Winters are changing: snow effects on Arctic and alpine tundra ecosystems

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Abstract

Snow is an important driver of ecosystem processes in cold biomes. Snow accumulation determines ground temperature, light conditions and moisture availability during winter. It also affects the growing season’s start and end, and plant access to moisture and nutrients. Here, we review the current knowledge of the snow cover’s role for vegetation, plant-animal interactions, permafrost conditions, microbial processes and biogeochemical cycling. We also compare studies of natural snow gradients with snow manipulation studies, altering snow depth and duration, to assess time scale difference of these approaches. The number of studies on snow in tundra ecosystems has increased considerably in recent years, yet we still lack a comprehensive overview of how altered snow conditions will affect these ecosystems. In specific, we found a mismatch in the timing of snowmelt when comparing studies of natural snow gradients with snow manipulations. We found that snowmelt timing achieved by manipulative studies (average 7.9 days advance, 5.5 days delay) were substantially lower than those observed over spatial gradients (mean range of 56 days) or due to interannual variation (mean range of 32 days). Differences between snow study approaches need to be accounted for when projecting snow dynamics and their impact on ecosystems in future climates.

Keywords: review, tundra, ground temperatures, snow experiments, ITEX

Introduction

In Arctic and alpine regions,snow and its specific properties such as depth, density, snow cover duration, and snow water equivalent plays acritical role for ecosystem processes across a wide range of temporal and spatial scales. Snowmelt timing, for example, may determine the beginning of the growing season and subsequent phenology and the growth responses of many organisms and growing season processes (Cooper 2014; Leffler et al. 2016; Kelsey et al. 2021). In addition, snow is also a critical driver of soil temperatures (Pattison and Welker 2014), albedo and atmospheric temperature regimes, spring freshet meltwater inputs (Lopez-Moreno et al. 2014), and snow influences decomposition rates and nutrient availability in the soil (Schimel et al. 2004; Brooks et al. 2011).

Reviews over the past two decades have emphasized the importance of snow for cold-climate ecosystems (Supplementary Table S2) beyond its importance as a driver of ecosystem processes: Jones et al. (2001) recognized snow as a complete ecosystem in itself with specialized organisms (e.g., Collembola, algae) living inside the snowpack (see also Körner 2003), while Kuhn (2001) addressed the snowpacks role in nutrient cycling. Since then, the importance of winter temperatures has been more widely recognized in Arctic and alpine (Callaghan and Johannson 2020) and boreal and temperate regions (Kreyling 2019). A main focus of recent reviews has been the changing duration of snow cover due to climate change, and its effects on ecosystem processes (Campbell et al. 2005; Brooks et al. 2011; Cooper 2014; Makoto et al. 2014; Kelsey et al. 2021) or society (Bokhorst et al. 2016b). Approaches to study snow cover changes though have been widely different (Jones et al. 1998; Welker et al. 2005b; Borner et al. 2008). However, even though the implications of snow cover changes on ecosystems may be heavily influenced by the methodology used, the differences between studies on natural snow gradients (spatially and temporally) and experimental manipulations has not been studied in detail.

A pioneering review and meta-analysis of snow manipulation experiments focusing on plant phenology analyzed 66 combinations of plant species and years clearly showed that flowering phenology, i.e. the timing of flowering, was linked to the timing of snowmelt (Wipf and Rixen 2010). The number of such experiments has increased considerably since then, and 20% of long-term (i.e., >30 years) climate change experiments in snow-covered systems include a snow manipulation treatment (Sanders-DeMott and Templer 2017). Most recently, Slatyer et al. (2021) reviewed 365 original research papers that used experimental field manipulations, natural snow gradients and/or long-term monitoring to test plant and animal responses at individual, population and community levels to changes in snow conditions. Although they confirmed strong links between snow cover and ecological processes, they concluded that many mechanisms of how snow affects ecosystems, i.e. by changes in snow timing, depth, type, subsequent thermal insulation properties, nutrient availability or meltwater sources etc., are not fully explored nor well understood.

Study types analysing natural snow gradients, i.e. gradients ranging from thin to deep snow cover due to topography, wind etc., and those using experimental snow manipulations often focus on different primary questions, making comparisons challenging (Billings 1969; Elmendorf et al. 2015). Along natural gradients, studies can be performed over a longer time frame, with plants that are adapted to the local environment, yet snow conditions co-varying with other factors such as microtopography or vegetation structure (Walker et al. 1993). Experiments, on the other hand, are designed for comparison to a specific control, and thus are better suited to establish causal relationships (Rieley et al. 1995; Welker et al. 2005a; De Boeck et al. 2015; Yang et al. 2018). Yet, experimental treatments may introduce artefacts or simulate scenarios not necessarily in line with predictions under climate change. To better understand which research questions require specific attention, we present a review of studies that include natural snow gradients and/or experimental snow manipulations, and demonstrate how these studies can collectively clarify the crucial role of snow cover in ecosystem processes. For this, we look at key snow variables with a focus on the timing of snowmelt, which can be derived from ground surface temperature data.

Specifically, we: 1) summarize how snow depth and snowmelt timing in cold environments affect plants, animals, microbial processes and biogeochemical cycling by updating the review by Wipf and Rixen (2010) to include studies published between 2010 and 2021 on snow and associated ecosystems; and 2) analyze soil temperature data from natural gradients of snowmelt timing (spatially and temporally) and from snow manipulation experiments (74 site-year combinations). We also assess whether such experiments change snowmelt timing realistically compared to natural spatial snow gradients and/or interannual variability and trends in snowmelt timing.

Direct effects of snow on ecosystems

Snow accumulation affects ecosystems in bothdirect and indirect ways. Snow properties, like its volume, water/ice content, timing and spatial distribution affect soil temperatures as well as light, water and nutrient availability (Starr and Oberbauer 2003; Welker et al. 2005a; Welker et al. 2005b; Bintanja 2018; Convey et al. 2018; Jespersen et al. 2018). In the following section, we discuss the mechanisms by which different snow properties, in particular snow depth and density and snowmelt timing, affect the environment.

1) Soil temperatures

One of the key attributes of snow is how it acts as a thermal insulator and decouples soils from winter air temperatures, so that soil temperature fluctuations under snow are smaller than air temperature fluctuations above the snowpack (Pruitt 1957; Goodrich 1982; Schimel et al. 2004; Schimel et al. 2006; Sullivan et al. 2008; Morgner et al. 2010; Zhang et al. 2018). Temperatures can remain very stable or even at 0°C for extended periods under thicker snow covers (Haeberli 1973; Grundstein et al. 2005; Pattison and Welker 2014; Convey et al. 2018; Way and Lewkowicz 2018) and soils may be up to 5°C warmer in the coldest period of winter, under deeper snow for instance in N Alaska (Pattison and Welker 2014). Haeberli (1973) found that a snow cover with a thickness of c. 80 cm was sufficient to completely decouple the soil from air temperatures though this threshold is dependent on the thermal conductivity, the density of the snowpack and the onset of the snow accumulation (Riseborough, 2004). Relatively mild conditions at the soil surface, compared to air temperatures, under the snowpack have been described as a ‘greenhouse’, accelerating soil microbial and other ecosystem processes (Cockell and Cordoba-Jabonero 2004; Cooper 2014). Both Way and Lewkowicz (2018) and Grünberg et al. (2020) found that snow depth and, most likely, snow structural differences, lead to pronounced differences in mean soil temperature, soil temperature variability and timing of snowmelt, across different vegetation types. Multiple field based studies have found that the thermal impacts of variations in snow thickness over natural gradients can explain more of the spatial variability in ground temperatures than key climate variables such as mean annual air temperature (Granberg 1988; Davesne et al. 2017; Way and Lewkowicz 2018; Pelletier et al. 2019; Davis et al. 2020; Garibaldi et al. 2021; Kropp et al. 2021). Some modelling studies have shown that deeper snow thicknesses found particularly in tall vegetation may altogether prevent the formation of permafrost in regions that would otherwise be climatically suitable (Smith and Riseborough 2002; Tutton and Way 2021; Way and Lapalme 2021). And, the deeper snow in tall shrub communities are the landscape locations where winter CO_2 emissions are found to be greatest, due to a combination of deeper snow and wetter conditions in riparian corridors. These water-tracks are winter CO_2 hot spots across the N Slope of AK (Fahnestock et al. 1998). While being occupying smaller spatial scales, these water tracks can have winter CO_2 emission rates that can be 2-3 times the rates of the surrounding, spatially extensive tussock tundra (Fahnestock et al. 1999a; Jones et al. 1999).

Many other studies show that taller vegetation can trap more snow and hence cause warmer ground temperatures leading to changes in numerous ecosystem processes (Sturm et al. 2001; Sturm et al. 2005b; Myers-Smith et al. 2011; Roy-Léveillée et al. 2014; Belke-Brea et al. 2020). With warming, tall shrubs have expanded (Myers-Smith et al. 2011; Ju and Masek 2016), which could result in a positive feedback loop of taller vegetation enhancing snow accumulation, which enhances shrubs (Sturm et al. 2001). However, this positive feedback may have limitations as climate warming progresses. Studies of early-winter processes in the low-Arctic showed that snowmelt and refreezing can be more pronounced in tall vegetation, which increase the release of soil heat and hence accelerate its cooling (Barrere et al. 2018).

A recent study by Way and Lapalme (2021) used numerical model simulations and a meta analysis of vegetation effects on ground temperature to explore whether changes in vegetation and its subsequent influence on snow cover would lead to a net ground temperature warming or cooling effect. Their results suggested that the long-term effects of vegetation change on ground temperature would be strongly influenced by soil moisture characteristics but that changes to snow cover would likely dominate the ground thermal regime leading to a net warming effect.

