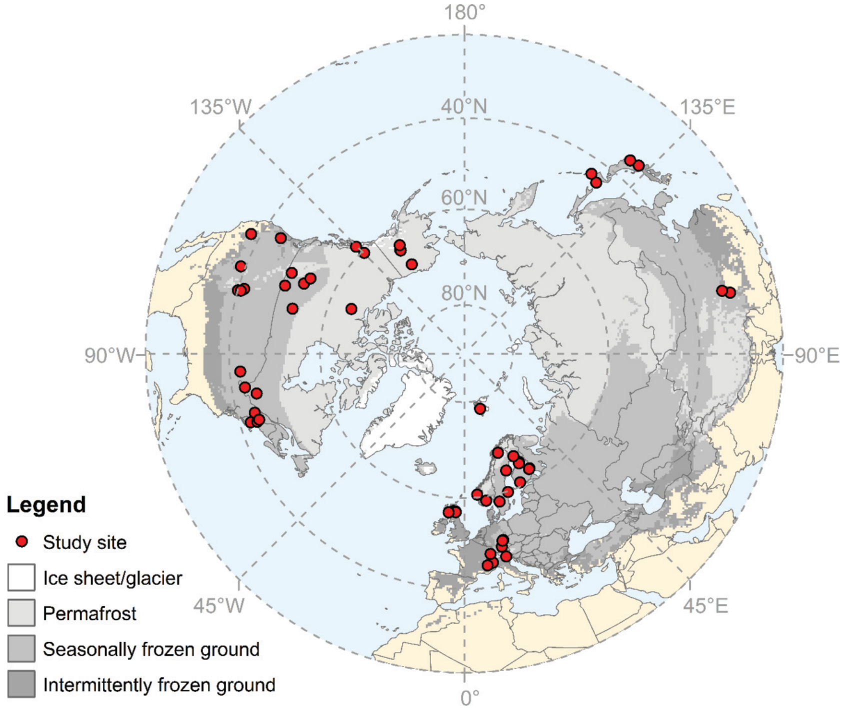
Fig. 1. Locations of study sites in the northern hemisphere where the effects of winter climate on carbon dynamics have been evaluated. The distribution of ice sheets and glaciers, permafrost, and the average maximum extent of seasonally and intermittently frozen ground are also shown (Zhang et al. 2003).



soil (Scharlemann et al. 2014). Data used in these estimates of soil organic carbon are typically from less than 1 m depth, which is sufficient for many regions. However, in the northern circumpolar permafrost region, inclusion of deeper soil carbon (0–3 m) and sediment deposits deeper than 3 m can markedly increase estimates (Hugelius et al. 2014; Schuur et al. 2015). When these deeper stores are included, the total estimated soil organic carbon for the permafrost region is ~1300 Pg (~60% in permanently frozen ground and ~40% in the seasonally thawed active layer or unfrozen pockets within permafrost (i.e., taliks)), which is substantial given that the total global estimate for organic carbon storage in the top 3 m of soil is 2344 Pg (Jobbágy and Jackson 2000).

Although estimates of carbon pools and fluxes have improved, the amount of carbon stored in, and lost from, northern ecosystems is not well established. Litter inputs, root exudation, and microbial biomass are the major sources of organic carbon in soils. Carbon is sequestered through photosynthesis and lost as autotrophic and heterotrophic carbon dioxide (CO_2) respiration, release of methane (CH_4) and volatile organic compounds, and through surface water export of dissolved organic carbon (DOC) and particulate organic carbon (POC). Soil carbon accumulation in northern ecosystems is mostly a result of slow turnover associated with cold and waterlogged soils and poor litter quality (Hobbie et al. 2000). Turnover times increase with soil depth and our knowledge of mechanisms controlling the stabilization of deep soil organic matter is limited, which makes it difficult to determine its vulnerability to change (Schmidt et al. 2011).

Since temperature and moisture strongly influence carbon cycling and loss, the large pool of soil organic carbon in northern ecosystems is susceptible to changes in climate. This soil organic carbon pool may be especially vulnerable because Arctic and Boreal biomes, as well as large parts of the northern Temperate region, are expected to experience some of the most drastic changes in climate (IPCC 2013). However, despite decades of research, there remains considerable uncertainty in how the carbon cycle at high latitudes is affected by climate change. Factors such as warming soil and thawing permafrost (Melillo et al. 2002; Schuur et al. 2015), changing hydrologic regimes (wetting and drying) in soil and wetlands (Lawrence et al. 2015; Trettin et al. 2006), increases in the frequency and severity of fire (Kasischke and Stocks 2000), and shifts in the composition of vegetation (Pearson et al. 2013) can impact the carbon cycle in complex ways that are difficult to predict. If these changes enhance the release of CO_2 or CH_4 to the atmosphere, it may result in a positive feedback that will accelerate change.

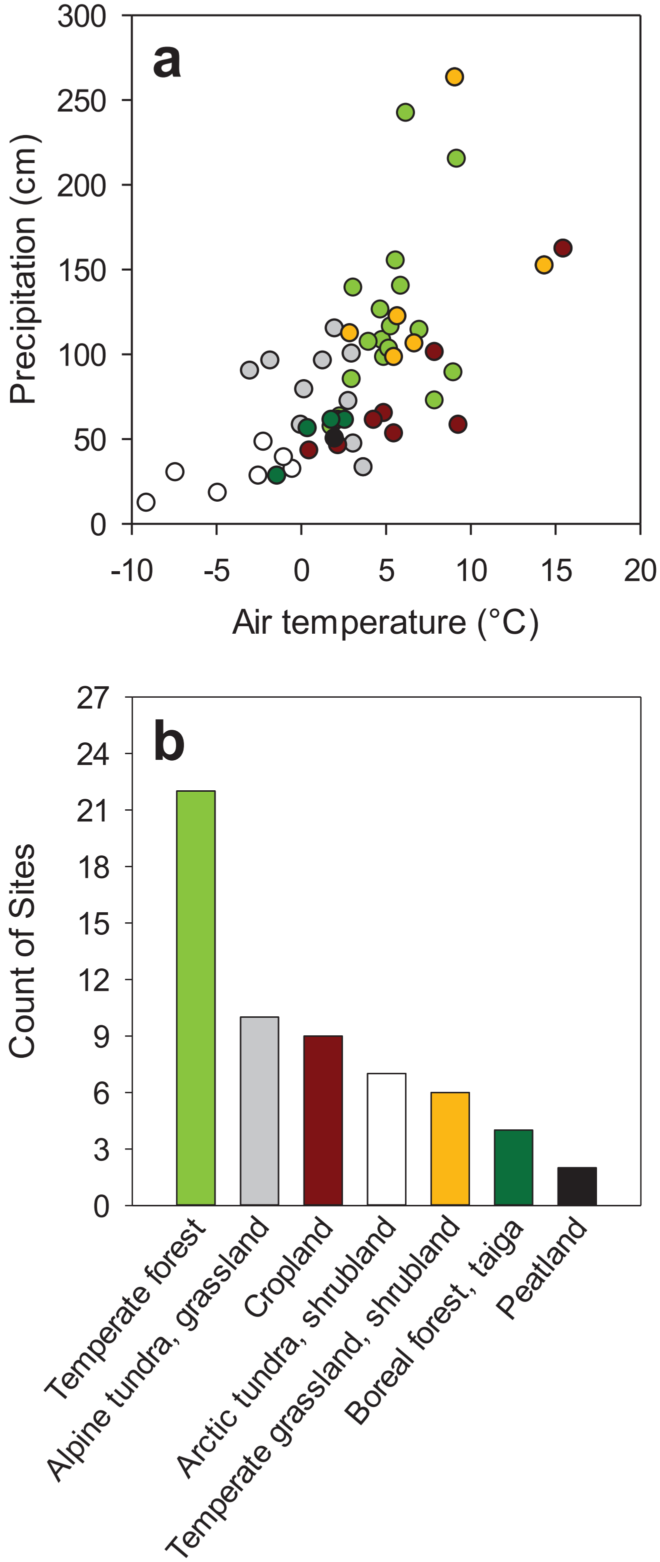
A major weakness in our understanding of the impact of climate change on northern ecosystems is how processes that occur during winter affect soil carbon stocks. Compared with numerous studies that have focused on carbon uptake and loss during the growing season, far less research has occurred over winter, even though biotic and abiotic processes at this time of year can make important contributions to annual soil carbon budgets (Ågren et al. 2010; Campbell et al. 2005; Monson et al. 2006*a*). Research in recent years has begun to address this issue, yet there has been no comprehensive assessment of general patterns and trends.

In this review, we highlight our current understanding of winter climate change and impacts on carbon cycling in northern ecosystems, providing critical information for predicting how this important pool may change in the future. We summarize results from empirical studies of winter climate and its influence on the fate and behavior of carbon in mid- to high-latitude regions that encompass Arctic, Boreal, and Temperate forest biomes (Figs. 1 and 2). These studies include field manipulations, gradient studies, laboratory experiments, and time series of carbon and hydroclimatological data. In this review we also identify major gaps in our understanding of how winter conditions influence carbon dynamics and highlight emerging topics and future research needs.

Approach

Winter is an inexact term that can be defined in many ways depending on the application. The term “cold season” is often

Fig. 2. Mean annual temperature (°C) and precipitation (cm) at each study site (*a*) and the number of study sites in each ecosystem type (*b*). Circle fill colors in (*a*) correspond to the ecosystem types in (*b*).



used instead of "winter" because it better describes regions with a long winter period, such as the Arctic where it can last nine months (Olsson et al. 2003); however, for the purposes of this review we used the term "winter" because it is widely recognized. In ecological studies, definitions of winter based on fixed dates (e.g., December–February; winter solstice to vernal equinox) are generally inadequate because they fail to capture how winter varies in time and space. A preferred approach is to use more biologically relevant indicators such as plant phenological phase, presence of snow cover, and temperature thresholds. Because these types of data were not available for all the studies we reviewed, we more loosely defined winter as periods with sustained freezing temperatures and snow cover. Winter is bookended by the fall and spring shoulder seasons (i.e., autumn–winter and winter–spring transition periods), which can also be defined in different ways. For our purposes, the fall shoulder season generally includes the period from autumnal senescence (brown down) to snow cover development, and the spring shoulder season is the period from snow cover melt to leaf development (green up).

Only winter climate change studies that evaluated carbon response variables were included in this review, although it is important to recognize that many other winter climate change studies have focused on other response variables, for example, those involving different elements such as nitrogen (see review by Blankinship and Hart (2012)). Studies that indirectly dealt with carbon production or allocation (e.g., vegetation and microbial responses) were also included. A literature search for suitable papers was initially performed in Web of Science (Clarivate Analytics; https://clarivate.com/products/web-of-science) and Google Scholar (https://scholar.google.com/) using combinations of keywords such as "carbon," "soil," "stream," "winter," "climate change," "cold season," "soil frost", and "snow." The search was then expanded using citations in the relevant papers and known existing literature. We identified a total of 55 study sites representing diverse ecosystems where the impacts of winter climate change on carbon cycling have been reported in the literature (Figs. 1 and 2; Table A1). Results from these studies were reported in a total of 99 publications, some of which evaluated multiple carbon response variables in the same article (Table A2).

