

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

2 ecosystems

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104 **Abstract**

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

120 **Keywords:** review, tundra, ground temperatures, snow experiments, ITEX
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126 Introduction

127 In Arctic and alpine regions, snow and its specific properties such as depth, density, snow cover
128 duration, and snow water equivalent plays a critical role for ecosystem processes across a wide range
129 of temporal and spatial scales. Snowmelt timing, for example, may determine the beginning of the
130 growing season and subsequent phenology and the growth responses of many organisms and
131 growing season processes (Cooper 2014; Leffler et al. 2016; Kelsey et al. 2021). In addition, snow is
132 also a critical driver of soil temperatures (Pattison and Welker 2014), albedo and atmospheric
133 temperature regimes, spring freshet meltwater inputs (Lopez-Moreno et al. 2014), and snow
134 influences decomposition rates and nutrient availability in the soil (Schimel et al. 2004; Brooks et al.
135 2011).

136
137 Reviews over the past two decades have emphasized the importance of snow for cold-climate
138 ecosystems (Supplementary Table S2) beyond its importance as a driver of ecosystem processes:
139 Jones et al. (2001) recognized snow as a complete ecosystem in itself with specialized organisms
140 (e.g., Collembola, algae) living inside the snowpack (see also Körner 2003), while Kuhn (2001)
141 addressed the snowpacks role in nutrient cycling. Since then, the importance of winter temperatures
142 has been more widely recognized in Arctic and alpine (Callaghan and Johannson 2020) and boreal
143 and temperate regions (Kreyling 2019). A main focus of recent reviews has been the changing
144 duration of snow cover due to climate change, and its effects on ecosystem processes (Campbell et
145 al. 2005; Brooks et al. 2011; Cooper 2014; Makoto et al. 2014; Kelsey et al. 2021) or society
146 (Bokhorst et al. 2016b). Approaches to study snow cover changes though have been widely different
147 (Jones et al. 1998; Welker et al. 2005b; Borner et al. 2008). However, even though the implications
148 of snow cover changes on ecosystems may be heavily influenced by the methodology used, the
149 differences between studies on natural snow gradients (spatially and temporally) and experimental
150 manipulations has not been studied in detail.

151

152 A pioneering review and meta-analysis of snow manipulation experiments focusing on plant
153 phenology analyzed 66 combinations of plant species and years clearly showed that flowering
154 phenology, i.e. the timing of flowering, was linked to the timing of snowmelt (Wipf and Rixen 2010).
155 The number of such experiments has increased considerably since then, and 20% of long-term (i.e.,
156 >30 years) climate change experiments in snow-covered systems include a snow manipulation
157 treatment (Sanders-DeMott and Templer 2017). Most recently, Slatyer et al. (2021) reviewed 365
158 original research papers that used experimental field manipulations, natural snow gradients and/or
159 long-term monitoring to test plant and animal responses at individual, population and community
160 levels to changes in snow conditions. Although they confirmed strong links between snow cover and
161 ecological processes, they concluded that many mechanisms of how snow affects ecosystems, i.e. by
162 changes in snow timing, depth, type, subsequent thermal insulation properties, nutrient availability
163 or meltwater sources etc., are not fully explored nor well understood.

164
165 Study types analysing natural snow gradients, i.e. gradients ranging from thin to deep snow cover
166 due to topography, wind etc., and those using experimental snow manipulations often focus on
167 different primary questions, making comparisons challenging (Billings 1969; Elmendorf et al. 2015).
168 Along natural gradients, studies can be performed over a longer time frame, with plants that are
169 adapted to the local environment, yet snow conditions co-varying with other factors such as
170 microtopography or vegetation structure (Walker et al. 1993). Experiments, on the other hand, are
171 designed for comparison to a specific control, and thus are better suited to establish causal
172 relationships (Rieley et al. 1995; Welker et al. 2005a; De Boeck et al. 2015; Yang et al. 2018). Yet,
173 experimental treatments may introduce artefacts or simulate scenarios not necessarily in line with
174 predictions under climate change. To better understand which research questions require specific
175 attention, we present a review of studies that include natural snow gradients and/or experimental
176 snow manipulations, and demonstrate how these studies can collectively clarify the crucial role of

177 snow cover in ecosystem processes. For this, we look at key snow variables with a focus on the
178 timing of snowmelt, which can be derived from ground surface temperature data.

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

186

187

188 **Direct effects of snow on ecosystems**

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

195

196 **1) Soil temperatures**

197 One of the key attributes of snow is how it acts as a thermal insulator and decouples soils from
198 winter air temperatures, so that soil temperature fluctuations under snow are smaller than air
199 temperature fluctuations above the snowpack (Pruitt 1957; Goodrich 1982; Schimel et al. 2004;
200 Schimel et al. 2006; Sullivan et al. 2008; Morgner et al. 2010; Zhang et al. 2018). Temperatures can

201 remain very stable or even at 0°C for extended periods under thicker snow covers (Haeberli 1973;
202 Grundstein et al. 2005; Pattison and Welker 2014; Convey et al. 2018; Way and Lewkowicz 2018) and
203 soils may be up to 5°C warmer in the coldest period of winter, under deeper snow for instance in N
204 Alaska (Pattison and Welker 2014). Haeberli (1973) found that a snow cover with a thickness of c. 80
205 cm was sufficient to completely decouple the soil from air temperatures though this threshold is
206 dependent on the thermal conductivity, the density of the snowpack and the onset of the snow
207 accumulation (Riseborough, 2004). Relatively mild conditions at the soil surface, compared to air
208 temperatures, under the snowpack have been described as a 'greenhouse', accelerating soil
209 microbial and other ecosystem processes (Cockell and Cordoba-Jabonero 2004; Cooper 2014). Both
210 Way and Lewkowicz (2018) and Grünberg et al. (2020) found that snow depth and, most likely, snow
211 structural differences, lead to pronounced differences in mean soil temperature, soil temperature
212 variability and timing of snowmelt, across different vegetation types. Multiple field based studies
213 have found that the thermal impacts of variations in snow thickness over natural gradients can
214 explain more of the spatial variability in ground temperatures than key climate variables such as
215 mean annual air temperature (Granberg 1988; Davesne et al. 2017; Way and Lewkowicz 2018;
216 Pelletier et al. 2019; Davis et al. 2020; Garibaldi et al. 2021; Kropp et al. 2021). Some modelling
217 studies have shown that deeper snow thicknesses found particularly in tall vegetation may
218 altogether prevent the formation of permafrost in regions that would otherwise be climatically
219 suitable (Smith and Riseborough 2002; Tutton and Way 2021; Way and Lapalme 2021). And, the
220 deeper snow in tall shrub communities are the landscape locations where winter CO₂ emissions are
221 found to be greatest, due to a combination of deeper snow and wetter conditions in riparian
222 corridors. These water-tracks are winter CO₂ hot spots across the N Slope of AK (Fahnestock et al.
223 1998). While being occupying smaller spatial scales, these water tracks can have winter CO₂ emission
224 rates that can be 2-3 times the rates of the surrounding, spatially extensive tussock tundra
225 (Fahnestock et al. 1999a; Jones et al. 1999).