Snow structural differences and soil moisture characteristics can affect physical snow properties such as density, thermal conductivity and albedo (Sturm et al. 2005a; Flanner and Zender 2006; Domine et al. 2016). For instance, shrubs in the Canadian high Arctic were found to increase snow depth up to their maximum height (c. 40 cm) but to also change snow properties (Domine et al. 2016): for instance, snow density and thermal conductivity of snow were lower under shrubs. Also, depth hoar, which develops under large temperature gradients and is highly insulating (Colbeck 1983), grew up to shrub height, but only up to 5-10 cm in the absence of shrubs. Hence, shrubs increase the insulating properties of snow for several reasons. On the other hand, Domine et al. (2016) also found that during times of snowmelt shrubs enhanced melting, e.g. through absorbed radiation, which reduced thermal resistance and hence counteracted the effects of shrubs detailed above. These examples illustrate the complex relationships between climate warming, plant cover, snow and soil temperatures. Different processes also happen at different times of the year and are likely to impact soil temperatures, nutrient cycling and also plant growth in the summer. These complex snow-climate-vegetation interactions require future research.

The timing of snow accumulation in autumn is crucial for the soil thermal regime in winter (Riseborough 2004; Jan and Painter 2020). Freezing temperatures prior to snow build-up result in colder soils during winter, whereas mild autumn air temperatures can lead to comparatively mild – or less cold – winter soil temperatures (Johansson et al. 2013; Lafreniere et al. 2013). In contrast, no or only a thin snow cover during the winter can cause soil cooling (previously described as “colder soils in a warmer world” in the context of climate change, Groffman et al. 2001; Davis et al. 2020). This has a profound effect on permafrost; for instance, in permafrost peatlands within the discontinuous and sporadic permafrost zones, wind-redistribution of snowfall leads to shallow snow covers on elevated peat plateaus, which in turn promotes permafrost aggradation and persistence due to extensive soil heat loss during winter (e.g., Seppälä 1982; Way et al. 2018). In contrast, wind-blown snow accumulates in depressions across the landscape, insulating soil microbes, invertebrates and plants from extreme cold temperatures (Convey et al. 2015; Convey et al. 2018; D'Imperio et al. 2018; Semenchuk et al. 2019). Thus, redistribution of snow within the landscape has the potential to accelerate or dampen permafrost thaw, which may impact and be impacted by vegetation greenness in the Arctic tundra (Wang et al. 2019).

In spring, deep snow usually promotes late snowmelt, which prevents solar radiation from reaching and heating the ground surface. This can lead to colder soils during the early growing season, delaying plant phenology and soil biogeochemical cycling (Convey et al. 2018). However, when snowmelt is not delayed, the insulating effect of deep snow on soil thermal regimes in winter may carry over, resulting in higher soil temperatures and permafrost thaw in summer (Natali et al. 2019).

This winter effect on summer permafrost thaw has been shown in N Alaska, where in an experimental deep snow zone, summer thaw was 25% greater compared to ambient snow areas (program by J. Welker). Radiocarbon (14C) analyses show that carbon emitted in summer in this experimental thermokarst area are derived from ancient C (Nowinski et al. 2010; Blanc-Betes et al. 2016) and that this permafrost C may be emitted as CO_2 and as CH_4. Whether ancient C where permafrost is experimentally thawed (as a result of experimentally enhanced snow depth)is emitted in winter or in the shoulder seasons is however still uncertain, but new integrative C capture techniques for ^{14}C analysis are proving useful for year-long studies of ancient C emissons in the Arctic (Pedron et al. 2021).

The timing of snowmelt is therefore a critical determinant for the legacy effects of winter snow regimes on the snow-free season (Wilcox et al. 2019). Changes in the depth of snow can have very different consequences for the energy balance of the ecosystem (Yoshino 1984; Klinges and Scheffers 2021) and for the ecology and activity of plants and soil microbes, depending on the timing of onset of snow accumulation in the autumn and the timing of snowmelt in the spring.

2) Light

Snow cover increases the albedo of the ground surface, reflecting much of the incoming solar radiation which could otherwise be absorbed by a darker ground or by photosynthetically active plant tissues (Liston et al. 2002). Hence, snow cover has a large influence on the energy budget of tundra ecosystems (Loranty et al. 2011). The magnitude of increase in albedo due to snow cover also depends on snow structure and the underlying surface composition, with tall-statured tundra vegetation showing lower albedo in snow-covered areas than low-statured vegetation or bare ground (Baker et al. 1991). For instance, in the study of Baker et al. (1991) 70% albedo (a value when most of the underlying surface is masked) was reached with c. 5 cm of snow on bare ground and with c. 15 cm in taller vegetation. Even with high albedo, light penetrates the snowpack. Measurements of solar radiation under different snow depths showed for instance under 10 cm of snow a daily photon flux density of c. 60-80% compared with open sky solar radiation (Starr and Oberbauer 2003). Light extinction continued under deeper snow, and c. 30% of light penetrated 20 cm and only 10% or less 30 cm of snow (Starr and Oberbauer 2003), which can compare to a cloudy day. These values of course can vary considerably depending on physical properties and purity of snow. Therefore, some plants, lichens and microbes are able to photosynthesize while snow-covered. For example, evergreen Arctic shrubs were found to photosynthesize under 30 cm of snow (Starr and Oberbauer 2003). Some plants, like the Australian Marsh Marigold (*Caltha introloba*), can even flower under snow, and the European *Soldanella pusilla* pushes its flowers through the snow in spring. These findings highlight that important processes continue even in the presence of snow and indicate that the vegetation under snow is not necessarily dormant (Bjork and Molau 2007).

3) Meltwater from snow

One important aspect of snow is the fate of meltwater and its role in aquatic ecology as it affects multiple physical, biological and ecological processes. It is key to freeze-thaw processes in spring that create ground patterns including frost boils, soil stripes and polygons (Hallet and Prestrud 1986; Kessler and Werner 2003; Walker et al. 2004; Horwath et al. 2008) . These physical influences of meltwater are complemented by differential frost heave, cryoturbation, frost boils, ‘polar stripe’ landscapes and other permafrost landforms (Kessler and Werner 2003; Walker et al. 2004), which is reflected in preferential growth of plants along patterns created by frost (Czimczik and Welker 2010). Furthermore, during spring melt the snowpack releases its content of nutrients and ions, with an early elution of water soluble species (e.g., Bales et al. 1989; Lilbaek and Pomeroy 2008; Björkman et al. 2014). With soil temperatures commonly close to zero and limited biological activity, most of these nutrients will flow on top of the soil to depressions or downstream ecosystems (Westergaard-Nielsen et al. 2020).

An illustrative example for the important role of meltwater is snowmelt timing in alpine and subalpine ecosystems in the Rocky Mountains. Summer rains usually arrive in July, terminating the typically dry period of May and June. As a result, the timing of meltwater release from the winter snowpack can be a critical factor shaping the composition of vegetation communities. Evidence for this comes from a 29-year experimental warming study at the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA (Harte et al. 1995). At the start of the experiment 30 years ago, meltwater release typically peaked in early June, and thus there was sufficient soil moisture for the vegetation through the low-precipitation months of June and early July. But in the experimentally heated plots and, in recent years even in the control plots, melt occurred already in March or April. By mid May, the meltwater had run through the system, leaving much drier soils until the summer monsoonal precipitation events arrived. The drought stress from this lengthened dry interval had caused a dramatic shift from a forb-dominated vegetation to shrubs such as sagebrush. This vegetation shift resulting from a changing spring water regime was especially strong in the warmed plots, yet could even be observed in the control plots in more recent years (Harte et al. 2015; Harte 2019).

Links between meltwater and ecosystem processes have been further extended recently into the ecophysiology and ecohydrology of tundra and boreal plants (Jespersen et al. 2018). It is clear that meltwater and the ionic pulse it carries are a key source of moisture and nutrients for tundra plants (Buckeridge and Grogan 2010). Just as important, this source of moisture appears to cause an extension of late-season high rates of leaf-level photosynthesis, linking meltwater to ecosystem C fixation and influencing annual tundra C fluxes and C source-sink attributes (Leffler et al. 2016; Wieder et al. 2017). Further evidence of snow meltwater as a key source of water that leads to changes in C cycling processes is provided by Welker et al. (2005b). This study shows that for years, in which snow pack is deeper, snow melt water is apparent ($\delta^{18}O$ values) in the growth segments of *Cassiope tetragona* that correspond with increases in leaf C isotope discrimination ($\delta^{13}C$-values) associated with greater degrees of leaf C fixation.

Knowledge concerning the complex dynamics between snow, snowmelt, hydrology, nutrient availability, plant growth and ecosystem dynamics has expanded significantly over the past 10-15 years using a host of new tools, incuding water isotope forensics (Welker et al. 2000; Jespersen et al. 2018) and remote sensing tools (Kelsey et al. 2021). Yet new studies are needed to fully resolve all connections between changes in snow and the function and structure of tundra vegetation and subsequent effects on herbivores that depend on these landscapes (Pedersen et al. 2021; Richert et al. 2021).