Of the studies identified, field experiments are the most common approach for evaluating how changing winter conditions affect carbon dynamics (67% of studies), followed by laboratory experiments (27%), and time-series analyses (6%). Field experiments consist largely of studies where snow depth has been manipulated by installing shelters to exclude snowfall, constructing snow fences to alter snow depth by wind redistribution, manually shoveling snow off (and on) plots, and adding insulation to simulate snow addition (Figs. 3*a* and 4; Table A2). In general, snow removal eliminates the insulating effect of snow cover and promotes deeper soil frost development, whereas insulation or snow addition results in warmer, more stable soil temperatures. Gradient studies are less common than snow depth manipulation experiments but work in much the same way. However, instead of manually altering snow depth, responses are evaluated along natural snow depth gradients, such as those that often occur with elevation. Because both manipulative experiments and gradient studies are conducted in the field, they have been used to evaluate a broad range of carbon response variables.

Laboratory experiments have consisted mainly of shorter duration (<1 year) soil incubations (homogenized soil samples or intact cores) performed at low temperatures of different ranges applied for different periods of time, as well as varied freeze–thaw cycles (Figs. 3*a*, 3*b* and 5; Table A2). Laboratory studies have most commonly included responses of carbon gases (CO_2 and in some cases CH_4), microbial C, and DOC (Fig. 3*c*).

Time-series analyses that specifically examine relationships between winter conditions and carbon response variables are less common than laboratory or field experiments and use data collected over longer time periods (3–60 years; Fig. 3*b*; Table A2). Carbon response variables for the time-series analyses mainly included DOC (Fig. 3*c*), sometimes with additional measures of DOC quality. However, some studies have also evaluated aboveground

Fig. 3. The percentage of each method used (*a*), study duration (*b*), and response variable (*c*) in laboratory, field, and time-series investigations.

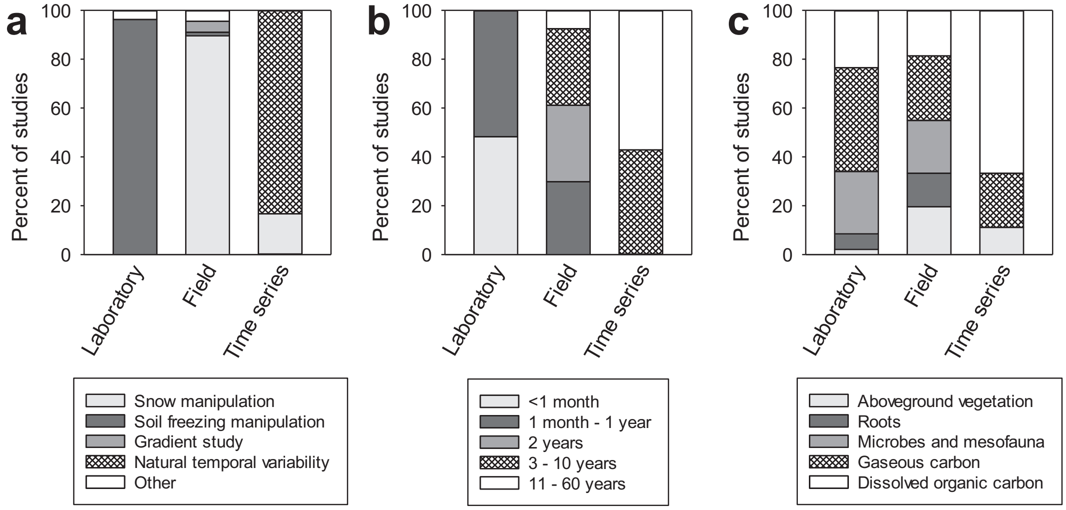
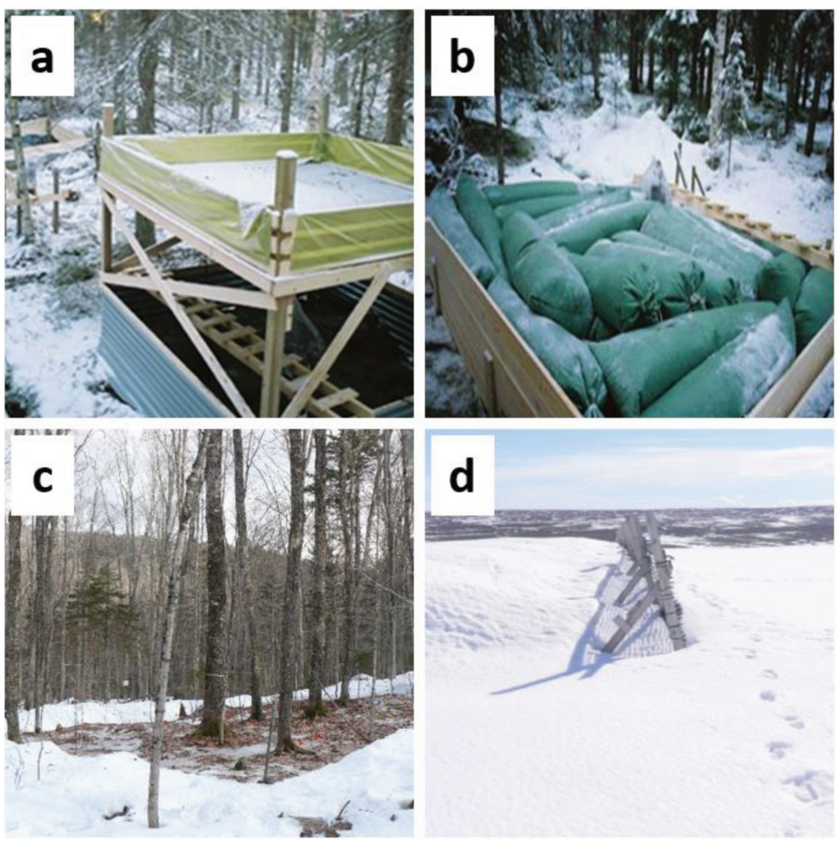


Fig. 4. Examples of experimental snow and temperature manipulation methods including: snow exclusion roof (*a*), insulation in a Boreal forest at Svartberget/Krycklan, Sweden (Haei et al. 2010; Öquist and Laudon 2008; photographs by Peder Blomkvist) (*b*), snow removal by shoveling at Hubbard Brook, USA (Groffman et al. 2001*a*; photograph by Annie Socci) (*c*) and snow fence at Toolik, USA (Walker et al. 1999; photograph by Yiwei Cheng) (*d*).



vegetation and trends in CO_2, based primarily on eddy covariance (tower) data. Although field and laboratory studies focused on the treatment effects of changes in snow cover and soil frost regimes, the time-series analyses focused mainly on other aspects of winter climate such as timing of snowmelt and air temperature changes. Many of these time-series analyses use natural climate variability to evaluate responses; however, some have also used long-term snow manipulations, primarily through installation of fencing (Fig. 3*a*).

Because of the many different experimental designs and methods applied, it is sometimes difficult to compare all studies and draw general conclusions (Henry 2007). These differences make it challenging to perform more quantitative meta-analyses, except in cases where there is a sufficient amount of data available across multiple sites (e.g., Blankinship and Hart 2012; Wipf and Rixen 2010). The intent of our analysis of the literature was to identify general patterns that have emerged from the limited number of comparable studies that have evaluated carbon responses to changing winter climate in northern regions.

Current understanding

Changing winter conditions

During the 20th century, northern regions have had a more pronounced increase in air temperature compared with the global mean (IPCC 2013; Serreze and Barry 2011), with the greatest increases occurring during winter and spring (Cayan et al. 2001; Parida and Buermann 2014). Global climate projections indicate a continued increasing trend in air temperature through the end of the century, again with greater warming at higher latitudes and during the winter season (Christensen and Christensen 2007; IPCC 2013). Precipitation is more variable than air temperature, and although there is evidence that annual precipitation has increased in northern regions, no clear trend in winter precipitation has been observed (Dore 2005; Hayhoe et al. 2007; Ren et al. 2013). The form of winter precipitation has changed though, with a decrease in the proportion of precipitation occurring as snow (Huntington et al. 2004; Knowles et al. 2006; Kozii et al. 2017). Modeled future precipitation trends differ somewhat from past observations, in that some projections show increases in winter precipitation of up to 30% (Giorgi and Bi 2005; Hayhoe et al. 2008). However, models generally do indicate shifts in the form of precipitation that are consistent with observed trends (i.e., less snow and more rain in most regions; Barnett et al. 2005; Bintanja and Andry 2017; Trenberth 2011).

Long-term data have shown that in the northern hemisphere, the depth of the snowpack is declining (Callaghan et al. 2011; Hodgkins and Dudley 2006), the snow-covered period is getting shorter (Dye 2002; Kreyling and Henry 2011), and snowmelt is occurring earlier (Déry et al. 2009; Hodgkins et al. 2003). These trends are expected to continue through the end of the century, as demonstrated with hydrologic models run under different climate change scenarios (Brown and Mote 2009; Callaghan et al. 2011; Campbell et al. 2010; Mellander et al. 2007).

Snow insulates soils, and a snowpack depth of 20–40 cm is generally sufficient to decouple air and soil temperatures under most conditions (Hirota et al. 2006; Zhang 2005). It has been suggested that decreases in snowpack depth will result in colder soils because there will be less snow insulating soils during winter, thereby exposing them to cold winter air (Brown and DeGaetano 2011; Groffman et al. 2001*a*). However, since winter air temperatures are getting warmer, soil temperatures may also increase (Campbell et al. 2010; Henry 2008), as demonstrated by long-term decreases in the depth of seasonally frozen ground (Frauenfeld et al. 2004), as well as an increase in the active layer in permafrost regions (Peng et al. 2018). Several modeling studies have predicted that the duration of frozen ground will become shorter in the future and there will be more freeze-thaw cycles, especially in areas where the snowpack is becoming increasingly intermittent (Campbell et al. 2010; Helama et al. 2011; Henry 2008). More frequent midwinter snowmelt events and earlier snowmelt will also decrease surface albedo, further enhancing snowmelt and soil temperature increase (Lawrence and Slater 2010).