226

227 Many other studies show that taller vegetation can trap more snow and hence cause warmer ground
228 temperatures leading to changes in numerous ecosystem processes (Sturm et al. 2001; Sturm et al.
229 2005b; Myers-Smith et al. 2011; Roy-Léveillé et al. 2014; Belke-Brea et al. 2020). With warming, tall
230 shrubs have expanded (Myers-Smith et al. 2011; Ju and Masek 2016), which could result in a positive
231 feedback loop of taller vegetation enhancing snow accumulation, which enhances shrubs (Sturm et
232 al. 2001). However, this positive feedback may have limitations as climate warming progresses.
233 Studies of early-winter processes in the low-Arctic showed that snowmelt and refreezing can be
234 more pronounced in tall vegetation, which increase the release of soil heat and hence accelerate its
235 cooling (Barrere et al. 2018).

236

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

243

244 Snow structural differences and soil moisture characteristics can affect physical snow properties
245 such as density, thermal conductivity and albedo (Sturm et al. 2005a; Flanner and Zender 2006;
246 Domine et al. 2016). For instance, shrubs in the Canadian high Arctic were found to increase snow
247 depth up to their maximum height (c. 40 cm) but to also change snow properties (Domine et al.
248 2016): for instance, snow density and thermal conductivity of snow were lower under shrubs. Also,
249 depth hoar, which develops under large temperature gradients and is highly insulating (Colbeck
250 1983), grew up to shrub height, but only up to 5-10 cm in the absence of shrubs. Hence, shrubs
251 increase the insulating properties of snow for several reasons. On the other hand, Domine et al.
252 (2016) also found that during times of snowmelt shrubs enhanced melting, e.g. through absorbed

253 radiation, which reduced thermal resistance and hence counteracted the effects of shrubs detailed
254 above. These examples illustrate the complex relationships between climate warming, plant cover,
255 snow and soil temperatures. Different processes also happen at different times of the year and are
256 likely to impact soil temperatures, nutrient cycling and also plant growth in the summer. These
257 complex snow-climate-vegetation interactions require future research.

258
259 The timing of snow accumulation in autumn is crucial for the soil thermal regime in winter
260 (Riseborough 2004; Jan and Painter 2020). Freezing temperatures prior to snow build-up result in
261 colder soils during winter, whereas mild autumn air temperatures can lead to comparatively mild –
262 or less cold – winter soil temperatures (Johansson et al. 2013; Lafreniere et al. 2013). In contrast, no
263 or only a thin snow cover during the winter can cause soil cooling (previously described as “colder
264 soils in a warmer world” in the context of climate change, Groffman et al. 2001; Davis et al. 2020).
265 This has a profound effect on permafrost; for instance, in permafrost peatlands within the
266 discontinuous and sporadic permafrost zones, wind-redistribution of snowfall leads to shallow snow
267 covers on elevated peat plateaus, which in turn promotes permafrost aggradation and persistence
268 due to extensive soil heat loss during winter (e.g., Seppälä 1982; Way et al. 2018). In contrast, wind-
269 blown snow accumulates in depressions across the landscape, insulating soil microbes, invertebrates
270 and plants from extreme cold temperatures (Convey et al. 2015; Convey et al. 2018; D'Imperio et al.
271 2018; Semenchuk et al. 2019). Thus, redistribution of snow within the landscape has the potential to
272 accelerate or dampen permafrost thaw, which may impact and be impacted by vegetation greenness
273 in the Arctic tundra (Wang et al. 2019).

274
275 In spring, deep snow usually promotes late snowmelt, which prevents solar radiation from reaching
276 and heating the ground surface. This can lead to colder soils during the early growing season,
277 delaying plant phenology and soil biogeochemical cycling (Convey et al. 2018). However, when

278 snowmelt is not delayed, the insulating effect of deep snow on soil thermal regimes in winter may
279 carry over, resulting in higher soil temperatures and permafrost thaw in summer (Natali et al. 2019).
280
281 This winter effect on summer permafrost thaw has been shown in N Alaska, where in an
282 experimental deep snow zone, summer thaw was 25% greater compared to ambient snow areas
283 (program by J. Welker). Radiocarbon (^{14}C) analyses show that carbon emitted in summer in this
284 experimental thermokarst area are derived from ancient C (Nowinski et al. 2010; Blanc-Betes et al.
285 2016) and that this permafrost C may be emitted as CO_2 and as CH_4 . Whether ancient C where
286 permafrost is experimentally thawed (as a result of experimentally enhanced snow depth) is emitted
287 in winter or in the shoulder seasons is however still uncertain, but new integrative C capture
288 techniques for ^{14}C analysis are proving useful for year-long studies of ancient C emissions in the Arctic
289 (Pedron et al. 2021).

290
291 The timing of snowmelt is therefore a critical determinant for the legacy effects of winter snow
292 regimes on the snow-free season (Wilcox et al. 2019). Changes in the depth of snow can have very
293 different consequences for the energy balance of the ecosystem (Yoshino 1984; Klinges and
294 Scheffers 2021) and for the ecology and activity of plants and soil microbes, depending on the timing
295 of onset of snow accumulation in the autumn and the timing of snowmelt in the spring.

296

297 **2) Light**

298 Snow cover increases the albedo of the ground surface, reflecting much of the incoming solar
299 radiation which could otherwise be absorbed by a darker ground or by photosynthetically active
300 plant tissues (Liston et al. 2002). Hence, snow cover has a large influence on the energy budget of
301 tundra ecosystems (Lorantý et al. 2011). The magnitude of increase in albedo due to snow cover also
302 depends on snow structure and the underlying surface composition, with tall-statured tundra
303 vegetation showing lower albedo in snow-covered areas than low-statured vegetation or bare

304 ground (Baker et al. 1991). For instance, in the study of Baker et al. (1991) 70% albedo (a value when
305 most of the underlying surface is masked) was reached with c. 5 cm of snow on bare ground and
306 with c. 15 cm in taller vegetation. Even with high albedo, light penetrates the snowpack.
307 Measurements of solar radiation under different snow depths showed for instance under 10 cm of
308 snow a daily photon flux density of c. 60-80% compared with open sky solar radiation (Starr and
309 Oberbauer 2003). Light extinction continued under deeper snow, and c. 30% of light penetrated 20
310 cm and only 10% or less 30 cm of snow (Starr and Oberbauer 2003), which can compare to a cloudy
311 day. These values of course can vary considerably depending on physical properties and purity of
312 snow. Therefore, some plants, lichens and microbes are able to photosynthesize while snow-
313 covered. For example, evergreen Arctic shrubs were found to photosynthesize under 30 cm of snow
314 (Starr and Oberbauer 2003). Some plants, like the Australian Marsh Marigold (*Caltha introloba*), can
315 even flower under snow, and the European *Soldanella pusilla* pushes its flowers through the snow in
316 spring. These findings highlight that important processes continue even in the presence of snow and
317 indicate that the vegetation under snow is not necessarily dormant (Bjork and Molau 2007).