Ecosystem responses to snow and climate change

Ongoing climate change can have a considerable influence on snow distribution patterns, snow redistribution, snow drift formation, and compaction as part of the general snowpack development as well as snow duration and depth (Bokhorst et al. 2016b). These processes are directly linked to natural variation in wind regimes and fluctuating air temperatures with implication for the thermal impacts of snow cover (Gisnås et al. 2016; Davesne et al. 2017). With increased warming, many areas have recorded a reduction in the duration and amount of snow during recent decades (Marty 2008; Bormann et al. 2018; Klein et al. 2018; Pulliainen et al. 2020). For example, the snow cover duration in Switzerland had decreased by 8.9 days per dedade (Klein et al. 2016). Some others areas though have experienced increased winter snow precipitation, which might to some degree compensate for warming-related snow reduction (Trenberth 2011; Notaro et al. 2014; Notaro et al. 2015). Changes in the distribution and duration of snow cover and their effects on ecosystems may vary significantly on local and regional scales (Cooper 2014). Less snow in winter may lead to decreased insulation and subsequently colder soils (see above, and Zhang et al. 2008). More snow in winter, on the other hand, generally has the opposite effect and causes warmer winter soils (Goodrich 1982; Schimel et al. 2004; Zhang 2005; Pattison and Welker 2014; Zhang et al. 2018).

With warming, periods of above-zero temperature during winter become more likely, which can create ground ice layers. Rain-on-snow (ROS) events also become more likely, which can lead to the formation of both ice lenses in the snow pack and on the ground with major consequences to ungulates and the forage they consume (Hansen et al. 2014; Beniston and Stoffel 2016; Hansen et al. 2019). In addition, ROS events are predicted to increase the risk of avalanche events and flooding, or extensive ground ice formation in the high Arctic (Vikhamar-Schuler et al. 2016). In addition, modelling studies have shown that large rain events could create warming effects on soil (Putkonen and Roe 2003) and accelerated permafrost degradation (Westermann et al. 2011). Ground ice formation can lead to deleterious effects on the biota, ranging from soil microarthropods (Coulson et al. 2000), evergreen dwarf shrubs (Milner et al. 2016) and vertebrates (Hansen et al. 2013) and affect plant phenology and reproduction (Le Moullec et al. 2019). Below we review effects of snow changes on plants, trophic interactions, plant pathogens and winter biogeochemical processes.

Plant phenology, growth and communities

Plant above-ground phenology, growth and community composition are very closely linked to the distribution and timing of snow (Tranquillini 1982; Sakai and Larcher 1987; Assmann et al. 2019). Snowmelt has been found to be a better predictor of tundra plant phenology dynamics that local temperatures (Assmann et al. 2019), and increasing snowfall and resulting snowmelt dynamics have been attributed as a reason for a lack of phenological change over time at some tundra sites (Bjorkman et al. 2015). Snowmelt timing is additionally strongly associated with snowbed species (Cooper et al. 2011; Semenchuk et al. 2016b), as snowmelt is often late in the season, and the remaining time for flowering and fruiting is thus very short, i.e. sometimes only a few weeks (Venn and Morgan 2007; Hülber et al. 2010; Wipf 2010; Carbognani et al. 2016; Kudo and Cooper 2019). Some species can emerge through a thin snow cover with their flowers (e.g., *Soldanella pusilla*) to advance the beginning of the growing season by a few days (Körner et al. 2019; Rixen 2020). Plants from ridges with little snow cover on the other hand potentially have a longer growing season, but risk freezing damage when flowering and losing winter frost resistance too early (Rixen et al. 2012; Venn et al. 2013). The phenology of many alpine plants is therefore often limited by photoperiod, and development only starts when days are long enough and the risk of freezing events is low (Keller and Körner 2003).

Plant species with no photoperiod limitation may need snow cover as protection from freezing (e.g., the evergreen shrub *Rhododendron ferrugineum*) and can suffer from freezing damage if snow cover is not sufficient (Larcher and Siegwolf 1985). Conversely, experimentally deepened snow may lead to substantial *R. subarcticum* growth, as the species' favoured microclimate conditions are prolonged in late-winter and early spring when competing species remain dormant (Christiansen et al. 2018a). Deeper snow cover can also protect the overwintering pre-formed flower buds from frost damage as a result of cold winter air temperatures; this is particularly evident from the damage done to buds during winters with little snow or extreme events in which mild periods (often accompanied by rain) melt away snow cover, followed by a return to freezing air temperatures (Semenchuk et al. 2013). In addition, extreme winter events that result in damaging snow conditions for plants can also delay spring phenology and reduce flowering (Le Moullec et al. 2019). For instance, extreme winter warming and associated loss of mid-winter snow resulted in delayed bud burst of the dwarf shrub *Vaccinium myrtillus* by up to three weeks in the following spring, though other species were less affected (Bokhorst et al. 2008). In contrast, experimental winter ice encasement (rain-on-snow simulation) caused earlier spring bud-burst in the same species (Preece et al. 2012). However, responses to extreme winter events appear species-specific and work is needed to further identify vulnerable/resistant groups and the mechanisms involved (Bokhorst et al. 2010a; Bokhorst et al. 2018; Le Moullec et al. 2019).

Variation in snowmelt timing not only leads to variation in the timing of phenological events, but also in the rate of developmental stages, which suggests different strategies of plants for responding to snowmelt timing (Semenchuk et al. 2016b; Gehrmann et al. 2017). Across all plant species in tundra ecosystems, however, most studies have reported advancing phenological development with climate warming and decreasing snow cover both in experiments (Wipf and Rixen 2010; Bjorkman et al. 2015; Rosa et al. 2015; Assmann et al. 2019; Jabis et al. 2020b; Collins et al. 2021) and in long-term monitoring (Wolkovich et al. 2012). In a global comparison, the phenology of plant populations from colder regions (High Arctic) was more sensitive to temperature than that of populations from warmer regions (Low Arctic) (Prevey et al. 2017; Prevey et al. 2019), which indicates that different plant species and populations from different regions can vary in their phenological response to climate and snow cover change.

Modifications of phenologies may disturb mutualistic interactions between species, i.e., phenological mismatch (see trophic interactions below; Memmott et al. 2007; Hegland et al. 2009; Green 2010; Forrest 2015). In studies along snowmelt gradients, changes in flowering phenology strongly affected the seed set and outcrossing rate of alpine plants visited by bumble bees (Kameyama and Kudo 2009; Kudo et al. 2011; Moriwaki et al. 2020). Therefore, phenological changes are also likely to affect interactions between flowers and pollinators (McKinney et al. 2012; Høye et al. 2013; Kudo and Ida 2013; Gillespie et al. 2016; Ogilvie et al. 2017; Robinson and Henry 2018; Kudo and Cooper 2019). For example, a study of bee pollinators in the subalpine found that their emergence, peak, and senescence phenology respond to snowmelt timing, but their rate of response is less sensitive than that of flowers (Stemkovski et al. 2020), creating the potential for reduced synchrony between bees and their flowers with earlier snowmelt timing.

While aboveground phenological responses to earlier or later snowmelt have been greatly expanded with the coupling of vegetation and snow remote sensing (Kelsey et al. 2021), much less is known about belowground root phenology and its interaction with the timing of snowmelt. A few studies do suggest, however, that root phenology may be much less responsive than aboveground responses, as it did not change with increased snow depth (and later snowmelt) in a wetland in Greenland (D'Imperio et al. 2018), nor with an earlier snowmelt in heath and meadow communities in the Swedish sub-Arctic (Blume-Werry et al. 2017). Makoto et al. (2020) showed for woody seedlings from Japanese forests with substantial winter snow cover that spring root and shoot growth phenology were decoupled across multiple species while they were coupled at the end of the growing season. Thus, root phenology cannot simply be inferred from aboveground phenology (Abramoff and Finzi 2015; Blume-Werry et al. 2016; Schwieger et al. 2018).

Tundra plant growth corresponds with growing season length and soil moisture availability in tundra ecosystems (Myers-Smith et al. 2015; Ackerman et al. 2017). Tundra shrub growth dynamics and the climate sensitivity of shrub growth is highly variable among species and sites (Dawes et al. 2011; Myers-Smith et al. 2015) and likely key climate drivers are both direct (e.g., snow melt timing, frost damage, snowmelt hydrology, etc.) and indirect (e.g., altered nutrient availability, accelerated permafrost thaw, etc.) (Myers-Smith et al. 2019). Dendroecology studies have found greater temperature sensitivity of tundra shrubs in wetter versus drier sites (Elmendorf et al. 2012; Myers-Smith et al. 2015; Ackerman et al. 2017) and the site-level soil moisture status is in part controlled by snowmelt dynamics (Westergaard-Nielsen et al. 2020). Deeper snow has been found to promote *Rhododendron subarcticum* shrub growth in Arctic tundra (Christiansen et al. 2018a, see above), and in contrast longer growing seasons have been found to promote *Rhododendron ferrugineum* shrub growth in alpine tundra (Francon et al. 2020). Both species grow in areas with long snow cover, but the seemingly contradicting results highlight the complexity in capturing responses of tundra plant growth to interacting climate drivers.

The patterns of plant community distributions strongly match those of the mean timing of snowmelt in heterogeneous landscapes (Friedel 1961; Körner 2003). In studies along snowmelt gradients, grasses and other tall and productive species encroached into snowbeds only a few years after snowmelt started to advance (Green and Pickering 2009; Pickering et al. 2014; Venn et al. 2014). With ongoing climate change, this could result in the long term in a reduction of habitat for snowbed specialists and a resultant decrease in biodiversity (Niittynen et al. 2018) as more competitive species encroach into these historically late-lying snow areas (Williams et al. 2015). Expansion of shrubs and graminoids is common in snow-meadow and snowbed habitats with climate change (e.g., Wipf et al. 2009; Spasojevic et al. 2013; Formica et al. 2014; Myers-Smith et al. 2019). Comparisons of community structure in snow-meadows revealed that the mosaic patterning of alpine vegetation has become obscured during the last 40 years and that the structure of alpine vegetation has become more uniform due to accelerated snowmelt and drier soil conditions linked to global warming (Amagai et al. 2018).