Because of the interacting effects of changes in air temperature, precipitation patterns, and snow cover, there are large uncertainties in how cold-season soil temperatures will change in the future. Predictions of soil temperature are further complicated by the influence of regional weather patterns as well as local site conditions (Kreyling and Henry 2011; Oni et al. 2017). Soil characteristics, such as organic matter and water content, influence soil temperature and the severity of freezing, type of soil frost that forms (e.g., concrete, granular), and the degree of frost heaving (Trimble et al. 1958), all of which influence physical, chemical, and biological processes in soil. In permafrost regions, warmer air temperatures and declines in the snowpack can cause a deepening of the active layer, but the relationships are complex and other factors, such as changes in shrub abundance, can also influence snow depth and soil temperatures (Grosse et al. 2016; Schuur et al. 2008). Since changes in soil temperature regimes can have both direct and indirect effects on carbon cycling, the uncertainty surrounding soil temperatures makes it challenging to predict future carbon responses. Nevertheless, we can make important inferences about future carbon responses to changing winter conditions based on observations from field experiments, gradients, laboratory studies, and long-term data and identify strengths and weaknesses in our understanding.

Carbon responses to winter climate

Aboveground vegetation

Photosynthesis is negligible in deciduous plants during the snow-covered period (e.g., Hamerlynck and Smith 1994); however, some conifer species (e.g., *Pinus sylvestris* (Vermeulen et al. 2015)) can assimilate carbon when average daily air temperatures are below freezing, having implications for winter carbon fluxes. Carbon uptake through photosynthesis during winter has also been shown for mosses and lichens, even when covered with snow (Kappen et al. 1996; Tieszen 1974). Starr and Oberbauer (2003) found that during spring when snow cover is still present, carbon uptake capacity of low stature, evergreen tundra plants is enhanced as a result of the favorable conditions of the subnivean environment, including sufficient light penetration, adequate temperatures, elevated CO_2, and available melt-water. In a sub-Arctic heath ecosystem in northern Sweden, winter season photosynthesis (19% of the annual gross CO_2 uptake) somewhat balanced the winter-season respiratory carbon loss, which comprised 22% of the annual respiratory flux (Larsen et al. 2007*b*).

Exceptionally cold temperatures can cause winter injury to woody plants. Damage to vegetation from these events can delay CO_2 uptake in the spring, thereby reducing growth and hence carbon storage (Parmentier et al. 2018). Some tree species, such as red spruce (*Picea rubens*), are particularly susceptible to cold temperature stresses (low temperatures, rapid freezing, freeze–thaw cycles), which can result in bud mortality and damage to current-year foliage (Lazarus et al. 2004). For lower stature vegetation, the presence of a deep snowpack can protect aboveground woody shoots from cold air temperatures, reducing winter injury to apical buds, branches, and leaves (Semenchuk et al. 2013). However, the weight and pressure of a deep snowpack can also break and deform plants and kill seedlings, especially when it contains layers of ice (Martz et al. 2016; Sonesson and Callaghan 1991; Weih and Karlsson 2002). Similarly, snowfall and ice storms can damage stems and branches of higher stature vegetation above the snowpack.

Shorter winters with less snow accumulation cause plant phenological shifts, although other factors, such as photoperiod, are also important (Keller and Körner 2003). The length of the growing season in the Northern Hemisphere has increased by approximately 3–6 days per decade from 1982–2012 (Wang et al. 2016) and earlier leaf-out dates of 1.2 days per decade have been reported (Schwartz et al. 2006). These trends can lead to increased plant production, as demonstrated by Berdanier and Klein (2011) in high-elevation meadows where growing season length constrained maximum aboveground net primary production (NPP) by an average of 4 g m^{-2} d^{-1}. However, results are not always consistent among studies because of confounding influences. For example, the snowpack affects soil moisture and nutrient availability, which further influence plant growth (Berdanier and Klein 2011; Knight et al. 1979; Weaver and Collins 1977). Earlier snowmelt and leaf-out can also increase the risk of spring frost damage to aboveground vegetation, causing a reduction in plant production (Arnold et al. 2014).

Because of the many different adaptive plant traits (growth strategies, frost hardening, plant architecture, etc.), there are inconsistencies in how winter conditions affect vegetation. Consequently, it is not possible to make broad generalizations about plant responses to winter conditions beyond the species level (Rumpf et al. 2014). It is clear however, that changes in winter conditions can cause shifts in the productivity and composition of vegetation, as demonstrated in many winter climate manipulation experiments (e.g., Christiansen et al. 2018; Dorrepaal et al. 2006; Weaver and Collins 1977). Since vegetation is a controlling factor for carbon fluxes, shifts in plant biomass and composition may alter carbon inputs to soil, causing potential changes to the carbon budget (Kreyling 2010; Neff and Hooper 2002; Vestgarden and Austnes 2009).

In addition to changes in vegetation that are attributed to the direct effects of climate, vegetation can also be altered by indirect climate effects, such as severe fires, outbreaks of pests and pathogens, and spread of invasive species (Dale et al. 2000). Some of these indirect effects are specifically linked to winter climate and include interactions that occur across trophic levels. For example, snow depth and soil temperatures affect animal physiological energetics, population dynamics, and community structure that impact vegetation by altering herbivory and nutrient inputs (Pauli et al. 2013; Post et al. 2009). These indirect effects of winter climate change on vegetation are complex and not well understood but are potentially important in regard to the carbon cycle and warrant further investigation.

Roots

Compared with aboveground vegetation, the impacts of winter climate on roots is more difficult to assess because of inherent problems in quantifying root systems and function. Nevertheless, some root response metrics have been evaluated, almost entirely through snow depth manipulation experiments that have focused on soil freezing effects (Table A2). Roots tend to be less frost hardy than the aboveground portion of plants and are therefore more susceptible to freezing injury (Schaberg et al. 2008; Sutinen et al. 1999). Many studies have demonstrated that soil freezing causes plant root injury during winter, reducing root vitality (Cleavitt et al. 2008) and cell membrane stability (Comerford et al. 2013) and increasing levels of root mortality and turnover (Gaul et al. 2008; Kreyling et al. 2012*b*; Tierney et al. 2001). Root injury has been attributed to physical damage associated with ice lens formation and frost heaving (Benninghoff 1952) as well as direct frost damage to root cells (Cleavitt et al. 2008).

While freezing clearly damages roots, impacts on root biomass and growth are not as straightforward. Some studies have shown that soil freezing reduces fine root production (Wipf et al. 2009) and biomass (Kreyling et al. 2012*a*) by as much as 50% in surface soils during the following growing season, whereas others have shown that it stimulates compensatory growth that leads to higher production, which in some cases balances or slightly exceeds the carbon loss from mortality (Cleavitt et al. 2008; Gaul et al. 2008; Repo et al. 2014; Sorensen et al. 2016*a*; Weih and Karlsson 2002).

The impact of soil freezing on roots may also affect carbon cycling by altering nutrient dynamics. Soil freezing can increase the amount of fine root necromass over winter, which is a potentially important source of nutrients made available through mineralization in the spring (Tierney et al. 2001). Shifts in the timing of root mortality and growth due to soil freezing may contribute to the availability of nutrients. Concentrations of biologically important nutrients, such as nitrogen, are typically greatest in early spring, so the loss and impairment of roots during this time can reduce root uptake (Campbell et al. 2014*b*) and increase nutrient leaching (Fitzhugh et al. 2001), even if soil freezing results in greater root production later in the growing season. This example demonstrates how soil freezing can disrupt the temporal synchrony between root production and uptake of nutrients belowground, having implications for aboveground plant growth. However, studies showing linkages between freezing effects on nutrient-root dynamics and aboveground productivity are lacking. There is a pressing need to explore and better understand these interactions through long-term data and new experiments, such as multi-factor manipulations of winter climate and nutrients.

Microbes

It is well documented that microbial biomass can increase during winter beneath the snowpack if there is sufficient free water and carbon substrate (see Schaefer and Jafarov 2016; Schmidt and Lipson 2004). Microbial biomass tends to decrease in late winter and early spring as the supply of available carbon becomes limiting and cold-adapted microbes die off (Lipson et al. 2000). Consequently, microbial populations are highly variable during spring snowmelt and can decline significantly over a period of days (Larsen et al. 2007*a*; Tan et al. 2014). Conditions that favor microbial processes (carbon supply, soil moisture, warmer temperatures) are important at this time of year because they enhance N mineralization and nitrification, and thus the supply of nutrients to plants early in the growing season (Schimel et al. 2004; Semenchuk et al. 2015).

It has been suggested that freeze–thaw cycles may cause rapid declines in microbial populations (Henry 2007; Larsen et al. 2002), which could also contribute to microbial die-off during snowmelt when there are cold snaps and insufficient amounts of snow to moderate soil temperatures. Although some experiments have shown declines in microbial biomass by as much as 40% in soils subjected to freezing (e.g., Larsen et al. 2002; Yanai et al. 2004), most have shown no significant effect (e.g., Bombonato and Gerdol 2012; Buckeridge and Grogan 2008; Groffman et al. 2001*b*; Koponen et al. 2006; Schmitt and Glaser 2011; Schmitt et al. 2008; Sjursen et al. 2005). Microbial cell lysis can fuel rapid recovery of microbial biomass, so it is possible that in most studies the sampling is not frequent enough to capture the variability in populations (Larsen et al. 2007*a*).

In addition to the total microbial biomass pool, studies have also investigated how winter conditions affect the composition of the microbial community. While there are reported shifts in the microbial community to more cold-adapted species during winter, the patterns are seasonal and not indicative of a long-term change (Aanderud et al. 2013; Monson et al. 2006*b*). These results suggest that soil freezing causes fluctuations in microbial populations in the short term that may influence the timing and availability of soil carbon, and that recovery is rapid with no apparent long-term effects on microbial community composition. Some winter climate change experiments have shown that fungal communities are sensitive to changing winter conditions (Semenova et al. 2016) and may be more susceptible to soil freezing than bacteria (Feng et al. 2007; Schmitt and Glaser 2011; Schmitt et al. 2008). Because microbial and fungal communities respond rapidly to biotic and abiotic factors, they can influence the timing and availability of soil carbon over short periods, making them useful indicators of change (Classen et al. 2015; Lau and Lennon 2012).

Although soil mesofauna contribute to decomposition, it is mainly driven by microbes (Kreyling et al. 2013), so any climate-induced changes in microbial dynamics may influence decomposition and soil respiration, thus affecting carbon feedbacks to rising CO_2. Decomposition also releases carbon compounds and nutrients to the soil through mineralization processes and therefore affects carbon leaching and NPP. Climate influences decomposition through abiotic factors that enhance the fragmentation and degradability of the substrate and the mesofauna and microorganisms that consume it. Studies have demonstrated that in high latitude regions, decomposition can occur at temperatures below freezing (Segura et al. 2017), and that a substantial amount of litter carbon loss occurs over winter. In Alaskan tussock tundra, Hobbie and Chapin (1996) showed an approximate 20% reduction in mass loss of fresh litter during the summer, followed by a 16% loss during the first winter, no clear change during the second summer, and an 8% loss during the second winter. However, some evidence suggests that much of the winter decomposition happens immediately after senescence in the late fall or early winter, highlighting the importance of this transition period (Bokhorst et al. 2010). Most winter climate change studies have investigated the decomposition of leaf litter on the surface of the ground, although as mentioned previously, damaged fine roots can also be an important source of litter (Tierney et al. 2001).