318

319 **3) Meltwater from snow**

320 One important aspect of snow is the fate of meltwater and its role in aquatic ecology as it affects
321 multiple physical, biological and ecological processes. It is key to freeze-thaw processes in spring that
322 create ground patterns including frost boils, soil stripes and polygons (Hallet and Prestrud 1986;
323 Kessler and Werner 2003; Walker et al. 2004; Horwath et al. 2008) . These physical influences of
324 meltwater are complemented by differential frost heave, cryoturbation, frost boils, 'polar stripe'
325 landscapes and other permafrost landforms (Kessler and Werner 2003; Walker et al. 2004), which is
326 reflected in preferential growth of plants along patterns created by frost (Czimczik and Welker
327 2010). Furthermore, during spring melt the snowpack releases its content of nutrients and ions, with
328 an early elution of water soluble species (e.g., Bales et al. 1989; Lilbaek and Pomeroy 2008;
329 Björkman et al. 2014). With soil temperatures commonly close to zero and limited biological activity,

330 most of these nutrients will flow on top of the soil to depressions or downstream ecosystems
331 (Westergaard-Nielsen et al. 2020).

332

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

347

348 Links between meltwater and ecosystem processes have been further extended recently into the
349 ecophysiology and ecohydrology of tundra and boreal plants (Jespersen et al. 2018). It is clear that
350 meltwater and the ionic pulse it carries are a key source of moisture and nutrients for tundra plants
351 (Buckeridge and Grogan 2010). Just as important, this source of moisture appears to cause an
352 extension of late-season high rates of leaf-level photosynthesis, linking meltwater to ecosystem C
353 fixation and influencing annual tundra C fluxes and C source-sink attributes (Leffler et al. 2016;
354 Wieder et al. 2017). Further evidence of snow meltwater as a key source of water that leads to

355 changes in C cycling processes is provided by Welker et al. (2005b). This study shows that for years,
356 in which snow pack is deeper, snow melt water is apparent ($\delta^{18}\text{O}$ values) in the growth segments of
357 *Cassiope tetragona* that correspond with increases in leaf C isotope discrimination ($\delta^{13}\text{C}$ -values)
358 associated with greater degrees of leaf C fixation.

359 Knowledge concerning the complex dynamics between snow, snowmelt, hydrology, nutrient
360 availability, plant growth and ecosystem dynamics has expanded significantly over the past 10-15
361 years using a host of new tools, including water isotope forensics (Welker et al. 2000; Jespersen et al.
362 2018) and remote sensing tools (Kelsey et al. 2021). Yet new studies are needed to fully resolve all
363 connections between changes in snow and the function and structure of tundra vegetation and
364 subsequent effects on herbivores that depend on these landscapes (Pedersen et al. 2021; Richert et
365 al. 2021).

366

367

368

369 **Ecosystem responses to snow and climate change**

370 Ongoing climate change can have a considerable influence on snow distribution patterns, snow
371 redistribution, snow drift formation, and compaction as part of the general snowpack development
372 as well as snow duration and depth (Bokhorst et al. 2016b). These processes are directly linked to
373 natural variation in wind regimes and fluctuating air temperatures with implication for the thermal
374 impacts of snow cover (Gisnås et al. 2016; Davesne et al. 2017). With increased warming, many
375 areas have recorded a reduction in the duration and amount of snow during recent decades (Marty
376 2008; Bormann et al. 2018; Klein et al. 2018; Pulliainen et al. 2020). For example, the snow cover
377 duration in Switzerland had decreased by 8.9 days per decade (Klein et al. 2016). Some other areas
378 though have experienced increased winter snow precipitation, which might to some degree

379 compensate for warming-related snow reduction (Trenberth 2011; Notaro et al. 2014; Notaro et al.
380 2015). Changes in the distribution and duration of snow cover and their effects on ecosystems may
381 vary significantly on local and regional scales (Cooper 2014). Less snow in winter may lead to
382 decreased insulation and subsequently colder soils (see above, and Zhang et al. 2008). More snow in
383 winter, on the other hand, generally has the opposite effect and causes warmer winter soils
384 (Goodrich 1982; Schimel et al. 2004; Zhang 2005; Pattison and Welker 2014; Zhang et al. 2018).

385
386 With warming, periods of above-zero temperature during winter become more likely, which can
387 create ground ice layers. Rain-on-snow (ROS) events also become more likely, which can lead to the
388 formation of both ice lenses in the snow pack and on the ground with major consequences to
389 ungulates and the forage they consume (Hansen et al. 2014; Beniston and Stoffel 2016; Hansen et
390 al. 2019). In addition, ROS events are predicted to increase the risk of avalanche events and flooding,
391 or extensive ground ice formation in the high Arctic (Vikhamar-Schuler et al. 2016). In addition,
392 modelling studies have shown that large rain events could create warming effects on soil (Putkonen
393 and Roe 2003) and accelerated permafrost degradation (Westermann et al. 2011). Ground ice
394 formation can lead to deleterious effects on the biota, ranging from soil microarthropods (Coulson
395 et al. 2000), evergreen dwarf shrubs (Milner et al. 2016) and vertebrates (Hansen et al. 2013) and
396 affect plant phenology and reproduction (Le Moullec et al. 2019). Below we review effects of snow
397 changes on plants, trophic interactions, plant pathogens and winter biogeochemical processes.

398

399

400 **Plant phenology, growth and communities**

401 Plant above-ground phenology, growth and community composition are very closely linked to the
402 distribution and timing of snow (Tranquillini 1982; Sakai and Larcher 1987; Assmann et al. 2019).

403 Snowmelt has been found to be a better predictor of tundra plant phenology dynamics than local

404 temperatures (Assmann et al. 2019), and increasing snowfall and resulting snowmelt dynamics have

405 been attributed as a reason for a lack of phenological change over time at some tundra sites
406 (Bjorkman et al. 2015). Snowmelt timing is additionally strongly associated with snowbed species
407 (Cooper et al. 2011; Semenchuk et al. 2016b), as snowmelt is often late in the season, and the
408 remaining time for flowering and fruiting is thus very short, i.e. sometimes only a few weeks (Venn
409 and Morgan 2007; Hülber et al. 2010; Wipf 2010; Carbognani et al. 2016; Kudo and Cooper 2019).
410 Some species can emerge through a thin snow cover with their flowers (e.g., *Soldanella pusilla*) to
411 advance the beginning of the growing season by a few days (Körner et al. 2019; Rixen 2020). Plants
412 from ridges with little snow cover on the other hand potentially have a longer growing season, but
413 risk freezing damage when flowering and losing winter frost resistance too early (Rixen et al. 2012;
414 Venn et al. 2013). The phenology of many alpine plants is therefore often limited by photoperiod,
415 and development only starts when days are long enough and the risk of freezing events is low (Keller
416 and Körner 2003).