Trophic interactions

Snow plays a vital role in the ontogeny and population dynamics of many animals (Korslund and Steen 2006; Bale and Hayward 2010), and has been proposed as one of the main climatic factors affecting trophic interactions in tundra ecosystems (Berg et al. 2008; Berteaux et al. 2017). For example, the timing and intensity of herbivory varies between habitats of contrasting snow cover

(Speed et al. 2009; Anderson et al. 2016b), and the snow sensitivity of tundra herbivore emergence and migration in turn influences higher trophic levels (Maclean and Pitelka 1971; Tulp and Schekkerman 2008). Climate-induced alterations in snow conditions will thus undoubtedly affect the interactions between plants and their herbivores, with consequences for other trophic levels.

Snow conditions, including spatial patterns, the onset and duration of winter snow cover, and thawing events during winter can influence plant-herbivore-predator interactions in a number of ways. First, snow distribution directly affects food accessibility to herbivores, which will influence their distribution (Berg et al. 2008; Pedersen et al. 2021). For example, during winter, muskoxen and reindeer/caribou prefer areas with thin snow cover where food is more easily accessible (Schaefer and Messier 1995; Riseth et al. 2011; Pedersen et al. 2021), while lemmings favour areas with deeper and more persistent snowpack that protects them from temperature extremes and predators (Gilg et al. 2009; Duchesne et al. 2011; Reid et al. 2012). Which habitats become available (snow-free) earlier in the season will also affect the spatial distribution of herbivores and their population dynamics (Layton-Matthews et al. 2020). For example, during the spring pre-breeding period prolonged snow cover restricts access of pink-footed geese (*Anser brachyrhynchus*) to their preferred foraging habitat on wet areas (Anderson et al. 2012; Pedersen et al. 2013).

In turn, snow provides plants with a physical barrier against some herbivores. For example, during winter, ptarmigan and hares have a limited ability to dig into the snow, and thus forage primarily on plants emerging through the snowpack or growing in wind-blown areas (Hakkarainen et al. 2007; Tape et al. 2010). In High-Arctic Greenland, Arctic hare and rock ptarmigan benefit from muskox opening the snowpack (Schmidt et al. 2018). A similar phenomenon has been observed in Svalbard, where reindeer cratering opens up foraging areas for rock ptarmigan (Pedersen et al. 2006). Conversely, plants are better protected from small mammal herbivory in areas with shallow snow, as small mammals will concentrate in areas with deeper snow in winter (Duchesne et al. 2011). Large herds of reindeer, caribou and muskoxen are not only affected by snow, but have direct impacts on snow properties; trampling on snow alter snow depth and density, and hence also winter soil temperatures, with cascading effects on summer soil temperatures (Roturier and Roué 2009; Riseth et al. 2011).

The timing of snowmelt is also one of the most important predictors of the phenology and activity of arthropods in the High Arctic (Høye and Forchhammer 2008; Coulson et al. 2014), although the responses seem to be group-specific (Dollery et al. 2006; Kankaanpää et al. 2018). Some studies have found increased invertebrate herbivory in earlier snowmelt areas (Roy et al. 2004; Berg et al. 2008; Little et al. 2016; Wheeler et al. 2016), but others have reported increased levels of herbivory in late snowmelt areas (Torp et al. 2010a; Torp et al. 2010b). Late snowmelt can increase plant palatability to herbivores by altering plant chemistry (Walsh et al. 1997; Semenchuk et al. 2015; Mörsdorf et al. 2019). In a snow fence experiment, the growth of moth larvae was higher when fed on leaves from the snow fence plots, suggesting that later snowmelt enhanced food quality for these herbivores (Torp et al. 2010a). Similarly, other studies have found that invertebrate herbivores like aphids and scale insects (Coccoidea) were most numerous in late snowmelt plots (Høye and Forchhammer 2008).

Finally, thawing events during winter and rain-on-snow (ROS) events can create ice crusts within the snowpack or ground ice, and episodes of heavy rain can cause flooding in the subnivean space and subsequent formation of a thick layer of ground ice (Hansen et al. 2014). Such ice layers prevent access to food by herbivores (Hansen et al. 2013), resulting in increased mortality and reduced fecundity. As an example, large ROS events in Yamal, Russia caused heavy mortality of reindeer (Sokolov et al. 2015; Forbes et al. 2016), with subsequent impacts across trophic levels causing increases of generalist predators (Sokolov et al. 2015). The occurrence of ROS events in the autumn determines the hardness of the basal snow layer and negatively influences brown lemming demographic parameters (Domine et al. 2018). The formation of ground ice also can lead to anoxia in the plant-soil interface and in the soil beneath, resulting in increased damage to, or mortality of plants (Bjerke et al. 2017), lichens (Bjerke et al. 2011) and soil invertebrate communities (Coulson et al. 2000) and hence decomposition and nutrient cycling processes (see below).

Climate change may have different consequences for different plant-herbivore systems, depending on the relative effects of temperature, snow and precipitation and the frequency and strength of climate related extreme events. Changes in snow patterns can affect herbivores in species-specific ways (Berteaux et al. 2017). Some herbivores, such as small mammals who actually live and reproduce under the snow, would be negatively affected by longer snow-free periods when predation risk is higher, whereas large herbivores that are less vulnerable to predation could potentially benefit from longer snow-free periods due to longer food accessibility (Berg et al. 2008). Changing snow conditions associated with climate warming have been proposed as a potential cause for the dampening of population cycles of small mammals (Domine et al. 2018), possibly due to increased cold stress when snow cover and depth are reduced (Kearney 2020) although the underlying mechanisms may differ across study locations (Kausrud et al. 2008; Gilg et al. 2009).

Fungal Pathogens

Snow molds are an important group of fungal pathogens that have a particularly clear relationship with snow cover (Smith et al. 1989). Snow molds are a taxonomically diverse group of fungi that occur throughout the Arctic tundra and attack overwintering plants under snow cover (Hsiang et al. 1999; Matsumoto 2009). Evergreen dwarf shrubs (Olofsson et al. 2011) and mosses (Moriana-Armendariz et al. 2021) are likely to be hit hardest by these pathogens since their growth form implies the presence of exposed green leaves under the snow. However, there are also snow molds that attack plants from other functional groups, such as grasses or trees at the treeline (Barbeito et al. 2012; Barbeito et al. 2013). Snow molds require snow cover to spread to new host plants and are often favoured by deep snow, as deeper snow cover usually results in warmer and more moist conditions, which are optimal for their spread (Snider et al. 2000; Matsumoto 2009). Outbreaks of snow molds are common during years with deep long-lasting snow cover and have considerable consequences for ecosystems, such as "winterkill" of plants (Matsumoto 2009). Snow molds are thus expected to increase in abundance and importance where future climate change results in deeper snow cover and warmer temperatures.

Fungal pathogens can even outweigh beneficial effects of snow cover changes to plants. For example, though plant growth may be increased by the warmer temperatures under a thicker winter snow cover, it may also facilitate outbreaks of parasitic fungi (Olofsson et al. 2011; Moriana-Armendariz et al. 2021). In northern Sweden, the evergreen shrub *Empetrum hermaphroditum* experienced a fungal outbreak of the pathogen *Arwidssonia empetri* that killed the majority of the plants and led to a reduction in net ecosystem carbon exchange during the growing season (Olofsson et al. 2011). Response of parasitic fungi to snow enhancement may thus contribute to the observed changes in vegetation composition (Cooper et al. 2019).

Snow distribution can also influence the effects of fungal pathogens by altering host plant abundance and susceptibility, or by influencing the spread of the pathogen (Matsumoto 2009). Thus, the effect of snow on pathogens will vary depending on traits of the host plants and the pathogens. Direct effects of snow on pathogens are expected to be mainly negative as fungi require high humidity conditions for spore dispersal, germination and infection. However, the effects on host plant abundance and susceptibility could range from positive to negative, and override the effects on pathogen spreading (Roy et al. 2004).

Winter biogeochemical processes

The most important control of winter soil microbial activity and biogeochemical cycling in cold regions is liquid water availability (Mikan et al. 2002; Brooks et al. 2011). Frozen soil water hinders diffusion of substrates and enzymes, effectively limiting microbial activity (Öquist et al. 2009). However, even when soils freeze, liquid water persists as unfrozen films around soil particles, particularly when temperatures remain above -5 to -10°C. Consequently, snow accumulation is critically important for facilitating winter microbial activity and biogeochemical cycling in Arctic and alpine environments.