Laboratory experiments have generally shown that repeated freezing and thawing accelerates decomposition, which is attributed to physical damage and chemical changes in plant matter that increase susceptibility to degradation (e.g., Taylor and Parkinson 1988). Field investigations on the other hand, have shown, with some exceptions (Bokhorst et al. 2010; Walker et al. 1999), that a thinner snowpack with greater frost development and freezing and thawing, substantially reduces decomposition rates (Christenson et al. 2010; Kreyling et al. 2013; Saccone et al. 2013; Walker et al. 1999; Wipf et al. 2015). For example, in a montane heathland in the Scottish Highlands, over-winter litter mass loss was 26% lower in areas with thin snow cover as compared with deep snow cover (Wipf et al. 2015). Similarly, at a boreal forest site in northern Sweden, snow removal reduced annual cellulose decomposition by 46% (Kreyling et al. 2013). These field observations showing reductions in decomposition rates when snow is lacking, are a result of the greater length of time the substrate remains frozen, and thus, is more resistant to degradation.

In addition to these more direct effects of winter climate on decomposition, indirect effects associated with shifts in the composition of vegetation and decomposer communities may also be important. For example, studies have found that vegetation type and associated quality of litter (e.g., lignin content) can be an equally, if not more important influence on decomposition than winter climate (Walker et al. 1999). Several studies have also shown that soil freezing can reduce the abundance and alter the community composition of soil mesofauna that contribute to decomposition (Sulkava and Huhta 2003; Templer et al. 2012).

While mesofauna can clearly be affected by winter climate, evaluating responses often prove challenging because of the low abundance of individual species and difficulties in attaining a complete census. These challenges are amplified for microbial community composition which is far more complex, consisting of thousands of low-abundance species (<0.1% of total; Luo et al. 2014). Consequently, the impact of microbial community composition on decomposition in general is not well known and microbial community responses to disturbances, such as soil freezing, are difficult to predict (Schimel and Schaeffer 2012; Shade et al. 2012). However, microbial investigations are entering an exciting new era with the advent of meta-omics and high-throughput fingerprinting and sequencing tools. These techniques are beginning to provide insight into microbial response to climate change (Luo et al. 2014) and will lead to better understanding of how winter climate impacts carbon cycling.

Gaseous carbon

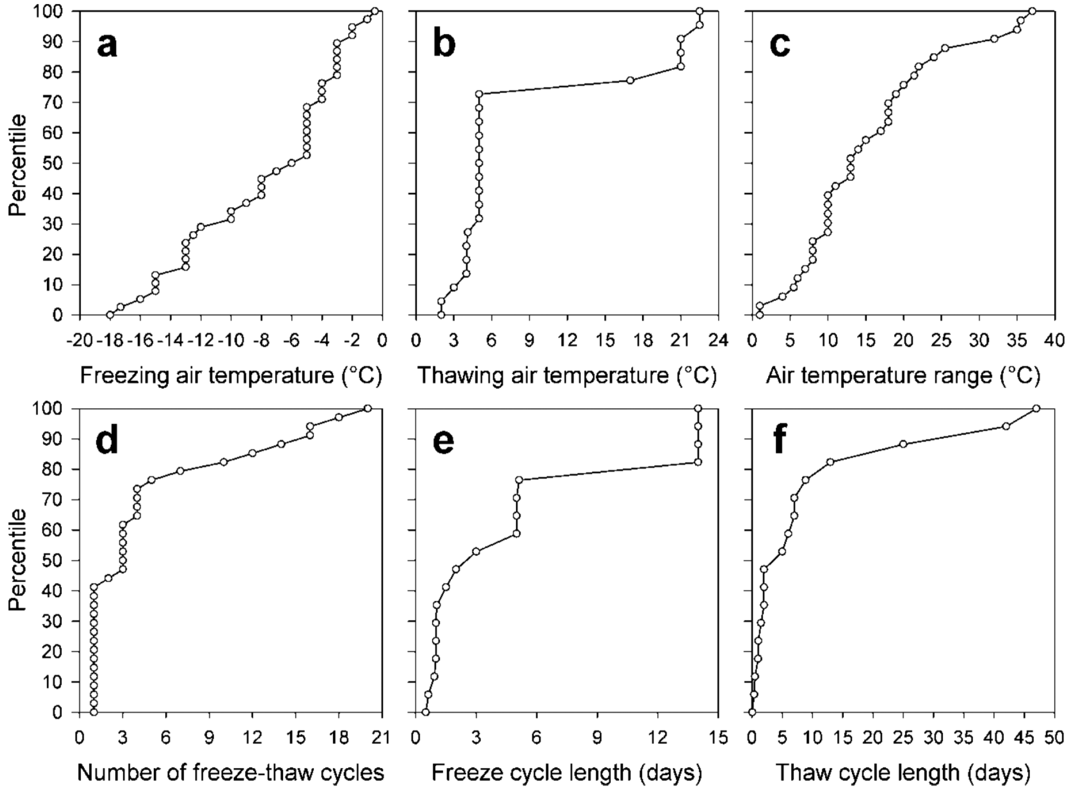
Soil CO_2 and CH_4 fluxes can be substantial during the snow-covered period, having potentially important impacts on annual trace-gas budgets. Soil CO_2 is produced by microbial and root respiration, the latter of which is typically minimal during winter due to limited plant activity. Soil CH_4 is consumed by aerobic and produced by anaerobic microorganisms; therefore, upland soils are generally a sink and wetlands are a source of CH_4, even during winter beneath the snowpack (Dise 1992; Groffman et al. 2006). The contribution of winter soil CO_2 efflux is typically ~5%–15% of the total annual efflux (see Groffman et al. 2006), although values as high as ~30% have been reported (e.g., Fahnestock et al. 1999; Liptzin et al. 2009). Reported winter CH_4 fluxes range from ~20% of annual uptake to about ~20% of annual emissions (see Dise 1992; Groffman et al. 2006). In Arctic ecosystems, cold season (approximately September–May) CH_4 emissions can be higher, contributing more than 50% of annual emissions (Zona et al. 2016). The large range in the production and consumption of gaseous carbon during winter may be due not only to natural variability, but also the methods used to determine fluxes (Björkman et al. 2010).

Since CO_2 and CH_4 are important greenhouse gases, knowledge of how winter climate change affects their fluxes is critical for predicting future carbon budgets and climate feedbacks. Winter climate change experiments that have investigated gaseous carbon fluxes have focused more on CO_2 than CH_4 (Table A2). A snow removal study in a northern hardwood forest where CH_4 was measured, showed lower CH_4 uptake in soil subjected to freezing (Groffman et al. 2006). However, in other experiments, there were no significant winter climate change treatment effects on CH_4 (Priemé and Christensen 2001; Reinmann et al. 2012), and CH_4 concentrations were typically low or below detection (Wang and Bettany 1993), making it difficult to detect trends.

Compared with CH_4, fluxes of CO_2 tend to be higher and show a wide range of responses to changing winter conditions. Qualities of the snowpack influence CO_2 exchange, and field experiments have shown that snow compaction and ice encasement can create a barrier that impedes CO_2 efflux (Martz et al. 2016; Morgner et al. 2010). Laboratory studies have demonstrated that soil freezing causes a respiratory burst upon thawing that is thought to be fueled by the release of simple sugars and amino acids from microbial cell lysis, which in turn increases the activity of surviving microbes (Feng et al. 2007; Schimel and Clein 1996; Skogland et al. 1988). However, recent field research suggests that increases in respiration following soil freezing may be associated with root mortality and subsequent decomposition of root necromass (Reinmann and Templer 2018). In field studies, soil freezing is one of many factors (e.g., temperature, soil moisture, carbon availability) that can control the amount and temporal patterns of CO_2 released from soil during winter. Eddy covariance data are becoming increasingly useful for evaluating these interactions, as records get longer and more sites operate throughout the year in cold regions. These studies have demonstrated strong relationships between CO_2 fluxes and winter conditions, especially the length of the snow-covered period (Bergeron et al. 2007; Galvagno et al. 2013; Monson et al. 2006*b*).

In addition to CO_2 and CH_4, carbon can be emitted to the atmosphere in the form of biogenic volatile organic compounds (BVOCs). BVOCs consist of a diverse group of reactive carbon compounds that typically remain in the atmosphere from minutes to days (Atkinson and Arey 2003). Emissions of BVOCs contribute to the global carbon cycle and while they are minor relative to NPP, they may be important relative to net ecosystem production, although current estimates are not well constrained due to a lack of data (Kesselmeier et al. 2002). Much of the recent interest in BVOCs has stemmed from their potential effects on the climate system (Peñuelas and Staudt 2010). In the atmosphere, BVOC oxidation products can form secondary organic aerosols that scatter and absorb light, and act as cloud condensation nuclei, creating a potentially important climate feedback (Kanakidou et al. 2005). BVOCs originate mainly from vegetation, and evidence suggests that they are produced in part as stress defense mechanism (Niinemets 2010; Peñuelas and Llusià 2003). A strong relationship between temperature and BVOC emissions has been demonstrated in Arctic ecosystems (Tiiva et al. 2008), along with secondary effects associated with plant cover and vegetation composition (Svendsen et al. 2016; Valolahti et al. 2015). However, few studies have evaluated the influence of climate change on BVOCs, and it is

Fig. 5. Cumulative distribution plots showing the conditions used in each laboratory freezing experiment and the corresponding percentile rank. The conditions evaluated include: freezing air temperature (*a*), thawing air temperature (*b*), range of freezing and thawing air temperature (*c*), number of freeze–thaw cycles (*d*), length of freezing cycle (*e*), and length of thawing cycle (*f*).



especially unclear how winter climate change specifically affects the release of BVOCs. Our knowledge of ecosystem-scale BVOC dynamics in general is limited by a lack of long-term data and experiments, highlighting an important research need.

Dissolved organic carbon

Like gaseous soil efflux, DOC export in soil leachate and stream water is also a pathway for carbon loss that may be affected by winter climate change. Although the flux of DOC is smaller than the amount of CO_2 released from most soils, it plays a fundamental role in biogeochemical processes. Some field experiments have shown that soil freezing can significantly increase soil solution DOC concentrations by a range of 1–35 mg L^{-1} (Groffman et al. 2011; Haei et al. 2010). However, other studies have found no detectable effects (e.g., Bombonato and Gerdol 2012; Fitzhugh et al. 2001; Hentschel et al. 2009; Sjursen et al. 2005). These different responses may be attributed to both the climatic conditions during the study (e.g., soil temperatures) and the characteristics of the ecosystem investigated (e.g., soil organic matter stock). Potential reasons for freezing-induced increases in DOC in soil solution include lysis of microbial cells (Soulides and Allison 1961), damage to fine roots (Tierney et al. 2001), and physical disruption of soil aggregates (Oztas and Fayetorbay 2003). Although freezing may enhance DOC concentrations in soil solution, water is a key determinant of DOC losses because of its role in carbon solubility and transport. A deeper snowpack produces more meltwater in spring, which enhances the water flux, and hence the DOC export during this period (Wipf et al. 2015).