417

418 Plant species with no photoperiod limitation may need snow cover as protection from freezing (e.g.,
419 the evergreen shrub *Rhododendron ferrugineum*) and can suffer from freezing damage if snow cover
420 is not sufficient (Larcher and Siegwolf 1985). Conversely, experimentally deepened snow may lead to
421 substantial *R. subarcticum* growth, as the species' favoured microclimate conditions are prolonged in
422 late-winter and early spring when competing species remain dormant (Christiansen et al. 2018a).
423 Deeper snow cover can also protect the overwintering pre-formed flower buds from frost damage as
424 a result of cold winter air temperatures; this is particularly evident from the damage done to buds
425 during winters with little snow or extreme events in which mild periods (often accompanied by rain)
426 melt away snow cover, followed by a return to freezing air temperatures (Semenchuk et al. 2013). In
427 addition, extreme winter events that result in damaging snow conditions for plants can also delay
428 spring phenology and reduce flowering (Le Moullec et al. 2019). For instance, extreme winter
429 warming and associated loss of mid-winter snow resulted in delayed bud burst of the dwarf shrub
430 *Vaccinium myrtillus* by up to three weeks in the following spring, though other species were less

431 affected (Bokhorst et al. 2008). In contrast, experimental winter ice encasement (rain-on-snow
432 simulation) caused earlier spring bud-burst in the same species (Preece et al. 2012). However,
433 responses to extreme winter events appear species-specific and work is needed to further identify
434 vulnerable/resistant groups and the mechanisms involved (Bokhorst et al. 2010a; Bokhorst et al.
435 2018; Le Moullec et al. 2019).

436
437 Variation in snowmelt timing not only leads to variation in the timing of phenological events, but
438 also in the rate of developmental stages, which suggests different strategies of plants for responding
439 to snowmelt timing (Semenchuk et al. 2016b; Gehrman et al. 2017). Across all plant species in
440 tundra ecosystems, however, most studies have reported advancing phenological development with
441 climate warming and decreasing snow cover both in experiments (Wipf and Rixen 2010; Bjorkman et
442 al. 2015; Rosa et al. 2015; Assmann et al. 2019; Jabis et al. 2020b; Collins et al. 2021) and in long-
443 term monitoring (Wolkovich et al. 2012). In a global comparison, the phenology of plant populations
444 from colder regions (High Arctic) was more sensitive to temperature than that of populations from
445 warmer regions (Low Arctic) (Prevey et al. 2017; Prevey et al. 2019), which indicates that different
446 plant species and populations from different regions can vary in their phenological response to
447 climate and snow cover change.

448
449 Modifications of phenologies may disturb mutualistic interactions between species, i.e.,
450 phenological mismatch (see trophic interactions below; Memmott et al. 2007; Hegland et al. 2009;
451 Green 2010; Forrest 2015). In studies along snowmelt gradients, changes in flowering phenology
452 strongly affected the seed set and outcrossing rate of alpine plants visited by bumble bees
453 (Kameyama and Kudo 2009; Kudo et al. 2011; Moriwaki et al. 2020). Therefore, phenological
454 changes are also likely to affect interactions between flowers and pollinators (McKinney et al. 2012;
455 Høye et al. 2013; Kudo and Ida 2013; Gillespie et al. 2016; Ogilvie et al. 2017; Robinson and Henry
456 2018; Kudo and Cooper 2019). For example, a study of bee pollinators in the subalpine found that

457 their emergence, peak, and senescence phenology respond to snowmelt timing, but their rate of
458 response is less sensitive than that of flowers (Stemkovski et al. 2020), creating the potential for
459 reduced synchrony between bees and their flowers with earlier snowmelt timing.

460

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

472

473 Tundra plant growth corresponds with growing season length and soil moisture availability in tundra
474 ecosystems (Myers-Smith et al. 2015; Ackerman et al. 2017). Tundra shrub growth dynamics and the
475 climate sensitivity of shrub growth is highly variable among species and sites (Dawes et al. 2011;
476 Myers-Smith et al. 2015) and likely key climate drivers are both direct (e.g., snow melt timing, frost
477 damage, snowmelt hydrology, etc.) and indirect (e.g., altered nutrient availability, accelerated
478 permafrost thaw, etc.) (Myers-Smith et al. 2019). Dendroecology studies have found greater
479 temperature sensitivity of tundra shrubs in wetter versus drier sites (Elmendorf et al. 2012; Myers-
480 Smith et al. 2015; Ackerman et al. 2017) and the site-level soil moisture status is in part controlled by
481 snowmelt dynamics (Westergaard-Nielsen et al. 2020). Deeper snow has been found to promote
482 *Rhododendron subarcticum* shrub growth in Arctic tundra (Christiansen et al. 2018a, see above), and

483 in contrast longer growing seasons have been found to promote *Rhododendron ferrugineum* shrub
484 growth in alpine tundra (Francon et al. 2020). Both species grow in areas with long snow cover, but
485 the seemingly contradicting results highlight the complexity in capturing responses of tundra plant
486 growth to interacting climate drivers.

487

488 The patterns of plant community distributions strongly match those of the mean timing of snowmelt
489 in heterogeneous landscapes (Friedel 1961; Körner 2003). In studies along snowmelt gradients,
490 grasses and other tall and productive species encroached into snowbeds only a few years after
491 snowmelt started to advance (Green and Pickering 2009; Pickering et al. 2014; Venn et al. 2014).

492 With ongoing climate change, this could result in the long term in a reduction of habitat for snowbed
493 specialists and a resultant decrease in biodiversity (Niittynen et al. 2018) as more competitive
494 species encroach into these historically late-lying snow areas (Williams et al. 2015). Expansion of
495 shrubs and graminoids is common in snow-meadow and snowbed habitats with climate change (e.g.,
496 Wipf et al. 2009; Spasojevic et al. 2013; Formica et al. 2014; Myers-Smith et al. 2019). Comparisons
497 of community structure in snow-meadows revealed that the mosaic patterning of alpine vegetation
498 has become obscured during the last 40 years and that the structure of alpine vegetation has
499 become more uniform due to accelerated snowmelt and drier soil conditions linked to global
500 warming (Amagai et al. 2018).