Continued soil organic matter decomposition during winter (Schimel et al. 2004; Schimel et al. 2006) results in significant emissions of CO_2 through the snow pack (e.g., Oechel et al. 1997; Fahnestock et al. 1999b; Grogan and Jonasson 2005; Sullivan et al. 2008; Euskirchen et al. 2012; Natali et al. 2019). Despite low absolute emission rates compared to summer, these winter emissions may accumulate to large magnitudes, as winter snow cover may be present for up to 75% of the year. As a result, cumulative winter CO_2 emissions are often greater than summer plant C uptake, and tundra ecosystems are now increasingly becoming net CO_2 sources on an annual basis (Belshe et al. 2013; Euskirchen et al. 2017; Natali et al. 2019). For instance, the current loss of carbon during the winter season from October to April amounted to 1622 Tg C per year for the entire permofrost regions, which is considerably more than the estimated carbon uptake of 1032Tg C during the growing season (Natali et al. 2019). These winter C emissions are even predicted to increase by 17% under a moderate mitigation scenario (Natali et al. 2019). While many models project increased snowfall for the Arctic in coming decades, there are still large uncertainties, including interannual variation and regional differences and shifts to increased rain, associated with future snowfall regimes (Callaghan et al. 2011; Bintanja 2018). Nevertheless, warmer winters with increased snowfall and earlier spring snowmelt date are expected for most regions, and these changes in winter climate are very likely to increase wintertime CO_2-release from arctic landscapes (Natali et al. 2019). With ongoing climate change, the magnitudes and patterns of net C emissions depend on different aspects of timing and depth of snow cover, which may affect these C source-sink relations in several ways. While it is generally expected that warmer soils in winter will lead to greater microbial respiration and greater winter C efflux, several recent studies have pointed to important complexities in the relationship between winter soil temperature and microbial respiration. For instance, experimental studies in the sub-alpine forest and near the southern limit of Arctic tundra have shown that soil microbes can exhaust the supply of labile C during warm winters and/or beneath deep insulative snowpacks, with important implications for both winter and summer CO_2 emissions and soil nutrient cycling (Brooks et al. 2005; Sullivan et al. 2020). Indeed, deepened snow increased wintertime CO_2 release in distinct Canadian and Svalbard tundra sites (Nobrega and Grogan 2007; Semenchuk et al. 2016a), leading to reduced soil C storage (Semenchuk et al. 2019) and ultimately lower summertime CO_2 release after 5-10 years (Semenchuk et al. 2016a; Christiansen et al. 2018a). Consequently, it seems clear that changes in winter climate will not only affect non-growing season carbon fluxes, as legacy effects also carry over to determine ecosystem carbon balance in summer.

Over the long-term, deeper snow may reduce soil cooling in winter, resulting in thawing permafrost and a deeper active layer in summer that facilitates emission of ancient labile permafrost C to the atmosphere (Czimczik and Welker 2010; Natali et al. 2014; Natali et al. 2015). These factors all play an important role in driving whether, and by how much, we can expect soil C losses in the Arctic (Crowther et al. 2016; Crowther et al. 2018; van Gestel et al. 2018).

Along with winter-long soil C mineralization and CO_2 emissions, mineralization of nutrients, such as nitrogen and phosphorus (Schimel et al. 2004; Schimel et al. 2006; Rixen et al. 2008; Buckeridge et al. 2013), results in annual microbial biomass peaking in late-winter (Buckeridge et al. 2013). Following snowmelt, enhanced nutrient supply from winter nutrient mineralization and lysing microbes can manifest during the growing season as higher tundra plant leaf N and P concentrations (Welker et al. 2005a; Semenchuk et al. 2015; Mörsdorf et al. 2019). These leaf nutrient concentrations are important as they contribute to leaf-level photosynthesis which, when considered at the plant community level, can influence C sequestration during summer (Pattison and Welker 2014). However, whether the net effect of summer C fixation in a warmer climate will exceed winter-long CO_2 emissions is still not fully resolved (Welker et al. 2000; Natali et al. 2019).

The temporal patterns of snowmelt in spring may either open the tundra to spring warmth when snow melts earlier, leading to early leaf out and rapid C gain, or delay snowmelt and thus the onset of spring growth, thereby prolonging snow-covered CO_2 emissions through a delayed snowmelt of deeper winter snow. These complexities and the net effect of deeper or shallower snowpack, earlier or later onset of snow cover in autumn and snow melt in spring will all affect the future C budget, with the integrated effect of these changes having either a positive or negative climate feedback effect (Welker et al. 1997; Oberbauer et al. 1998; Starr et al. 2000; Starr et al. 2008; Steltzer et al. 2009; Grogan 2012; Livensperger et al. 2016; Darrouzet-Nardi et al. 2019).

An important aspect of climate change effects on biogeochemical processes is the occurrence of extreme events in winter (see above). Extreme winter warming events associated with loss of snow, frost-drought or ice layer development can cause plant damage and mortality and lead to substantial reductions in gross primary productivity (Bokhorst et al. 2009). They can also lead to reduced ecosystem respiration as a result of the lower GPP, with a net effect of an overall reduction in ecosystem carbon sequestration (net primary productivity) in the following growing season (Treharne et al. 2019; Treharne et al. 2020).

While below-ground soil organic matter decomposition rates increase with enhanced snowfall and accumulation (see above), the effects of warmer winter temperatures on foliar litter decay rates on the ground surface seem variable. Recent experimental studies in diverse tundra landscapes across the circumpolar Arctic suggest that deepened snow alone has negligible effect on litter mass loss (Walker et al. 1999; Aerts et al. 2012; Myers-Smith and Hik 2013; DeMarco et al. 2014; Christiansen et al. 2017; Christiansen et al. 2018b) although alpine snow gradient studies showed positive relationships between snow depth (Saccone et al. 2013) or snow-cover duration (Carbognani et al. 2014) and litter decomposition. Experimental snow reduction, however, showed negligible effects on litter decay rates (Bokhorst et al. 2013b), suggesting that changes in winter microclimate may have little impact on the litter layer. This apparent site- and year-dependent discrepancy between ground surface and belowground soil microbial activities in winter could be due to more pronounced frost desiccation, and therefore unfrozen water limitation, of the surface litter layer relative to soil organic matter. While there is still uncertainty on the responsiveness of the decomposers and physical breakdown of leaf litter material during winter and the role snow plays in this process (Hobbie and Chapin 1996; Bokhorst et al. 2010b; Bokhorst et al. 2013b), it appears that snow accumulation by itself has little impact on mid-winter litter mass losses, when temperatures are well below freezing. However, where changes in snow cover cause community change (see below), this may lead to changes in litter quality and thereby decomposability. For instance, an experimental study on tundra biome litter decomposability indicated that a change from herbaceous to shrub-dominated tundra would lead to lower litter decomposability (Cornelissen et al. 2007). How changes in litter quality and overall microbial decomposition rates as induced by changes in snow cover, in combination, lead to changing litter decomposition rates is a question in need of in-depth study.

Studying effects of snow changes on ecosystems

Given the critical role of snow cover in numerous ecosystem processes and the disruption to prevailing patterns of snow cover predicted under climate change, many studies have investigated the various effects of changing snow parameters (e.g. snow duration, depth and quality) on ecosystems (e.g., Rixen et al. 2004), as well snow-related extreme events such as icing (Coulson et al. 2000; Preece et al. 2012; Hansen et al. 2014) and extreme winter warming (Bokhorst et al. 2008; Bokhorst et al. 2011a). Here, we review two types of snow studies: those that aim to understand natural gradients and those that manipulate snow depth experimentally. To contrast snow manipulation experiments with natural snow gradient studies, we gathered temperature data from snow studies (74 site-year combinations of manipulations and natural gradients) to analyze and compare timing of snowmelt (defined as end of the zero degree curtain, i.e. the increase in temperature after disappearance of snow) (Figs. 1 and 3; methods in Appendix). We also consider the seasonal setting of snow studies, in order to account for studies being carried out at sites with naturally early, mid or late snowmelt.

Fig. 1.

Remote sensing approaches

A promising approach to quantifying natural gradients of snow cover over different and large spatio-temporal scales is to use remote sensing data from satellites, drones and other types of photographic data (Malnes et al. 2016; Kankaanpää et al. 2018). Satellite snow products, such as simulated potential snow accumulation patterns (Randin et al. 2009), first snow-free day (Dedieu et al. 2016), and snow cover duration (Niittynen et al. 2018), demonstrate the importance of snow cover in explaining vegetation composition, distribution and phenology in cold biomes (Walker et al.

1993; Zeng and Jia 2013; Kelsey et al. 2021). However, as many Arctic ecosystem properties are scale-dependent (Siewert 2018; Assmann et al. 2020; Siewert and Olofsson 2020) , the spatial resolution of satellite-based remote sensing approaches with a coarse resolution (e.g., 30 - 500 m pixel widths) may only detect large-scale changes in snow cover (Hall et al. 2002; Nagler et al. 2008) and in land-surface greenness (Zeng and Jia 2013; Myers-Smith et al. 2020), but do not detect small-scale ecosystem processes driven by snow cover (Myers-Smith et al. 2020).

Snow cover is spatially and temporally heterogeneous and, in particular, snowmelt and snow accumulation patterns can vary across landscapes with varied topography (Marsh et al. 1997; Aalstad et al. 2020; Pedersen et al. 2021). Recently, drones have successfully been used for recording and seasonal monitoring of ecosystem properties even in climatically challenging tundra environments (Fraser et al. 2016; Assmann et al. 2020; Siewert and Olofsson 2020). Drones and high-resolution satellite imagery can resolve small scale variability in snow extent, often measured as fractional snow-covered area (fSCA) (Liang et al. 2017; Aalstad et al. 2020), or snow thickness (Grünberg et al. 2020; Harder et al. 2020) or snow depth (Pedersen et al. 2018; Pedersen et al. 2021). Snow cover can be coupled with hydrological analyses, for example by estimating the snow water equivalent (Liston and Sturm 2002; Dozier et al. 2016; Niedzielski et al. 2019), or to understand the impact of snowbeds on vegetation productivity (Borner et al. 2008; Siewert and Olofsson 2020).