Laboratory experiments, under closely controlled conditions, have been used to investigate types of freezing events that may alter DOC concentrations in soil solution. These experiments have evaluated how factors such as the number of freeze–thaw cycles, duration of freezing, temperatures used, and soil water content affect the DOC response. Results from these experiments can be highly variable, possibly in part because of the wide range of freezing manipulations that have been employed (Fig. 5). Nevertheless, these laboratory studies have consistently shown that mild soil freezing (0 to −5 °C) under any type of freezing scenario, generally has no effect on the amount of DOC leached (Campbell et al. 2014*a*; Freppaz et al. 2007; Hentschel et al. 2008; Sjursen et al. 2005). In contrast, severe soil freezing (below −5 °C) has been shown to increase soil solution DOC. Hentschel et al. (2008) found that severe soil freezing increases the release of DOC only after the initial freeze–thaw cycle, providing some indication of a limited source of C, such as freezing-induced physical breakdown of soil aggregates. Other studies have shown that more DOC is released after multiple freeze–thaw cycles, which may indicate a source of carbon that is not readily depleted, such as microbial cell lysis (Grogan et al. 2004; Wipf et al. 2015). Laboratory experiments using different soil moisture levels indicate that pretreatment water content influences the amount of DOC released from soils subjected to freezing. When soils are wetter when they freeze, they tend to release more DOC (Haei et al. 2012; Wang and Bettany 1993).

In addition to evaluating the impacts of soil freezing on the quantity of DOC, several laboratory and field experiments have also evaluated impacts of freezing on the quality of DOC, which reflects its source and composition. Most of these studies have used carbon-specific ultraviolet absorbance and, less commonly, fluorescence spectroscopy to assess the origin of DOC. In general, these studies have found that DOC leaching from previously frozen soil is more labile than DOC from unfrozen soil (Austnes et al. 2008; Campbell et al. 2014*a*; Panneer et al. 2016; Wipf et al. 2015), indicating release of more recent, highly degradable carbon of biological origin, such as microbial biomass or fine roots. Despite this general finding, inconsistent DOC quality responses to soil freezing (Austnes and Vestgarden 2008), and in one case even slight declines in lability were reported, suggesting more aromatic DOC from humic material, such as that which may be released after soil aggregates break up (Hentschel et al. 2008).

Time series of DOC responses to winter climate mainly consist of data from streams and rivers and reflect the seasonal variations in both climatic and hydrological conditions. It is well established that hydrology regulates the export and concentrations of DOC in northern latitude streams (Laudon et al. 2012). Changes in hydrological conditions due to alterations in temperature and precipitation patterns may therefore affect the export of carbon prior to the winter season and offset the impact of winter climate on carbon dynamics during spring snowmelt (Ågren et al. 2010; Haei et al. 2010). In many regions, the riparian zone acts as a significant source of carbon to aquatic systems, particularly during high-flow episodes (Dick et al. 2015; Hinton et al. 1998; Seibert et al. 2009), and significantly controls stream DOC concentrations. Therefore, even small changes in riparian soil organic carbon production and runoff can have important implications for adjacent streams. Most results from existing time-series analyses agree that longer and colder winter seasons with frozen soils are followed by higher concentrations of DOC in streams during the following spring. Carbon export is primarily controlled by changes in discharge, and there are indications of higher DOC export during warmer winters with higher winter stream flows (Laudon et al. 2013; Spence et al. 2015). Change in soil water flow-paths is another key effect of soil freezing on hydrology and DOC. When soil is frozen, runoff leaches the organic-rich litter layers rather than deeper soil horizons that can promote more DOC loss to streams (Dittman et al. 2007; Finlay et al. 2006). However, if the frozen soil prevents infiltration and causes overland flow, it could reduce streamwater DOC (Laudon et al. 2004; Semenchuk et al. 2019). Improved predictions of DOC export in a changing climate require better understanding of how extreme winter weather events such as soil freezing, rain on snow, and mid-winter thaws alter the production and transport of DOC to streams.

Emerging topics and research needs

Seasonal carry-over effects

Although winter climate can clearly affect carbon cycling within seasons, it is important to recognize that climate impacts from one season can also manifest in other seasons (Cornelissen and Makoto 2014; Tiwari et al. 2018). These carry-over effects from one season to another highlight how climate change alters carbon pools and fluxes in complex ways. For example, in a tundra snow fence experiment in Svalbard, deepened snow reduced growing season ecosystem respiration after 5–9 years, which was attributed to depletion of labile carbon substrate due to warmer winter soils (Semenchuk et al. 2016, 2019). Deepened snow in these ecosystems has also been shown to increase soil nutrient availability in early spring, with implications for vegetation growth during warmer months (Semenchuk et al. 2015).

Ample evidence shows that winter climate influences carbon dynamics during the growing season by shifting the balance between production and consumption. For example, in boreal forests of northern Sweden, deep soil freezing in winter has been shown to enhance the rate of heterotrophic CO_2 production and the concentration of soil solution DOC during the following summer, although the mechanistic underpinnings are not well established (Haei et al. 2013). The carry-over effects associated with climatic conditions during winter are also evident in hydrological records. Long-term data have shown increases in streamflow and export of DOC during warm winters, followed by lower export during spring and summer; thus, during warm winters streamflow is modulated and the variability in DOC export throughout the year is reduced (Laudon et al. 2013; Spence et al. 2015). A more thorough understanding of these carry-over effects and interactions among seasons is critical for characterizing and predicting impacts of climate change on carbon cycling. Because climate change occurs over the entire year, and not just within one season, more experiments that evaluate responses to climate change across seasons are needed (Natali et al. 2014; Templer et al. 2017).

Shoulder seasons

Research has shown that environmental conditions and ecological processes during the winter shoulder seasons have important implications for carbon cycling. For example, although soil respiration is typically greatest during the growing season, cold-season CO_2 production can also make substantial contributions to the annual carbon budget and is generally highest during shoulder seasons when conditions are favorable for CO_2 release (Fahnestock et al. 1999; Raz-Yaseef et al. 2017). Factors such as air temperature, soil temperature and moisture, and the timing of snowpack development and melt, strongly regulate carbon gains and losses during these times.

Meteorological conditions during the fall–winter shoulder season determine soil temperatures during winter. If air temperatures are cold and snowpack development is delayed, the ensuing cold soil temperatures and formation of deep soil frost can impact overwinter carbon cycling. Additionally, greater amounts of precipitation during the fall–winter transition increase soil water content, creating concrete soil frost that can act as a barrier, affecting infiltration rates, hydrologic flow paths, and soil trace gas exchange (Harris 1972; Shanley and Chalmers 1999; van Bochove et al. 2001). In permafrost regions, the impacts of meteorological conditions during the fall–winter transition can have longer-lasting effects because they set the stage for freezing conditions that influence the depth of the active layer in summer months (Zhang 2005).

During the winter–spring shoulder season, warm air temperatures and rain on snow events can cause snowmelt to occur earlier. Soil temperatures rise rapidly in spring when the insulating layer of snow melts, and soils are exposed to warmer spring air temperatures. This "spring trigger" induces biological activity, putting in motion a sequence of ecological events (e.g., microbial processing, root activity, leaf development; Groffman et al. 2012). It has been suggested that the "vernal window" between snowmelt and leaf-out is longer during warmer winters with less snow, resulting in longer time lags between these events, which may impact flows of energy, water, and carbon (Contosta et al. 2017).

Extreme events

While it is critical to evaluate responses to long-term changes in mean winter climate and impacts on ecosystems, it is also important to understand the more acute effects of extreme winter weather events because even though they occur over short time periods, they can have dramatic and enduring impacts on the carbon cycle. Ice storms are an example of an extreme winter event that causes canopy damage, resulting in large deposits of woody debris to the forest floor that can last for decades (Fahey et al. 2005). Some extreme events occur in the winter shoulder seasons and are exacerbated by phenological change. For example, snowstorms that occur before leaf drop can cause canopy damage that is far more severe than that caused by snowstorms after leaves senesce (Kane and Finn 2014). Similarly, vegetation can be damaged by hard spring freeze events, killing newly formed leaves, shoots, and developing flowers and fruits (Gu et al. 2008; Hufkens et al. 2012; Semenchuk et al. 2013). Although trees can recover from these events, the disturbance causes a substantial loss of carbon and nutrients with potentially longer-term effects on plant productivity.

While time-series data are useful for studying natural variations in climate, shorter-term manipulations in the field and laboratory provide some advantages for evaluating impacts of extreme weather events. The stochastic nature of extreme events makes it difficult to predict when and where they will occur and how severe they will be. Experiments make it possible to conduct studies under highly controlled conditions, effectively eliminating the uncertainty associated with actual events. Although it is more difficult to predict how the frequency and severity of extreme events will change in the future compared with changes in mean climatic conditions, it is central to understanding the full impacts of winter climate change on carbon cycling.

Methodological considerations

Both field studies and laboratory experiments have provided valuable insights into carbon responses to winter climate change; however, these investigations have not always produced consistent results, possibly in part because of artifacts associated with experimental design. In field studies, root systems remain intact, in contrast to laboratory studies where roots are typically severed when a sample or core is extracted from the soil. Further disturbance can occur when soil samples are sieved and homogenized. Additionally, in nearly all cases, there are differences in the way that temperatures are manipulated in the laboratory and field. In laboratory experiments, there is a tendency to use unrealistically cold temperatures or rates of freezing and thawing that do not reflect what occurs naturally in the field, potentially producing misleading results (Fig. 5; Lipson et al. 2000).

Compared with laboratory experiments, field manipulations generally have less severe experimental artifacts; however, there are some issues that warrant consideration. Snow removal experiments may not represent conditions associated with actual climate change because the snowpack is reduced without concurrent increases in air temperature (Campbell et al. 2010; Henry 2008). Additionally, snow removal can perturb the soil, and attempts to protect it with a synthetic covering or layer of packed snow may influence responses. It is also important to consider the impacts of snow removal on the water balance and how it affects microbial dynamics and DOC export (Haei et al. 2012; Heimann and Reichstein 2008). Snow additions can affect the density of snow, potentially altering processes such as trace gas exchange, oxygen diffusion into the soil, and snowmelt and infiltration.