501

502

503 **Trophic interactions**

504

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

509 (Speed et al. 2009; Anderson et al. 2016b), and the snow sensitivity of tundra herbivore emergence
510 and migration in turn influences higher trophic levels (Maclean and Pitelka 1971; Tulp and
511 Schekkerman 2008). Climate-induced alterations in snow conditions will thus undoubtedly affect the
512 interactions between plants and their herbivores, with consequences for other trophic levels.
513
514 Snow conditions, including spatial patterns, the onset and duration of winter snow cover, and
515 thawing events during winter can influence plant-herbivore-predator interactions in a number of
516 ways. First, snow distribution directly affects food accessibility to herbivores, which will influence
517 their distribution (Berg et al. 2008; Pedersen et al. 2021). For example, during winter, muskoxen and
518 reindeer/caribou prefer areas with thin snow cover where food is more easily accessible (Schaefer
519 and Messier 1995; Riseth et al. 2011; Pedersen et al. 2021), while lemmings favour areas with
520 deeper and more persistent snowpack that protects them from temperature extremes and
521 predators (Gilg et al. 2009; Duchesne et al. 2011; Reid et al. 2012). Which habitats become available
522 (snow-free) earlier in the season will also affect the spatial distribution of herbivores and their
523 population dynamics (Layton-Matthews et al. 2020). For example, during the spring pre-breeding
524 period prolonged snow cover restricts access of pink-footed geese (*Anser brachyrhynchus*) to their
525 preferred foraging habitat on wet areas (Anderson et al. 2012; Pedersen et al. 2013).
526
527 In turn, snow provides plants with a physical barrier against some herbivores. For example, during
528 winter, ptarmigan and hares have a limited ability to dig into the snow, and thus forage primarily on
529 plants emerging through the snowpack or growing in wind-blown areas (Hakkarainen et al. 2007;
530 Tape et al. 2010). In High-Arctic Greenland, Arctic hare and rock ptarmigan benefit from muskox
531 opening the snowpack (Schmidt et al. 2018). A similar phenomenon has been observed in Svalbard,
532 where reindeer cratering opens up foraging areas for rock ptarmigan (Pedersen et al. 2006).
533 Conversely, plants are better protected from small mammal herbivory in areas with shallow snow, as
534 small mammals will concentrate in areas with deeper snow in winter (Duchesne et al. 2011). Large

535 herds of reindeer, caribou and muskoxen are not only affected by snow, but have direct impacts on
536 snow properties; trampling on snow alter snow depth and density, and hence also winter soil
537 temperatures, with cascading effects on summer soil temperatures (Roturier and Roué 2009; Riseth
538 et al. 2011).

539

540 The timing of snowmelt is also one of the most important predictors of the phenology and activity of
541 arthropods in the High Arctic (Høye and Forchhammer 2008; Coulson et al. 2014), although the
542 responses seem to be group-specific (Dollery et al. 2006; Kankaanpää et al. 2018). Some studies
543 have found increased invertebrate herbivory in earlier snowmelt areas (Roy et al. 2004; Berg et al.
544 2008; Little et al. 2016; Wheeler et al. 2016), but others have reported increased levels of herbivory
545 in late snowmelt areas (Torp et al. 2010a; Torp et al. 2010b). Late snowmelt can increase plant
546 palatability to herbivores by altering plant chemistry (Walsh et al. 1997; Semenchuk et al. 2015;
547 Mörsdorf et al. 2019). In a snow fence experiment, the growth of moth larvae was higher when fed
548 on leaves from the snow fence plots, suggesting that later snowmelt enhanced food quality for these
549 herbivores (Torp et al. 2010a). Similarly, other studies have found that invertebrate herbivores like
550 aphids and scale insects (Coccoidea) were most numerous in late snowmelt plots (Høye and
551 Forchhammer 2008).

552

553 Finally, thawing events during winter and rain-on-snow (ROS) events can create ice crusts within the
554 snowpack or ground ice, and episodes of heavy rain can cause flooding in the subnivean space and
555 subsequent formation of a thick layer of ground ice (Hansen et al. 2014). Such ice layers prevent
556 access to food by herbivores (Hansen et al. 2013), resulting in increased mortality and reduced
557 fecundity. As an example, large ROS events in Yamal, Russia caused heavy mortality of reindeer
558 (Sokolov et al. 2015; Forbes et al. 2016), with subsequent impacts across trophic levels causing
559 increases of generalist predators (Sokolov et al. 2015). The occurrence of ROS events in the autumn
560 determines the hardness of the basal snow layer and negatively influences brown lemming

561 demographic parameters (Domine et al. 2018). The formation of ground ice also can lead to anoxia
562 in the plant-soil interface and in the soil beneath, resulting in increased damage to, or mortality of
563 plants (Bjerke et al. 2017), lichens (Bjerke et al. 2011) and soil invertebrate communities (Coulson et
564 al. 2000) and hence decomposition and nutrient cycling processes (see below).

565
566 Climate change may have different consequences for different plant-herbivore systems, depending
567 on the relative effects of temperature, snow and precipitation and the frequency and strength of
568 climate related extreme events. Changes in snow patterns can affect herbivores in species-specific
569 ways (Berteaux et al. 2017). Some herbivores, such as small mammals who actually live and
570 reproduce under the snow, would be negatively affected by longer snow-free periods when
571 predation risk is higher, whereas large herbivores that are less vulnerable to predation could
572 potentially benefit from longer snow-free periods due to longer food accessibility (Berg et al. 2008).
573 Changing snow conditions associated with climate warming have been proposed as a potential cause
574 for the dampening of population cycles of small mammals (Domine et al. 2018), possibly due to
575 increased cold stress when snow cover and depth are reduced (Kearney 2020) although the
576 underlying mechanisms may differ across study locations (Kausrud et al. 2008; Gilg et al. 2009).

577

578

579 **Fungal Pathogens**

580 Snow molds are an important group of fungal pathogens that have a particularly clear relationship
581 with snow cover (Smith et al. 1989). Snow molds are a taxonomically diverse group of fungi that
582 occur throughout the Arctic tundra and attack overwintering plants under snow cover (Hsiang et al.
583 1999; Matsumoto 2009). Evergreen dwarf shrubs (Olofsson et al. 2011) and mosses (Mariana-
584 Armendariz et al. 2021) are likely to be hit hardest by these pathogens since their growth form
585 implies the presence of exposed green leaves under the snow. However, there are also snow molds
586 that attack plants from other functional groups, such as grasses or trees at the treeline (Barbeito et

587 al. 2012; Barbeito et al. 2013). Snow molds require snow cover to spread to new host plants and are
588 often favoured by deep snow, as deeper snow cover usually results in warmer and more moist
589 conditions, which are optimal for their spread (Snider et al. 2000; Matsumoto 2009). Outbreaks of
590 snow molds are common during years with deep long-lasting snow cover and have considerable
591 consequences for ecosystems, such as “winterkill” of plants (Matsumoto 2009). Snow molds are thus
592 expected to increase in abundance and importance where future climate change results in deeper
593 snow cover and warmer temperatures.