Mapping snow extent can be easily achieved from optical sensors due to the high spectral contrast of snow. Similarly, snow algae can be measured as they influence the optical properties of snow (Davey et al. 2019; Gray et al. 2020). Estimating snow thickness using drones typically relies on the generation of a digital elevation model (DEM) using either structure from motion (SfM) or Lidar approaches, followed by subtracting a snow-free reference DEM (Niedzielski et al. 2019; Harder et al. 2020; Walker et al. 2021). Drones can be particularly useful in spring, when snowmelt dynamics are fast but cloud cover can prevent satellite observations. Here, repeated drone flights provide temporally resolved estimates of snowmelt (Siewert and Olofsson 2020). Another approach is the use of near-remote sensing, for example with instruments (e.g., time-lapse camera networks) permanently mounted on poles 2 m above a given plot and able to take multiple measurements of the same plots (Anderson et al. 2016a; Parmentier et al. 2021) to follow the vegetation development from snowmelt throughout the growing season and relate this to environmental conditions experienced.

Natural gradients

An obvious approach to studying effects of snow is along natural gradients of snowmelt resulting e.g. from microtopography under the same climatic conditions or along large climate gradients (Borner et al. 2008; Rammig et al. 2010; Vandvik et al. 2020). However, these natural gradients, as with any observational approach, often co-vary with features such as aspect, slope etc. (Dunne et al. 2004). Our snow timing data show by how much snowmelt date can vary within a single gradient and year (Fig. 2, see methods). The timespan between the earliest and the latest snowmelt date along a gradient can be up to two months. The earliest snowmelt recorded in our data was day 58 (equating to 27 February in the Northern Hemisphere – for dates from Southern Hemisphere studies we subtracted 182 from the day of year to give consistency in numbers) and the latest was day 230 (equating to 18 August). Mean site differences in snowmelt timing due to micro-topographic gradients was 56 days. At sites with extremely late snowmelt, vegetation is dominated by snowbed specialists with low above-ground biomass (such as *Salix herbacea*) (Wheeler et al. 2016). On the other hand, at sites with early snowmelt such as ridges or hummocks, specialists adapted to freezing temperatures and dry conditions dominate. At sites with an intermediate snowmelt timing, the most favourable conditions for plant growth can be found, with intermediate soil moisture levels, a moderate growing season length and a moderate level of protection from freezing events (Walker et al. 1993).

Alongside geographical gradients, snowmelt date can vary over time. For example, a site that has been monitored daily since 1975 for snowpack and snowmelt at the RMBL (south-west Colorado, at 2,915 m a.s.l.) has an average snowmelt date of 20 May, ranging from 24 April to 19 June, paralleling the snowfall variation in the preceding winter (mean maximum snow depth of 10.6 m, ranging from 4.74 m to 16.41 m). The wide range of microhabitats available in an environment can create an even greater range of snowmelt dates through a combination of spatial and interannual variability.

Fig. 2.

Snow manipulation experiments

In many studies, snow cover has been manipulated experimentally, either by removing snow and hence advancing snowmelt or by adding snow and postponing snowmelt. A convenient way to add snow is by installing fences in areas with a dominant wind direction. A snowdrift forms on the lee side of the fence, while snow depth can additionally be reduced on the exposed side (Jones et al. 1998; Walker et al. 1999; Morgner et al. 2010; Mark et al. 2015; Ricketts et al. 2016; D'Imperio et al. 2018; Jespersen et al. 2018). If fences are sufficiently long, the area of increased snow may well be large enough to have a considerable effect on both above and belowground parts of the vegetation (Welker et al. 2005a), and thus avoid the problems associated with other approaches as discussed below, with small treatment plots with proportionately large edge effects.

Manipulating snow manually by shoveling is more labour-intensive and may alter snow properties, yet has the advantage that a higher number of well-defined plots in a given area can be treated. Also, removals and additions can be realized in close proximity under controlled conditions (Wipf et al. 2006; Anderson and Wadgymar 2019; Wadgymar et al. 2019; Frei and Henry 2021). Snowmelt can also be accelerated by positioning dark cloth on the snow surface that increases the absorption of solar radiation (Steltzer et al. 2009; Blume-Werry et al. 2017). Experimental snowmelt change has also been achieved using infrared heaters (Harte and Shaw 1995; Harte et al. 1995; Harte et al. 2015; Winkler et al. 2016; Panetta et al. 2018; Harte 2019; Jabis et al. 2020a), heating cables in the ground (Rixen et al. 2012), the combination of both (Bokhorst et al. 2008; Bokhorst et al. 2011a), dust or black sand on snow (Blankinship et al. 2014) or reflective surfaces on snow (Blankinship et al. 2014).

By analyzing the snowmelt date based on the marked increase in temperature fluctuation after the extended period of the zero curtain we could quantify delays and advances in the meltout date caused by the snow manipulation experiments (Fig. 3). On average, snow addition delayed snowmelt by 5.5 days (± 8.2 SD), and snow removal advanced snowmelt by 7.9 days (± 8.4 SD). The experiments varied considerably in their timing of snowmelt with respect to day of the year, from day 49 to day 188 (equating to 18 February and early July in the Northern Hemisphere). We do not have complete information of the amounts of snow that were added or removed in the experiments. But from those studies where snow depth information is available, we see that on average 80 cm of snow is added (ranging from c. 40 to 150 cm, see SupplementaryTable S1). This addition of snow corresponded to c. 10 days delay in snowmelt. The amount of snow added did not correlate with days of delay in snowmelt (results not shown), which indicates that temperatures and radiation are just as important, if not more important, for snowmelt timing as the amounts of snow.
The experimental manipulations of snow cover only caused minor changes in snowmelt timing compared with the large natural differences in snowmelt that exist because of topography, wind drift, interannual variation, etc., and impacts on the studied ecosystems should thus always be interpreted with these numbers in mind. However, the change in snowmelt timing depended upon the natural timing of snowmelt, as snow treatments at sites with earlier natural snowmelt had larger experimental effects than those at sites with late natural snowmelt (Fig. 4).

One way to use the natural snow gradient experimentally is to carry out transplants across the snow gradient. In a transplant study with the dwarf willow *Salix herbacea*, the difference in snowmelt timing between snowbeds and ridges was about one month, and phenological responses of *S. herbacea* to the very different times of melt-out were highly plastic (Sedlacek et al. 2015).

Fig. 3

Fig. 4.

The variability of responses to snow manipulation experiments is in general very high (Wipf and Rixen 2010). The timing in the season when a snow manipulation is carried out can to some degree explain seemingly contradictory plant responses in different studies. If for instance a snow addition is made in a system where the natural snowmelt is already very late (e.g., Jespersen et al. 2018), the experiment is likely to make the growing conditions more extreme, effectively by shortening the already short growing season. Plant growth and productivity are hence likely to be reduced. On the other hand, if snow addition is carried out early in spring or summer, it is likely to make growing conditions more benign, for instance by providing protection from freezing events and cold temperatures (Klein et al. 2018; Vitasse et al. 2018), or by improving soil moisture conditions. The opposite can be expected for the advancement of snowmelt by snow removal. In a long-term snow removal study, all species of a plant community responded with decreased growth during the subsequent summer, with the exception of *Loiseleuria procumbens*, a species characteristic of the most extreme end of the snow gradient, where early snowmelt and extreme temperature fluctuations are experienced (see above) (Wipf et al. 2009).

Open Top Chambers (OTCs) x snow manipulations

An increasing number of studies have combined snow manipulations with warming by OTCs (Dorrepaal et al. 2004; Weedon et al. 2012; Drescher 2014; Suzuki 2014; Weedon et al. 2014; Gillespie et al. 2016; Christiansen et al. 2017; D'Imperio et al. 2018; Darrouzet-Nardi et al. 2019; Mörsdorf et al. 2019; Frei and Henry 2021; Thompson et al. 2021). Both treatments can affect plant growth and biogeochemical processes, but can have different effects depending on mechanisms at work. Warming can for instance cause drying of soils, while snow addition by snow fences can increase soil moisture (Schollert et al. 2017). The combined effects of warming and increased snow depth can change the plant community composition and increase primary productivity (Leffler et al. 2016). Warmer spring temperatures and deeper snow can also have opposing effects, e.g. on litter decomposition (Farrer et al. 2015; Blok et al. 2016).

An unintended consequence of the widely-used ‘open top chamber’ methodology of experimentally manipulating air temperature in polar field experiments studying potential consequences of warming can be the accumulation of snow within the chambers when left in place over winter. This can lead to artifacts in the data obtained both in terms of winter temperature regime and extended snow cover within the experiment (Dorrepaal et al. 2009; Bokhorst et al. 2011b; Bokhorst et al. 2013a). For instance, increased snow depth in OTCs led to near complete disappearance of a previously dominant lichen species (Bokhorst et al. 2016a). We would therefore encourage authors to state whether their OTCs are removed or left on the plots during winter when reporting their results. Nevertheless, leaving OTCs in place in winter remains advantageous as it enables a combination of snow increase in winter and summer warming (for a comparison of effects of winter and summer warming on tundra see Pold et al. 2021).

Future Research Priorities

1. New technology to sense snow and snowmelt dynamics

New technology including drones (Assmann et al. 2020; Siewert and Olofsson 2020), lidar and radar observations (Harder et al. 2020) and higher-resolution optical satellite imagery will allow us to capture snow and snowmelt dynamics missed by historical data collection. Integrating these new technologies into future *in-situ* ecological data collection will allow for a better understanding of the fine spatial and temporal scale dynamics of snowmelt and resulting ecological processes such as plant phenology. There is a continued need, however, for improving the validation between remotely-sensed and ground-based observations of phenology (see, e.g. Karlsen et al. 2021 for an approach). Further development of *in-situ* low-cost snow monitoring techniques (e.g., Lewkowicz 2008; Siren et al. 2018; Tutton and Way 2021) and expanded winter field data collection should also be prioritized to provide better validation of remotely-sensed snow products (Walker et al. 2021).