A complicating factor in field experiments is that they are superimposed on natural climate variability, and inter-annual differences in climate can affect results. Time-series analyses capitalize on this natural variability for assessing responses to winter climate, but the records are often not long enough to capture the full range of potential future change, especially considering that some of the projected changes are unprecedented. As in time-series analyses, the length of record is also an important consideration for experiments. With few exceptions, such as passive snow fence experiments (e.g., Semenchuk et al. 2016) and a snow exclusion experiment in a boreal forest in northern Sweden that started in 2002 and still continues (Haei et al. 2010), most winter climate change manipulation experiments to date have been short-term investigations (Table A1). Studies that last less than a few years may fail to capture important long-term, cumulative, or transient effects (Blume-Werry et al. 2016). While short-term experiments can provide some valuable information about winter conditions and seasonal changes in carbon cycling, the cumulative effects and long-term impacts are important from a carbon budget perspective. More long-term field experiments and time series data are needed to better characterize carbon response trajectories so that estimates of future carbon pools and fluxes can be refined.

New studies that minimize experimental artifacts and utilize innovative approaches to address different aspects of winter climate change will improve predictions of carbon cycling in the future. Understanding responses to winter climate change requires knowledge of impacts from multiple, simultaneous, interacting environmental factors (e.g., soil moisture, temperature, CO_2, nutrients). Multi-factor laboratory and field manipulations have proved useful for investigating these interactions (e.g., soil freezing × nitrogen addition; Vankoughnett and Henry 2014), and although they are costly and results can sometimes be difficult to interpret, they remain an important and underutilized tool in this area of research, and more of these types of experiments would be valuable.

More nonmanipulative, observational studies are also needed. Since the 1970s, satellite remote sensing and associated airborne measurements have been critical for documenting changes in climate and vegetation that have occurred over broad spatial scales, such as snow cover extent (Estilow et al. 2015) and Arctic greening (Sitch et al. 2007). More recently, near-surface remote sensing (e.g., webcams, unmanned aerial vehicles) has also been used to investigate relationships between carbon and climate (e.g., Richardson et al. 2009). Near-surface remote sensing has gained popularity largely because the equipment is now widely available and relatively inexpensive, and it can make observations at high temporal frequency. The value of remote and near-surface sensing will continue to increase in the future as sensors improve and records become longer.

Modeling

Empirical data have improved knowledge and provided some mechanistic understanding of the influence of winter conditions on carbon cycling. However, computer simulation models are the only feasible approach to evaluate how winter climate affects carbon dynamics under changing environmental conditions over long periods. Future climate scenarios, that include changes in temperature and precipitation, have been used in models that depict carbon cycling. However, most carbon modeling studies have primarily focused on long-term temporal changes in carbon exchange at global (e.g., Cramer et al. 2001; Sitch et al. 2008) and regional (e.g., Morales et al. 2007; Sitch et al. 2007) scales, and mainly at coarse time-steps (e.g., annual basis). As the spatial and temporal resolution of climate input data improves, so will predictions of winter climate effects on carbon cycling.

Because winter conditions strongly influence carbon dynamics, there is a critical need to more explicitly incorporate these winter variables and processes into models so that we can better predict future changes and evaluate seasonal shifts and impacts (Commane et al. 2017; Yi et al. 2015). For example, field studies have demonstrated that soil freezing is an important belowground disturbance that causes root damage and nutrient loss (Campbell et al. 2014*b*) with consequences for aboveground production (e.g., Reinmann and Templer 2016), yet these types of processes have not yet been incorporated into computer simulation models. Deep carbon stores are greater than previously thought, yet models typically only represent processes in shallow soils (Schmidt et al. 2011). We have a poor understanding of the stability of deep soil carbon, which makes it difficult to predict responses to changes in climate (Marschner et al. 2008; Schmidt et al. 2011). This topic is especially pertinent to permafrost soils where deeper soil carbon stores are large and becoming exposed as a result of thaw, creating a potentially important climate change feedback (Schuur et al. 2015). Extreme winter events discussed previously are also not adequately represented in models because they are not well characterized and because of the uncertainty in future changes.

A more comprehensive modeling approach that includes winter climate change impacts and other simultaneous drivers of change, such as increases in atmospheric CO_2, will improve our predictive ability and understanding of how carbon dynamics are influenced by winter processes. Additional steps that would improve modeling efforts include: (*i*) harmonization of existing data so that models can be run using comparable values for input, parameterization, and verification; (*ii*) development of a coordinated network of large-scale field experiments to better evaluate and understand the magnitude of carbon responses represented in models; (*iii*) collection of long-term data for model calibration and validation; (*iv*) use of innovative approaches, such as hierarchical Bayesian modeling, machine learning, and model-data fusion; and (*v*) cross-model comparisons to assess uncertainty in modeled carbon responses.

Conclusions

As the literature indicates, the ongoing changes in winter climate in northern ecosystems is altering carbon cycling in complex ways. Over the last several decades, there have been many different types of laboratory and field experiments conducted in northern ecosystems around the world. Additionally, long-term monitoring has occurred at some sites, enabling the evaluation of relationships between variation in winter climate and carbon fluxes. Because of the many differences among studies and ecosystems observed, it can be challenging to make generalities about carbon responses; however, some common patterns have emerged from this body of research. Vegetation responses to winter climate have shown that although the longer growing season can enhance production of aboveground biomass, it can be offset by extreme events, such as spring freeze events, that are expected to become more common in the future. Changes in soil temperature regimes are among the more important factors affecting ecosystems during winter and can alter the carbon cycle by damaging roots and slowing decomposition rates. Effects of winter climate on microbial communities are mixed, and although microbial communities are highly variable, they appear to respond to and recover rapidly from winter climate events. The response of soil carbon gas flux to winter climate is highly variable and inconsistent among studies, but it is critically important from a carbon budget perspective. Fluxes of DOC in stream water are also highly variable and largely regulated by hydrology, but soil freezing has also been shown to enhance the concentrations and lability of DOC, which can have numerous ecological consequences.

Although much knowledge has been gained from the first wave of winter climate change studies, we still are just beginning to disentangle the complex relationships between winter climate and carbon cycling and export. More controlled, long-term field and laboratory experiments that resemble more realistic future winter climatic conditions are needed. Extending the duration of field and laboratory experiments over a period of many years to decades would enable evaluation of longer lasting, cumulative effects. These long-term data are essential not only for evaluating trends over time, but also for model development and validation. Many of the winter climate manipulations that have been performed thus far, have occurred within the winter season only. These experiments can be strengthened by extending studies throughout the year, and by emphasizing the shoulder seasons and other transition periods.

To date, most winter climate change studies have been conducted by individual groups of scientists at their respective sites. This insular research approach, combined with the great diversity of experiments established (type of treatment, timing of treatment, methods used, response data collected, etc.), makes it challenging to synthesize results from these studies. Some of the sites included in this review are part of the International Tundra Experiment (ITEX), which is a research network that uses standard approaches to examine the impacts of warming on tundra ecosystems and has included long-term comparative snow fence experiments at some sites (Walker et al. 1999). Building on the success of ITEX and other similar international cooperative networks, there is a pressing need to establish a winter climate change research network designed to put site-based results in a broader context. This network would leverage the value of existing experiments and enable the planning and coordination of new, multiyear manipulations using common protocols. Creating this platform for more rigorous cross-site syntheses and meta-analyses would improve knowledge of patterns and processes at regional and global scales. By fostering opportunities for collaboration and making comparisons across sites, we would gain a more complete understanding of the complex effects of winter climate change on carbon cycling and ecosystems in general.

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Appendix A

Appendix Tables A1–A2 appear on the following pages.

Table A1. Description of sites where effects of winter conditions on carbon cycling have been evaluated.

Study site	Location	Latitude, longitude	Elevation. (m)	Ecosystem	Study type	Temperature (°C)	Precipitation (cm)	Representative reference
Abisko	Lappland, Sweden	68°21′N, 18°49′E	430	Sub-Arctic tundra	Field, lab	–0.5	320	Larsen et al. (2007*b*)
Allt a'Mharcaidh	Highland, Scotland	57°06′N, 3°50′W	315	Moorland	Time series	5.7	1220	Laudon et al. (2013)
Bangtail Mesa	Montana, USA	49°47′N, 110°44′W	2380	Alpine meadow	Field	1.3	960	Weaver and Collins (1977)
Bayreuth	Bavaria, Germany	49°55′N, 11°35′E	365	Conifer forest; grassland	Lab	7.9	724	Kreyling et al. (2012*b*)
Bergen	Western Norway, Norway	60°34′N, 5°19′E	205	Broadleaf forest	Lab	6.2	2420	Skogland et al. (1988)
Bipenggou	Tibetan Plateau, China	31°15′N, 102°53′E	3580	Alpine conifer forest	Field	3.0	850	Tan et al. (2014)
Bonanza Creek	Alaska, USA	64°45′N, 148°18′W	440	Boreal forest	Lab	–1.4	280	Clein and Schimel (1995)
Coulissenhieb II	Bavaria, Germany	50°03′N, 11°51′E	770	Conifer forest	Field, Lab	5.3	1160	Hentschel et al. (2009)
Daring Lake	Northwest Territories, Canada	64°52′N, 111°35′W	400	Low-Arctic tundra	Field	–9.1	120	Buckeridge and Grogan (2008)
Donaumoos	Bavaria, Germany	48°40′N, 11°04′E	440	Grassland; cropland	Lab	9.3	580	Priemé and Christensen (2001)
Dorset	Ontario, Canada	45°23′N, 79°08′W	330	Broadleaf forest	Time series	4.9	980	Laudon et al. (2013)
Eight Mile Lake	Alaska, USA	63°53′N, 149°14′W	700	Sub-Arctic tundra	Field, time series	–1.0	390	Webb et al. (2016)
Ellerslie	Alberta, Canada	53°25′N, 113°33′W	800	Grassland; cropland	Lab	2.2	460	Feng et al. (2007)
Falköping	Västergötland, Sweden	58°20′N, 13°30′E	130	Grassland; cropland	Lab	4.9	650	Priemé and Christensen 2001
Girnock	Aberdeenshire, Scotland	57°02′N, 3°06′W	350	Moorland	Time series	6.7	1060	Laudon et al. (2013)
Glas Maol	Angus, Scotland	56°53′N, 3°02′W	1068	Montane heathland	Field, lab	2.9	1120	Wipf et al. (2015)
H.J. Andrews	Oregon, USA	44°12′N, 122°09′W	760	Conifer forest	Time series	9.2	2150	Laudon et al. (2013)
Harvard Forest	Massachusetts, USA	42°30′N, 72°10′W	380	Broadleaf forest	Field	7.0	1140	Reinmann and Templer (2016)
Hubbard Brook	New Hampshire, USA	43°56′N, 71°45′W	472	Broadleaf forest	Field, lab	5.9	1400	Groffman et al. (2001*b*)
Huntington	New York, USA	43°59′N, 74°14′W	515	Broadleaf forest	Time series	4.8	1080	Park et al. (2005)
Joensuu	North Karelia, Finland	62°36′N, 29°43′E	84	Boreal forest	Field	2.6	610	Repo et al. (2014)
Jokioinen	Tavastia, Finland	60°49′N, 23°30′E	100	Cropland	Lab	4.3	610	Koponen et al. (2006)
Juneau	Alaska, USA	58°22′N, 134°37′W	5	Conifer forest	Field	5.6	1550	Schaberg et al. (2008)
Kananaskis	Alberta, Canada	50°02′N, 115°03′W	1400	Broadleaf forest	Lab	2.3	630	Taylor and Parkinson (1988)
Korentosuo	N. Ostrobothnia, Finland	64°53′N, 26°50′E	200	Sub-Arctic peatland	Field	2.0	500	Eskelinen et al. (2016)
London	Ontario, Canada	43°02′N, 81°13′W	265	Cropland	Field	7.9	1010	Vankoughnett and Henry (2014)
Lys Valley	Aosta Valley, Italy	45°30′N, 7°51′E	1450	Alpine meadow; conifer forest	Field, lab	4.0	1070	Freppaz et al. (2008)
Medicine Bow	Wyoming, USA	41°20′N, 106°22′W	3100	Alpine meadow, shrubland	Field	0.0	580	Knight et al. (1979)
Melfort	Saskatchewan, Canada	52°52′N, 104°37′W	460	Cropland	Lab	0.5	430	Wang and Bettany (1993)
Mount Kaka	Tibetan Plateau, China	32°59′N, 103°40′E	4100	Alpine meadow	Field	2.8	720	Liu et al. (2010)
Murphy Dome	Alaska, USA	64°57′N, 148°22′W	850	Sub-Arctic tundra	Field	–2.5	280	Wipf et al. (2006)
Nagoya	Aichi, Japan	35°07′N, 137°05′E	70	Cropland; Broadleaf forest	Lab	15.5	1620	Yanai et al. (2004)
Niwot Ridge	Colorado, USA	40°03′N, 105°35′W	3500	Alpine tundra	Field	–3.0	900	Brooks et al. (1995)
Passo San Pellegrino	Trento, Italy	46°21′N, 11°44′E	1800	Alpine bog	Field	3.0	1000	Bombonato and Gerdol (2012)