594
595 Fungal pathogens can even outweigh beneficial effects of snow cover changes to plants. For
596 example, though plant growth may be increased by the warmer temperatures under a thicker winter
597 snow cover, it may also facilitate outbreaks of parasitic fungi (Olofsson et al. 2011; Moriana-
598 Armendariz et al. 2021). In northern Sweden, the evergreen shrub *Empetrum hermaphroditum*
599 experienced a fungal outbreak of the pathogen *Arwidssonia empetri* that killed the majority of the
600 plants and led to a reduction in net ecosystem carbon exchange during the growing season (Olofsson
601 et al. 2011). Response of parasitic fungi to snow enhancement may thus contribute to the observed
602 changes in vegetation composition (Cooper et al. 2019).

603
604 Snow distribution can also influence the effects of fungal pathogens by altering host plant
605 abundance and susceptibility, or by influencing the spread of the pathogen (Matsumoto 2009). Thus,
606 the effect of snow on pathogens will vary depending on traits of the host plants and the pathogens.
607 Direct effects of snow on pathogens are expected to be mainly negative as fungi require high
608 humidity conditions for spore dispersal, germination and infection. However, the effects on host
609 plant abundance and susceptibility could range from positive to negative, and override the effects
610 on pathogen spreading (Roy et al. 2004).

611
612

613 **Winter biogeochemical processes**

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

621
622 Continued soil organic matter decomposition during winter (Schimel et al. 2004; Schimel et al. 2006)
623 results in significant emissions of CO₂ through the snow pack (e.g., Oechel et al. 1997; Fahnestock et
624 al. 1999b; Grogan and Jonasson 2005; Sullivan et al. 2008; Euskirchen et al. 2012; Natali et al. 2019).
625 Despite low absolute emission rates compared to summer, these winter emissions may accumulate
626 to large magnitudes, as winter snow cover may be present for up to 75% of the year. As a result,
627 cumulative winter CO₂ emissions are often greater than summer plant C uptake, and tundra
628 ecosystems are now increasingly becoming net CO₂ sources on an annual basis (Belshe et al. 2013;
629 Euskirchen et al. 2017; Natali et al. 2019). For instance, the current loss of carbon during the winter
630 season from October to April amounted to 1622 Tg C per year for the entire permafrost regions,
631 which is considerably more than the estimated carbon uptake of 1032Tg C during the growing
632 season (Natali et al. 2019). These winter C emissions are even predicted to increase by 17% under a
633 moderate mitigation scenario (Natali et al. 2019). While many models project increased snowfall for
634 the Arctic in coming decades, there are still large uncertainties, including interannual variation and
635 regional differences and shifts to increased rain, associated with future snowfall regimes (Callaghan
636 et al. 2011; Bintanja 2018). Nevertheless, warmer winters with increased snowfall and earlier spring
637 snowmelt date are expected for most regions, and these changes in winter climate are very likely to
638 increase wintertime CO₂-release from arctic landscapes (Natali et al. 2019). With ongoing climate

639 change, the magnitudes and patterns of net C emissions depend on different aspects of timing and
640 depth of snow cover, which may affect these C source-sink relations in several ways. While it is
641 generally expected that warmer soils in winter will lead to greater microbial respiration and greater
642 winter C efflux, several recent studies have pointed to important complexities in the relationship
643 between winter soil temperature and microbial respiration. For instance, experimental studies in the
644 sub-alpine forest and near the southern limit of Arctic tundra have shown that soil microbes can
645 exhaust the supply of labile C during warm winters and/or beneath deep insulative snowpacks, with
646 important implications for both winter and summer CO₂ emissions and soil nutrient cycling (Brooks
647 et al. 2005; Sullivan et al. 2020). Indeed, deepened snow increased wintertime CO₂ release in distinct
648 Canadian and Svalbard tundra sites (Nobrega and Grogan 2007; Semenchuk et al. 2016a), leading to
649 reduced soil C storage (Semenchuk et al. 2019) and ultimately lower summertime CO₂ release after
650 5-10 years (Semenchuk et al. 2016a; Christiansen et al. 2018a). Consequently, it seems clear that
651 changes in winter climate will not only affect non-growing season carbon fluxes, as legacy effects
652 also carry over to determine ecosystem carbon balance in summer.

653
654
655 Over the long-term, deeper snow may reduce soil cooling in winter, resulting in thawing permafrost
656 and a deeper active layer in summer that facilitates emission of ancient labile permafrost C to the
657 atmosphere (Czimczik and Welker 2010; Natali et al. 2014; Natali et al. 2015). These factors all play
658 an important role in driving whether, and by how much, we can expect soil C losses in the Arctic
659 (Crowther et al. 2016; Crowther et al. 2018; van Gestel et al. 2018).

660
661 Along with winter-long soil C mineralization and CO₂ emissions, mineralization of nutrients, such as
662 nitrogen and phosphorus (Schimel et al. 2004; Schimel et al. 2006; Rixen et al. 2008; Buckeridge et
663 al. 2013), results in annual microbial biomass peaking in late-winter (Buckeridge et al. 2013).
664 Following snowmelt, enhanced nutrient supply from winter nutrient mineralization and lysing

665 microbes can manifest during the growing season as higher tundra plant leaf N and P concentrations
666 (Welker et al. 2005a; Semenchuk et al. 2015; Mörsdorf et al. 2019). These leaf nutrient
667 concentrations are important as they contribute to leaf-level photosynthesis which, when
668 considered at the plant community level, can influence C sequestration during summer (Pattison and
669 Welker 2014). However, whether the net effect of summer C fixation in a warmer climate will
670 exceed winter-long CO₂ emissions is still not fully resolved (Welker et al. 2000; Natali et al. 2019).

671
672
673 The temporal patterns of snowmelt in spring may either open the tundra to spring warmth when
674 snow melts earlier, leading to early leaf out and rapid C gain, or delay snowmelt and thus the onset
675 of spring growth, thereby prolonging snow-covered CO₂ emissions through a delayed snowmelt of
676 deeper winter snow. These complexities and the net effect of deeper or shallower snowpack, earlier
677 or later onset of snow cover in autumn and snow melt in spring will all affect the future C budget,
678 with the integrated effect of these changes having either a positive or negative climate feedback
679 effect (Welker et al. 1997; Oberbauer et al. 1998; Starr et al. 2000; Starr et al. 2008; Steltzer et al.
680 2009; Grogan 2012; Livensperger et al. 2016; Darrouzet-Nardi et al. 2019).

681
682 An important aspect of climate change effects on biogeochemical processes is the occurrence of
683 extreme events in winter (see above). Extreme winter warming events associated with loss of snow,
684 frost-drought or ice layer development can cause plant damage and mortality and lead to substantial
685 reductions in gross primary productivity (Bokhorst et al. 2009). They can also lead to reduced
686 ecosystem respiration as a result of the lower GPP, with a net effect of an overall reduction in
687 ecosystem carbon sequestration (net primary productivity) in the following growing season
688 (Treharne et al. 2019; Treharne et al. 2020).