2. Changing phenology and trophic interactions under altered snow regimes

New technologies will allow us to answer questions about how changing snow regimes are altering the landscape heterogeneity of tundra plant productivity. Earlier snowmelt in the tundra can advance plant phenological stages (e.g., Assmann et al. 2020), and altered snow regimes can influence trophic interactions by changing the availablity of plant resources across the landscape (e.g., Berteaux et al. 2017; Gillespie and Cooper 2021). A research priority will also be to improve quantitative (and not only qualitative) impacts of climate and vegetation changes on snow properties.

3. Influence of changing snowmelt dynamics and winter extreme events on tundra biodiversity

Changing snow regimes and more frequent winter extreme events could have cumulative impacts on tundra biodiversity. Longer summer growing seasons or frost tolerance could alter community composition (Bokhorst et al. 2018). Experiments that test the sensitivity of plants to snow regimes and winter conditions beyond those currently experienced in tundra ecosystems will shed light on the composition of tundra that could be expected with future climate change.

Conclusions

Snow and changes in snow cover are key drivers of ecological processes in cold ecosystems. Snow and snowmelt dynamics alter plant growing season length, phenology, growth, community composition, soil moisture and biogeochemistry, carbon sequestration and trophic interactions. We find that the difference in snow-free season length can be up to two months in snow manipulation studies and along natural local and regional snowmelt gradients. However, most snow manipulation experiments change the snowmelt timing by a much shorter amount, often by only a few days. In addition., the time of the year when snow studies have been carried out varies markedly. In this review, we have taken the first steps in providing an improved baseline for future studies of the influence of snow on terrestrial ecosystems. Differences between snow study approaches need to be accounted for when drawing ecological conclusions and projecting snow dynamics and their impact on ecosystems in future climates. Along with these temporal considerations, questions of the spatial scale of effects must be addressed using study designs that incorporate multiple spatial extents and resolutions of snow cover and depth measurements, to better link plot-level observations to landscape-scale dynamics, and we thus recommend further comparisons between natural gradient and experimental studies (see e.g. Moriana-Armendariz et al. 2021; Gehrmann et al. this issue). Our analysis of temperature data across many studies and years can and should be expanded, to quantify winter temperature fluctuations, the frequency and intensity of freezing events, freeze-thaw cycles, rain-on-snow events and build-up of the snow cover in autumn. Gathering global data focusing on the impacts of snow on tundra ecosystems has the potential to considerably improve our understanding of cold ecosystems in times of climate change.

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Contributors’ statement

CR, TTH, PM, EJC, ED, CTC and SW conceived the idea for the paper. The following people contributed substantially to the acquisition of data, and the analysis and interpretation of data: CR, TTH, PM, RA, JA, JTA, PAA, ICB, JWB, MPB, DB, GBW, JB, SB, MC, CTC, PC, EJC, JHCC, SJC, ED, BE, SCE, CE, TGWF, ERF, SRG, FG, CG, PG, JH, GHRH, DI, REI, GJ, ISJ, JYJ, DK, GK, JL, HL, JJL, SL, MM, JM, IMS, JO, RP, AP, GKP, HMRM, PS, MBS, RS, MS, KS, PS, KLT, MV, VV, SV, JW, RW, JMW, SW and SZ. CR led the writing of the manuscript with substantial contributions from TTH, PM, ICB, MPB, CTC, EJC, REI, JO, PS, MBS, JMW, RA, JA, JTA, PAA, JWB, DB, GBW, JB, SB, MC, PC, JHCC, SJC, ED, BE, SCE, CE, TGWF, ERF, SRG, FG, CG, PG, JH, GHRH, DI, GJ, ISJ, JYJ, DK, GK, JL, HL, JJL, SL, MM, JM, IMS, RP, AP, GKP, HMRM, PS, RS, MS, KS, KLT, MV, VV, SV, JW, RW, SW and SZ. All co-authors provided editorial writing to one or more manuscript drafts, all co-authors approved the final version of the manuscript and agree to be accountable for the work.

Data availability statement

The data used for the paper can be requested from the corresponding author.

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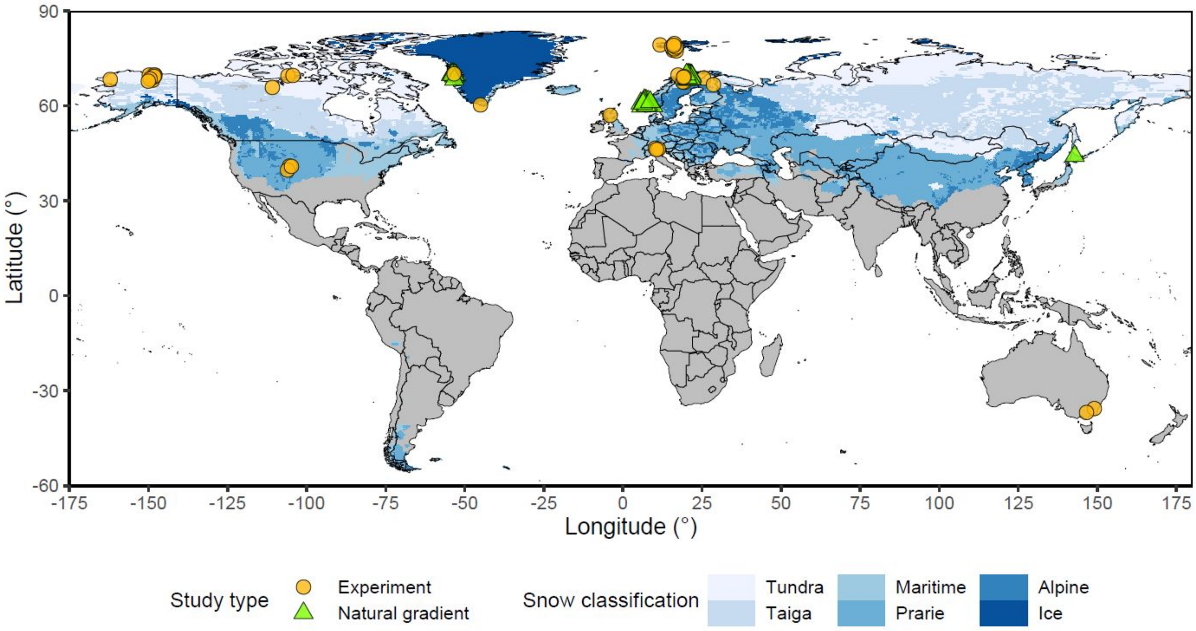

Fig. 1. Map of studies used in our analysis. Yellow dots indicate a snow manipulation experiment, green triangles indicate studies along a natural snow gradient (i.e. plots within a given region with

different abouts of snow due to topography). The snow classification and the shape files for projecting these layers follows Sturm et al. (1995) and the Atlas of the Cryosphere (Maurer 2007), where darkest blue to lightest blue colours in order represent ice, alpine, prarie, maritime, taiga, and tundra. Some regions with seasonal snow, primarily in the Southern Hemisphere, do not have a classification according to the system of Sturm et al. (1995). The base map was produced in R using the 'ggplot2' R package (Wickham 2016) to project a 2013 world map that is freely available from the Natural Earth project (https://www.naturalearthdata.com/, 1:50m scale, no permission for reuse required). The map and the snow classification layers were projected using a WGS84 geographic coordinate system from the 'raster' R package (Hijmans 2021), which aligned coordinates from the map and snow layers with the GPS coordinates of the study locations.