Table A1 (*concluded*).

Study site	Location	Latitude, longitude	Elevation. (m)	Ecosystem	Study type	Temperature (°C)	Precipitation (cm)	Representative reference
Rocky Mtn. Natl. Park	Colorado, USA	40°43′N, 105°43′W	3550	Alpine meadow	Field	3.1	470	Bell and Bliss (1979)
Rokua	Kainuu, Finland	64°34′N, 26°33′E	200	Peatland	Field	2.0	500	Eskelinen et al. (2016)
Romanche Valley	Hautes-Alpes, France	45°02′N, 6°20′E	1850	Grassland	Field	–1.8	960	Saccone et al. (2013)
Shibecha	Hokkaido, Japan	43°24′N, 144°39′E	120	Broadleaf forest	Field	5.2	1030	Hosokawa et al. (2017)
Sierra Nevada	California, USA	37°56′N, 119°17′W	3100	Alpine meadow	Time series	0.2	790	Arnold et al. (2014)
Siiskasalmi	North Karelia, Finland	62°31′N, 29°23′E	80	Broadleaf forest; cropland	Lab	2.2	610	Priemé and Christensen (2001)
Sleepers River	Vermont, USA	44°29′N, 72°09′W	475	Broadleaf forest	Time series	4.7	1260	Laudon et al. (2013)
Spitsbergen	Svalbard	78°10′N, 16°04′E	40	High-Arctic tundra	Field	–4.9	180	Semenchuk et al. (2016)
Stillberg	Graubünden, Switzerland	46°46′N, 9°52′E	2200	Alpine tundra	Field	2.0	1150	Wipf et al. (2009)
Storgama	Telemark, Norway	59°03′N, 8°34′E	560	Montane heathland	Field, lab	5.5	980	Austnes et al. (2008)
Strontian	Highland, Scotland	56°45′N, 5°36′W	20	Heathland; conifer forest	Time series	9.1	2630	Laudon et al. (2013)
Svartberget	Västerbotten, Sweden	64°14′N, 19°46′E	250	Boreal forest	Field, lab, time series	1.8	610	Haei et al. (2010)
Tavivaara	Rovaniemi, Finland	66°26′N, 25°42′E	110	Boreal forest	Field	0.4	560	Martz et al. (2016)
Toolik Lake	Alaska, USA	68°38′N, 149°34′W	760	Low-Arctic tundra	Field, lab	–7.4	300	Walker et al. (1999)
Tsukui	Kanagawa, Japan	35°33′N, 139°16′E	160	Grassland; broadleaf forest	Lab	14.4	1520	Yanai et al. (2004)
Ultuna	Uppland, Sweden	59°49′N, 17°38′E	30	Cropland	Lab	5.5	530	Herrmann and Witter (2002)
Uryu	Hokkaido, Japan	44°21′N, 142°15′E	307	Mixed broadleaf and conifer forest	Field	3.1	1390	Shibata et al. (2013)
Wasatch Plateau	Utah, USA	39°00′N,111°18′W	2800	Broadleaf forest; alpine meadow	Field	3.7	330	Conner et al. (2017)
Whitecourt	Alberta, Canada	54°15′N, 116°00′W	810	Conifer forest	Lab	1.8	571	Taylor and Parkinson (1988)
W.K. Kellogg	Michigan, USA	42°24′N, 85°24′W	288	Broadleaf forest	Field	9.0	890	Aanderud et al. (2013)
Wolf Creek	Yukon, Canada	60°32′N, 135°11′W	1360	Sub-Arctic Tundra	Time series	–2.2	480	Laudon et al. (2013)

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Table A2. Description of studies that have evaluated effects of winter conditions on carbon pools and fluxes.

Study site*	Study type	Method	Response variable	Reference
Aboveground vegetation				
Abisko	Field	Snow addition (open-top chamber)	Moss length, density	Dorrepaal et al. (2003)
	Field	Snow addition (open-top chamber)	Shrub growth	Dorrepaal et al. (2006)
	Field	Soil freezing (mesocosm experiment)	Seedling biomass	Weih and Karlsson (2002)
	Lab	Soil freezing intensity, FTC (mesocosm experiment)	Plant biomass	Grogan et al. (2004)
Bangtail Mesa	Field	Snow addition (snow fence)	Plant biomass	Weaver and Collins (1977)
Daring Lake	Field	Snow addition (snow fence)	Plant biomass, cover	Christiansen et al. (2018)
Eight Mile Lake	Field	Snow addition (snow fence)	Plant biomass	Mauritz et al. (2017)
Harvard Forest	Field	Snow removal (shoveling)	Tree radial growth	Reinmann and Templer (2016)
Medicine Bow	Field	Snow addition (shoveling during spring)	Plant biomass	Knight et al. (1979)
	Field	Snow addition (snow fence)	Plant cover	Tucker et al. (2016)
Murphy Dome	Field	Snow addition/removal (shoveling)	Plant growth	Wipf et al. (2006); Wipf and Rixen (2010)
Niwot Ridge	Field	Snow addition (snow fence)	Foliage production	Seastedt and Vaccaro (2001)
Rocky Mt. Natl. Park	Field	Natural snow gradient	Plant biomass	Bell and Bliss (1979)
Sierra Nevada	Time series	Length of winter	Plant growth	Arnold et al. (2014)
Spitsbergen	Field	Snow addition (snow fence) and removal (shoveling)	Plant biomass, seeds, leaf length, flower abundance	Rumpf et al. (2014); Semenchuk et al. (2016); Mallik et al. (2011); Semenchuk et al. (2015); Semenchuk et al. (2013)
Stillberg	Field	Snow removal (shoveling)	Shrub growth	Wipf et al. (2009)
Svartberget	Field	Snow removal (roof) and insulation	Plant cover	Kreyling et al. (2012*a*)
	Field	Snow removal (roof)	Plant biomass	Zhao et al. (2017)
Tavivaara	Field	Snow manipulation (shoveling, watering, compacting)	Seedling survival, growth	Martz et al. (2016)
Wasatch Plateau	Field	Snowmelt advance (dust)	Plant biomass, flowers, seeds	Conner et al. (2017)
Roots				
Abisko	Field	Soil freezing (mesocosm experiment)	Root biomass	Weih and Karlsson (2002)
	Lab	Soil freezing intensity, FTC (mesocosm experiment)	Root biomass	Grogan et al. (2004)
Bangtail Mesa	Field	Snow addition (snow fence)	Root biomass	Weaver and Collins (1977)
Bayreuth	Lab	FTC	Relative electrolyte leakage, mortality	Kreyling et al. (2012*b*)
Coulissenhieb II	Field	Snow removal (shoveling)	Root biomass, production, mortality	Gaul et al. (2008)
Daring Lake	Field	Snow addition (snow fence)	Root biomass	Buckeridge and Grogan (2008)
Harvard Forest	Field	Snow removal (shoveling)	Root biomass	Reinmann and Templer (2016)
	Field	Snow removal (shoveling)	Root mortality	Reinmann and Templer (2018)
Hubbard Brook	Field	Snow removal (shoveling)	Root production, mortality	Tierney et al. (2001)
	Lab	Soil freezing (mesocosm experiment)	Root production, mortality	Tierney et al. (2001)
	Field	Snow removal (shoveling)	Root vitality, growth	Cleavitt et al. (2008)
	Field	Snow removal (shoveling)	Relative electrolyte leakage	Comerford et al. (2013)
	Field	Natural snow gradient	Root production	Sorensen et al. (2016*a*)
Joensuu	Field	Snow removal (shoveling) and insulation	Root production, mortality	Repo et al. (2014)
Juneau	Field	Insulation	Relative electrolyte leakage	Schaberg et al. (2008)
Spitsbergen	Field	Snow addition (snow fence) and removal (shoveling)	Root biomass	Semenchuk et al. (2016)
Stillberg	Field	Snow removal (shoveling)	Root production	Wipf et al. (2009)
Svartberget	Field	Snow removal (roof) and insulation	Root biomass	Kreyling et al. (2012*a*)

Table A2 (*continued*).