689

690 While below-ground soil organic matter decomposition rates increase with enhanced snowfall and
691 accumulation (see above), the effects of warmer winter temperatures on foliar litter decay rates on
692 the ground surface seem variable. Recent experimental studies in diverse tundra landscapes across
693 the circumpolar Arctic suggest that deepened snow alone has negligible effect on litter mass loss
694 (Walker et al. 1999; Aerts et al. 2012; Myers-Smith and Hik 2013; DeMarco et al. 2014; Christiansen
695 et al. 2017; Christiansen et al. 2018b) although alpine snow gradient studies showed positive
696 relationships between snow depth (Saccone et al. 2013) or snow-cover duration (Carbognani et al.
697 2014) and litter decomposition. Experimental snow reduction, however, showed negligible effects
698 on litter decay rates (Bokhorst et al. 2013b), suggesting that changes in winter microclimate may
699 have little impact on the litter layer. This apparent site- and year-dependent discrepancy between
700 ground surface and belowground soil microbial activities in winter could be due to more pronounced
701 frost desiccation, and therefore unfrozen water limitation, of the surface litter layer relative to soil
702 organic matter. While there is still uncertainty on the responsiveness of the decomposers and
703 physical breakdown of leaf litter material during winter and the role snow plays in this process
704 (Hobbie and Chapin 1996; Bokhorst et al. 2010b; Bokhorst et al. 2013b), it appears that snow
705 accumulation by itself has little impact on mid-winter litter mass losses, when temperatures are well
706 below freezing. However, where changes in snow cover cause community change (see below), this
707 may lead to changes in litter quality and thereby decomposability. For instance, an experimental
708 study on tundra biome litter decomposability indicated that a change from herbaceous to shrub-
709 dominated tundra would lead to lower litter decomposability (Cornelissen et al. 2007). How changes
710 in litter quality and overall microbial decomposition rates as induced by changes in snow cover, in
711 combination, lead to changing litter decomposition rates is a question in need of in-depth study.

712
713
714

715 **Studying effects of snow changes on ecosystems**

716

717 Given the critical role of snow cover in numerous ecosystem processes and the disruption to
718 prevailing patterns of snow cover predicted under climate change, many studies have investigated
719 the various effects of changing snow parameters (e.g. snow duration, depth and quality) on
720 ecosystems (e.g., Rixen et al. 2004), as well snow-related extreme events such as icing (Coulson et al.
721 2000; Preece et al. 2012; Hansen et al. 2014) and extreme winter warming (Bokhorst et al. 2008;
722 Bokhorst et al. 2011a). Here, we review two types of snow studies: those that aim to understand
723 natural gradients and those that manipulate snow depth experimentally. To contrast snow
724 manipulation experiments with natural snow gradient studies, we gathered temperature data from
725 snow studies (74 site-year combinations of manipulations and natural gradients) to analyze and
726 compare timing of snowmelt (defined as end of the zero degree curtain, i.e. the increase in
727 temperature after disappearance of snow) (Figs. 1 and 3; methods in Appendix). We also consider
728 the seasonal setting of snow studies, in order to account for studies being carried out at sites with
729 naturally early, mid or late snowmelt.

730

731 Fig. 1.

732

733 **Remote sensing approaches**

734

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

741 1993; Zeng and Jia 2013; Kelsey et al. 2021). However, as many Arctic ecosystem properties are
742 scale-dependent (Siewert 2018; Assmann et al. 2020; Siewert and Olofsson 2020) , the spatial
743 resolution of satellite-based remote sensing approaches with a coarse resolution (e.g., 30 - 500 m
744 pixel widths) may only detect large-scale changes in snow cover (Hall et al. 2002; Nagler et al. 2008)
745 and in land-surface greenness (Zeng and Jia 2013; Myers-Smith et al. 2020), but do not detect small-
746 scale ecosystem processes driven by snow cover (Myers-Smith et al. 2020).

747
748 Snow cover is spatially and temporally heterogeneous and, in particular, snowmelt and snow
749 accumulation patterns can vary across landscapes with varied topography (Marsh et al. 1997;
750 Aalstad et al. 2020; Pedersen et al. 2021). Recently, drones have successfully been used for
751 recording and seasonal monitoring of ecosystem properties even in climatically challenging tundra
752 environments (Fraser et al. 2016; Assmann et al. 2020; Siewert and Olofsson 2020). Drones and high-
753 resolution satellite imagery can resolve small scale variability in snow extent, often measured as
754 fractional snow-covered area (fSCA) (Liang et al. 2017; Aalstad et al. 2020), or snow thickness
755 (Grünberg et al. 2020; Harder et al. 2020) or snow depth (Pedersen et al. 2018; Pedersen et al.
756 2021). Snow cover can be coupled with hydrological analyses, for example by estimating the snow
757 water equivalent (Liston and Sturm 2002; Dozier et al. 2016; Niedzielski et al. 2019), or to
758 understand the impact of snowbeds on vegetation productivity (Borner et al. 2008; Siewert and
759 Olofsson 2020).

760
761 Mapping snow extent can be easily achieved from optical sensors due to the high spectral contrast
762 of snow. Similarly, snow algae can be measured as they influence the optical properties of snow
763 (Davey et al. 2019; Gray et al. 2020). Estimating snow thickness using drones typically relies on the
764 generation of a digital elevation model (DEM) using either structure from motion (SfM) or Lidar
765 approaches, followed by subtracting a snow-free reference DEM (Niedzielski et al. 2019; Harder et
766 al. 2020; Walker et al. 2021). Drones can be particularly useful in spring, when snowmelt dynamics

767 are fast but cloud cover can prevent satellite observations. Here, repeated drone flights provide
768 temporally resolved estimates of snowmelt (Siewert and Olofsson 2020). Another approach is the
769 use of near-remote sensing, for example with instruments (e.g., time-lapse camera networks)
770 permanently mounted on poles 2 m above a given plot and able to take multiple measurements of
771 the same plots (Anderson et al. 2016a; Parmentier et al. 2021) to follow the vegetation development
772 from snowmelt throughout the growing season and relate this to environmental conditions
773 experienced.

774

775 **Natural gradients**

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

793 Alongside geographical gradients, snowmelt date can vary over time. For example, a site that has
794 been monitored daily since 1975 for snowpack and snowmelt at the RMBL (south-west Colorado, at
795 2,915 m a.s.l.) has an average snowmelt date of 20 May, ranging from 24 April to 19 June, paralleling
796 the snowfall variation in the preceding winter (mean maximum snow depth of 10.6 m, ranging from
797 4.74 m to 16.41 m). The wide range of microhabitats available in an environment can create an even
798 greater range of snowmelt dates through a combination of spatial and interannual variability.