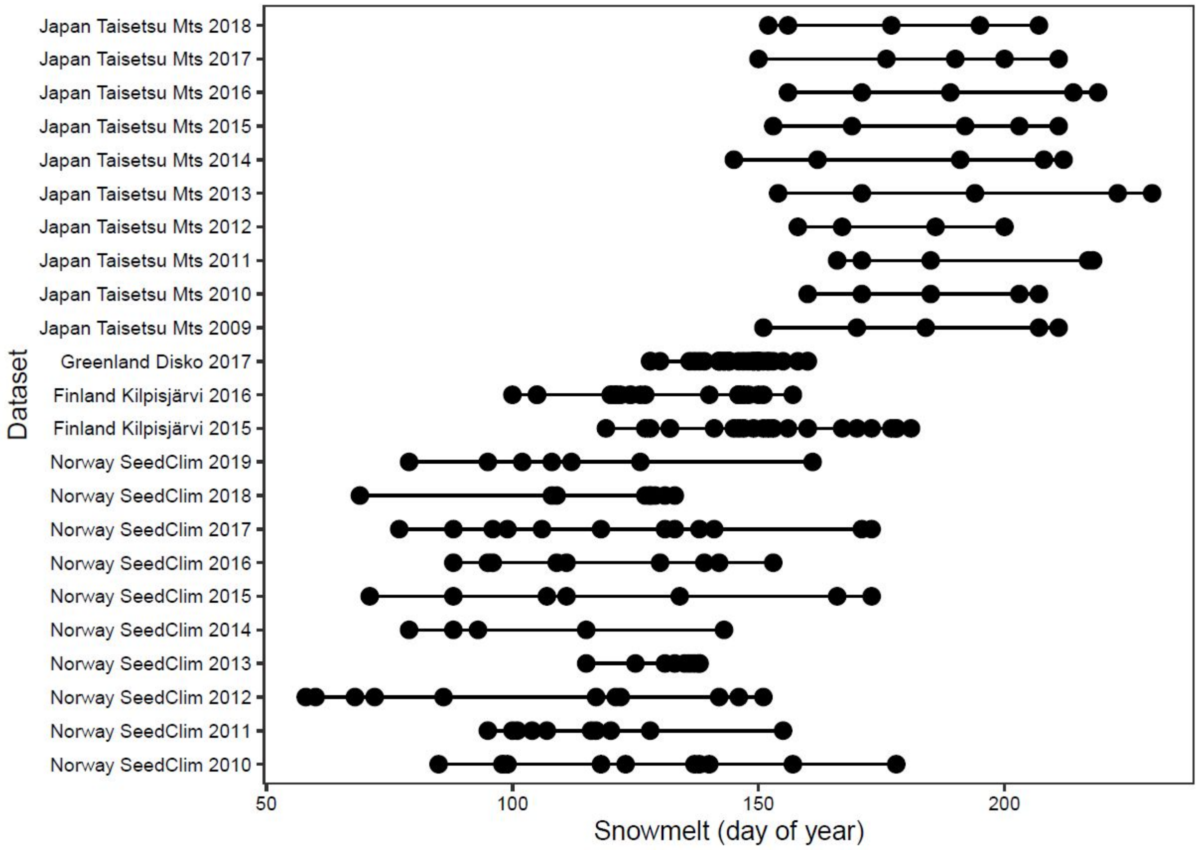

Fig. 2. Snowmelt timing along natural snow gradients (caused by topography, wind etc.) varies considerably at individual sites (multiple sites across western Norway in the SeedClim data) and between years (see methods for site selection, calculations etc.). The X axis represents the day of the year (DOY) on which snowmelt occurs. Different dots represent plots within one studied gradient in a given year. Site-year combinations are ordered first by mean snowmelt date of sites (across years per site) and then by year. Different site-year combinations can be from the same study. Most studies include only small elevation differences (except Norway), hence the snow differences are caused by micro-topography, wind drift and other factors. Japan: 43.67°N, 142.91°E, 1800 m asl (Kudo 2016); Greenland: 69.27°N 53.50°E, 90 m asl; Finland: 69.06°N 20.81°E, 697-768 m asl; Norway: 60.54-61.09°N 5.96-8.70°E, 346-1213 m asl.

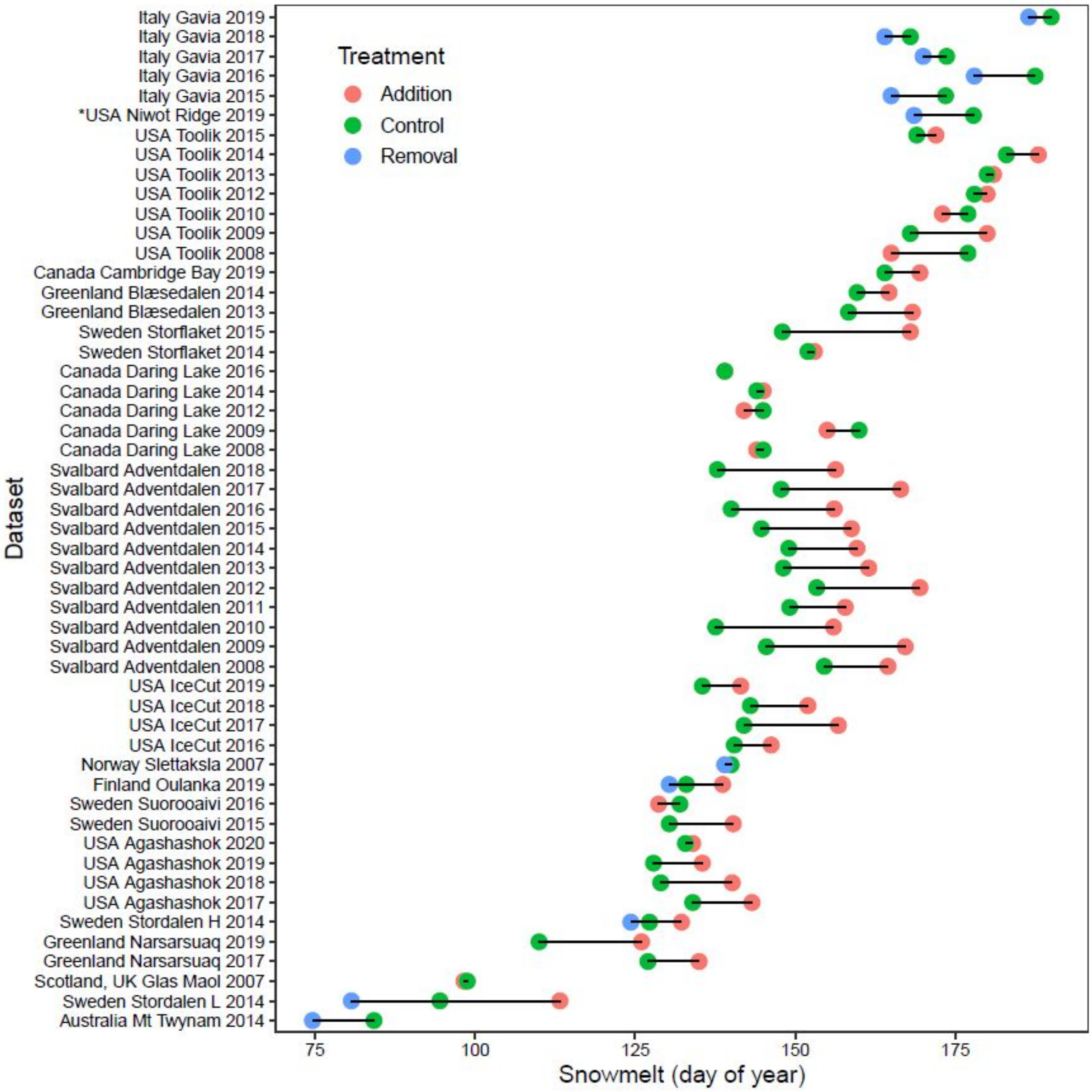

Fig. 3. Most snow manipulation experiments change the snowmelt date by less than what can be observed due to variation in space or time (Fig. 2). Treatment x year combinations are ordered by site day of snowmelt (i.e. day of year for sites from the Northern Hemisphere and day of year – 182 for sites from the Southern Hemisphere) first per site, then by year within site. Type of snow manipulation is indicated for each site/experiment. All experiments with snow addition only (represented by only green and red dots) were realized by snow fences. All experiment that included snow removal or represented only snow removal (represented by a blue dot) were carried out by snow shoveling (exeption USA Niwot Ridge, marked with *, were black sand was used to advance snowmelt).

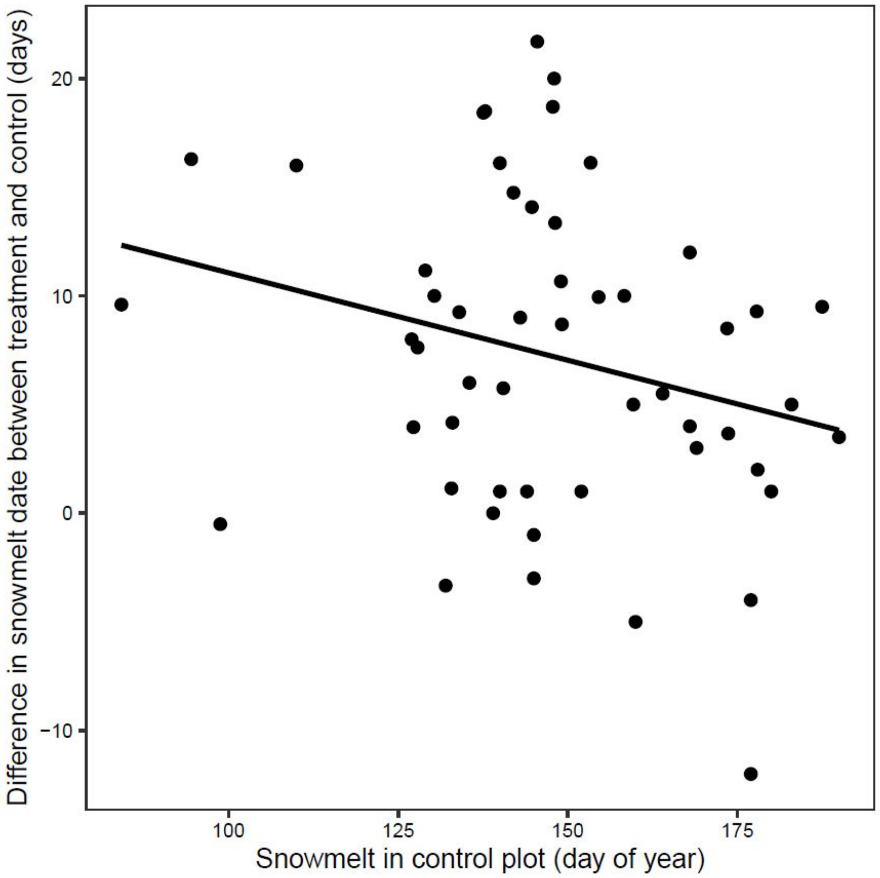

Fig. 4. Effect size of snow treatments is more pronounced at plots with early snowmelt. The effect size is the number of days advancement or delay in snowmelt timing caused by both snow addition and removal and was calculated for removals as control – removal, and for additions as addition – control. See fig. 3 for origin of data points. Effect size is larger at sites with earlier natural snowmelt ($p<0.01$) and equally driven by addition and removal treatments (interaction treatment type x snowmelt day in control plot n.s.).