Study site*	Study type	Method	Response variable	Reference
Microbes and mesofauna				
Abisko	Field	Snow addition (snow fence)	Microbial C	Larsen et al. (2007*a*)
	Field	Winter warming (heating lamps and soil cables)	Litter decomposition	Bokhorst et al. (2010)
	Lab	Freezing intensity, FTC	Microbial C	Larsen et al. (2002)
	Lab	Freezing intensity, FTC	Microbial C	Sjursen et al. (2005)
	Lab	Soil freezing intensity, FTC (mesocosm experiment)	Microbial C	Grogan et al. (2004)
	Lab	Winter warming (climate chambers)	Litter decomposition	Bokhorst et al. (2010)
Bergen	Lab	Freezing intensity	Microbial C	Skogland et al. (1988)
Bipenggou	Field	Snow removal (roof) and irrigation	Microbial C	Tan et al. (2014)
Coulissenhieb II	Field	Snow removal (shoveling)	Microbial composition	Schmitt and Glaser (2011)
	Lab	FTC	Microbial composition	Schmitt et al. (2008)
Daring Lake	Field	Snow addition (snow fence)	Microbial C	Buckeridge and Grogan (2008); Buckeridge and Grogan (2010); Buckeridge et al. (2010); Christiansen et al. (2018)
Ellerslie	Lab	FTC	Microbial composition	Feng et al. (2007)
Glas Maol	Field	Snow addition (snow fence)	Litter decomposition	Wipf et al. (2015)
Harvard Forest, Hubbard Brook	Field	Snow removal (shoveling)	Microbial C	Sorensen et al. (2016*b*)
Hubbard Brook	Field	Snow removal (shoveling)	Microbial C	Groffman et al. (2001*b*)
	Field	Snow removal (shoveling)	Microbial C	Christenson et al. (2010)
	Field	Snow removal (shoveling)	Litter decomposition	Christenson et al. (2010)
Jokioinen	Lab	FTC	Microbial composition	Koponen et al. (2006)
Kananaskis, Whitecourt	Lab	FTC	Litter decomposition	Taylor and Parkinson (1988)
Lys Valley	Field	Snow removal (shoveling)	Microbial C	Freppaz et al. (2008)
	Lab	Freezing intensity	Microbial C	Freppaz et al. (2007)
Medicine Bow	Field	Snow addition (snow fence)	Microbial C	Tucker et al. (2016)
Nagoya, Tsukui	Lab	FTC	Microbial C	Yanai et al. (2004)
	Lab	FTC	Chitin/rice straw decomposition	Yanai et al. (2004)
Niwot Ridge, Toolik Lake	Field	Snow addition (snow fence)	Litter decomposition	Walker et al. (1999)
Passo San Pellegrino	Field	Snow removal, addition (shoveling), delayed melt (cover snow)	Microbial C	Bombonato and Gerdol (2012)
Romanche Valley	Field	Natural snow gradient	Litter decomposition	Saccone et al. (2013)
Shibecha	Field	Snow removal (shoveling)	Microbial C	Hosokawa et al. (2017)
Svartberget	Lab	Freezing intensity, FTC, freezing duration, water content	Microbial composition	Haei et al. (2011)
	Field	Snow removal (roof and insulation)	Cellulose decomposition	Kreyling et al. (2013)
Toolik Lake	Field	Snow addition (snow fence)	Microbial composition	Ricketts et al. (2016)
W.K. Kellogg Biological Station	Field	Snow addition/removal (shoveling)	Microbial composition	Aanderud et al. (2013)
Wasatch Plateau	Field	Snowmelt advance (dust)	Microbial C	Conner et al. (2017)
Gaseous carbon				
Abisko	Field	Snow addition (snow fence)	CO_2	Larsen et al. (2007*a*)
	Field	FTC (chamber)	CO_2	Larsen et al. (2007*b*)
	Lab	Freezing intensity, FTC	CO_2	Larsen et al. (2002)
	Lab	Freezing intensity, FTC	CO_2	Sjursen et al. (2005)
	Lab	Soil freezing intensity, FTC (mesocosm experiment)	CO_2	Grogan et al. (2004)
Bergen	Lab	Freezing intensity	CO_2	Skogland et al. (1988)
Bonanza Creek, Toolik Lake	Lab	Freezing intensity	CO_2	Clein and Schimel (1995)
	Lab	Freezing intensity, FTC	CO_2	Schimel and Clein (1996)
Coulissenhieb II	Field	Snow removal (shoveling)	CO_2, $\Delta^{14}C$-CO_2	Muhr et al. (2009)
	Lab	Freezing intensity, FTC	CO_2	Goldberg et al. (2008)

Table A2 (*continued*).

Study site*	Study type	Method	Response variable	Reference
Daring Lake	Field	Snow addition (snow fence)	CO_2, CH_4	Buckeridge et al. (2010); Christiansen et al. (2018); Grogan (2012); Nobrega and Grogan (2007); Semenchuk et al. (2016)
Donaumoos, Falköping, Siiskasalmi	Lab	Freezing intensity	CO_2, CH_4	Priemé and Christensen (2001)
Eight Mile Lake	Field	Snow addition (snow fence)	CO_2	Mauritz et al. (2017); Webb et al. (2016)
	Time series	Snow addition (snow fence)	CO_2	Celis et al. (2017)
Ellerslie	Lab	FTC	CO_2	Feng et al. (2007)
Glas Maol	Lab	Freezing intensity, FTC	CO_2	Wipf et al. (2015)
Harvard Forest, Hubbard Brook	Field	Snow removal (shoveling)	CO_2	Sorensen et al. (2016*b*)
Harvard Forest	Field	Snow removal (shoveling)	CO_2	Reinmann and Templer (2018)
Hubbard Brook	Field	Snow removal (shoveling)	CO_2, CH_4	Groffman et al. (2006)
	Lab	Freezing intensity	CO_2	Nielsen et al. (2001)
	Lab	Freezing intensity	CO_2, CH_4	Reinmann et al. (2012)
Jokioinen	Lab	FTC	CO_2	Koponen et al. (2006)
Medicine Bow	Field	Snow addition (snow fence)	CO_2	Tucker et al. (2016)
Melfort	Lab	FTC and flooding	CO_2, CH_4	Wang and Bettany (1993)
Niwot Ridge, Toolik Lake	Field	Snow addition (snow fence)	CO_2	Walker et al. (1999)
Niwot Ridge	Field	Snow addition (snow fence)	CO_2	Brooks et al. (1995)
Passo San Pellegrino	Field	Snow removal, addition (shoveling), delayed melt (cover snow)	CO_2	Bombonato and Gerdol (2012)
Sierra Nevada	Time series	Length of winter	CO_2	Arnold et al. (2014)
Spitsbergen	Field	Snow addition (snow fence)	CO_2, $\Delta^{14}C$-CO_2	Lupascu et al. (2018); Morgner et al. (2010); Semenchuk et al. (2016)
Storgama	Lab	Freezing intensity, FTC	CO_2	Austnes and Vestgarden (2008); Vestgarden and Austnes (2009)
Svartberget	Lab	Freezing intensity, FTC, freezing duration, water content	CO_2	Haei et al. (2011)
	Lab	Freezing intensity	CO_2	Drotz et al. (2010)
	Field	Snow removal (roof/insulation)	CO_2	Öquist and Laudon (2008)
	Field	Snow removal (roof) and insulation	CO_2	Haei et al. (2013)
	Field	Snow removal (roof)	CO_2	Zhao et al. (2017)
Tavivaara	Field	Snow manipulation (shoveling, watering, compacting)	CO_2	Martz et al. (2016)
Toolik Lake	Field	Snow addition (snow fence)	CO_2	Schimel et al. (2004)
	Field	Snow removal (shoveling, roof), warming (heating cable)	CO_2	La Puma et al. (2007)
	Field	Snow removal (shoveling, roof), warming (heating cable)	CO_2, CH_4	Oberbauer et al. (1998)
	Field	Snow addition (snow fence)	CO_2, CH_4	Blanc-Betes et al. (2016)
Ultuna	Lab	FTC	CO_2	Herrmann and Witter (2002)
W.K. Kellogg Biological Station	Field	Snow addition/removal (shoveling)	CO_2	Aanderud et al. (2013)
Wasatch Plateau	Field	Snowmelt advance (dust)	CO_2	Conner et al. (2017)
Dissolved Organic Carbon				
Abisko	Field	Snow addition (snow fence)	Soil extractable DOC	Larsen et al. (2007*a*)
	Lab	Soil freezing intensity, FTC (mesocosm experiment)	Soil extractable DOC	Grogan et al. (2004)
	Lab	Freezing intensity, FTC	Soil extractable DOC	Sjursen et al. (2005)
Bipenggou	Field	Snow removal (roof) and irrigation	Soil extractable DOC	Tan et al. (2014)

Table A2 (*concluded*).

Study site*	Study type	Method	Response variable	Reference
Coulissenhieb II	Field	Snow removal (shoveling)	Soil water DOC, Soil extractable DOC	Hentschel et al. (2009)
	Lab	Freezing intensity, FTC	Soil water DOC	Hentschel et al. (2008)
Daring Lake	Field	Snow addition (snow fence)	Soil extractable DOC	Buckeridge and Grogan (2008); Buckeridge and Grogan (2010); Buckeridge et al. (2010); Christiansen et al. (2018)
Glas Maol	Field	Snow manipulation (snow fence)	Soil water DOC	Wipf et al. (2015)
	Lab	Freezing intensity, FTC	Soil water DOC	Wipf et al. (2015)
Hubbard Brook	Field	Snow removal (shoveling)	Soil water DOC	Fitzhugh et al. (2001)
	Field	Snow removal (shoveling)	Soil water DOC	Groffman et al. (2011)
	Lab	Freezing intensity	Soil water DOC	Campbell et al. (2014*b*)
Huntington Forest	Time series	Long-term data	Stream DOC	Park et al. (2005)
Lys Valley	Field	Snow removal (shoveling)	Soil extractable DOC	Freppaz et al. (2008)
	Lab	Freezing intensity	Soil extractable DOC	Freppaz et al. (2007)
Melfort	Lab	FTC and flooding	Soil water DOC	Wang and Bettany (1993)
Allt a'Mharcaidh, Dorset, Girnock, H.J. Andrews, Sleepers River, Strontian, Svartberget, Wolf Creek	Time series	Long-term data	Stream DOC	Laudon et al. (2013)
Passo San Pellegrino	Field	Snow removal, addition (shoveling), delayed melt (cover snow)	Soil extractable DOC	Bombonato and Gerdol (2012)
Shibecha	Field	Snow removal (shoveling)	Soil extractable DOC	Hosokawa et al. (2017)
Spitsbergen	Field	Snow addition (snow fence)	Soil extractable DOC	Semenchuk et al. (2015)
Storgama	Field	Snow manipulation (shoveling/ insulation)	Stream TOC	Austnes et al. (2008)
	Lab	Freezing intensity, FTC	Soil water DOC	Austnes and Vestgarden (2008); Vestgarden and Austnes (2009)
Svartberget	Time series	Long-term data	Stream DOC	Ågren et al. (2010)
	Time series	Long-term data	Stream DOC	Ågren et al. (2012)
	Time series	Long-term data	Stream DOC	Haei et al. (2010)
	Field	Snow removal (roof) and insulation	Soil water DOC	Haei et al. (2010); Haei et al. (2013); Panneer et al. (2016)
	Lab	Freezing intensity, FTC, freezing duration, water content	Soil extractable DOC	Haei et al. (2011); Haei et al. (2012)
W. K. Kellogg Biological Station	Field	Snow removal/addition (shoveling)	Soil extractable DOC	Aanderud et al. (2013)
Wasatch Plateau	Field	Snowmelt advance (dust)	Soil extractable DOC	Conner et al. (2017)

Note: FTC, freeze–thaw cycle; DOC, dissolved organic carbon; TOC, total organic carbon.
*See Table A1 for location of study site.