799

800 Fig. 2.

801

802 **Snow manipulation experiments**

803

804 In many studies, snow cover has been manipulated experimentally, either by removing snow and
805 hence advancing snowmelt or by adding snow and postponing snowmelt. A convenient way to add
806 snow is by installing fences in areas with a dominant wind direction. A snowdrift forms on the lee
807 side of the fence, while snow depth can additionally be reduced on the exposed side (Jones et al.
808 1998; Walker et al. 1999; Morgner et al. 2010; Mark et al. 2015; Ricketts et al. 2016; D'Imperio et al.
809 2018; Jespersen et al. 2018). If fences are sufficiently long, the area of increased snow may well be
810 large enough to have a considerable effect on both above and belowground parts of the vegetation
811 (Welker et al. 2005a), and thus avoid the problems associated with other approaches as discussed
812 below, with small treatment plots with proportionately large edge effects.

813

814

815 Manipulating snow manually by shoveling is more labour-intensive and may alter snow properties,
816 yet has the advantage that a higher number of well-defined plots in a given area can be treated.

817 Also, removals and additions can be realized in close proximity under controlled conditions (Wipf et
818 al. 2006; Anderson and Wadgymar 2019; Wadgymar et al. 2019; Frei and Henry 2021). Snowmelt can

819 also be accelerated by positioning dark cloth on the snow surface that increases the absorption of
820 solar radiation (Steltzer et al. 2009; Blume-Werry et al. 2017). Experimental snowmelt change has
821 also been achieved using infrared heaters (Harte and Shaw 1995; Harte et al. 1995; Harte et al. 2015;
822 Winkler et al. 2016; Panetta et al. 2018; Harte 2019; Jabis et al. 2020a), heating cables in the ground
823 (Rixen et al. 2012), the combination of both (Bokhorst et al. 2008; Bokhorst et al. 2011a), dust or
824 black sand on snow (Blankinship et al. 2014) or reflective surfaces on snow (Blankinship et al. 2014).

825

826 By analyzing the snowmelt date based on the marked increase in temperature fluctuation after the
827 extended period of the zero curtain we could quantify delays and advances in the meltout date
828 caused by the snow manipulation experiments (Fig. 3). On average, snow addition delayed snowmelt
829 by 5.5 days (± 8.2 SD), and snow removal advanced snowmelt by 7.9 days (± 8.4 SD). The

830 experiments varied considerably in their timing of snowmelt with respect to day of the year, from
831 day 49 to day 188 (equating to 18 February and early July in the Northern Hemisphere). We do not
832 have complete information of the amounts of snow that were added or removed in the experiments.

833 But from those studies where snow depth information is available, we see that on average 80 cm of
834 snow is added (ranging from c. 40 to 150 cm, see SupplementaryTable S1). This addition of snow
835 corresponded to c. 10 days delay in snowmelt. The amount of snow added did not correlate with
836 days of delay in snowmelt (results not shown), which indicates that temperatures and radiation are
837 just as important, if not more important, for snowmelt timing as the amounts of snow.

838 The experimental manipulations of snow cover only caused minor changes in snowmelt timing
839 compared with the large natural differences in snowmelt that exist because of topography, wind
840 drift, interannual variation, etc., and impacts on the studied ecosystems should thus always be
841 interpreted with these numbers in mind. However, the change in snowmelt timing depended upon
842 the natural timing of snowmelt, as snow treatments at sites with earlier natural snowmelt had larger
843 experimental effects than those at sites with late natural snowmelt (Fig. 4).

844

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

849

850 Fig. 3

851

852 Fig. 4.

853

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

868

869

870 **Open Top Chambers (OTCs) x snow manipulations**

871

872 An increasing number of studies have combined snow manipulations with warming by OTCs
873 (Dorrepaal et al. 2004; Weedon et al. 2012; Drescher 2014; Suzuki 2014; Weedon et al. 2014;
874 Gillespie et al. 2016; Christiansen et al. 2017; D'Imperio et al. 2018; Darrouzet-Nardi et al. 2019;
875 Mörsdorf et al. 2019; Frei and Henry 2021; Thompson et al. 2021). Both treatments can affect plant
876 growth and biogeochemical processes, but can have different effects depending on mechanisms at
877 work. Warming can for instance cause drying of soils, while snow addition by snow fences can
878 increase soil moisture (Schollert et al. 2017). The combined effects of warming and increased snow
879 depth can change the plant community composition and increase primary productivity (Leffler et al.
880 2016). Warmer spring temperatures and deeper snow can also have opposing effects, e.g. on litter
881 decomposition (Farrer et al. 2015; Blok et al. 2016).

882

883 An unintended consequence of the widely-used 'open top chamber' methodology of experimentally
884 manipulating air temperature in polar field experiments studying potential consequences of
885 warming can be the accumulation of snow within the chambers when left in place over winter. This
886 can lead to artifacts in the data obtained both in terms of winter temperature regime and extended
887 snow cover within the experiment (Dorrepaal et al. 2009; Bokhorst et al. 2011b; Bokhorst et al.
888 2013a). For instance, increased snow depth in OTCs led to near complete disappearance of a
889 previously dominant lichen species (Bokhorst et al. 2016a). We would therefore encourage authors
890 to state whether their OTCs are removed or left on the plots during winter when reporting their
891 results. Nevertheless, leaving OTCs in place in winter remains advantageous as it enables a
892 combination of snow increase in winter and summer warming (for a comparison of effects of winter
893 and summer warming on tundra see Pold et al. 2021).

894

895 **Future Research Priorities**

896 1. *New technology to sense snow and snowmelt dynamics*

897 New technology including drones (Assmann et al. 2020; Siewert and Olofsson 2020), lidar and radar
898 observations (Harder et al. 2020) and higher-resolution optical satellite imagery will allow us to
899 capture snow and snowmelt dynamics missed by historical data collection. Integrating these new
900 technologies into future *in-situ* ecological data collection will allow for a better understanding of the
901 fine spatial and temporal scale dynamics of snowmelt and resulting ecological processes such as
902 plant phenology. There is a continued need, however, for improving the validation between
903 remotely-sensed and ground-based observations of phenology (see, e.g. Karlsen et al. 2021 for an
904 approach). Further development of *in-situ* low-cost snow monitoring techniques (e.g., Lewkowicz
905 2008; Siren et al. 2018; Tutton and Way 2021) and expanded winter field data collection should also
906 be prioritized to provide better validation of remotely-sensed snow products (Walker et al. 2021).

907 2. *Changing phenology and trophic interactions under altered snow regimes*

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

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

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

921 **Conclusions**

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

940 the impacts of snow on tundra ecosystems has the potential to considerably improve our
941 understanding of cold ecosystems in times of climate change.

942

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972

973 **Contributors' statement**

974 CR, TTH, PM, EJC, ED, CTC and SW conceived the idea for the paper. The following
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987

988 **Data availability statement**

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

990

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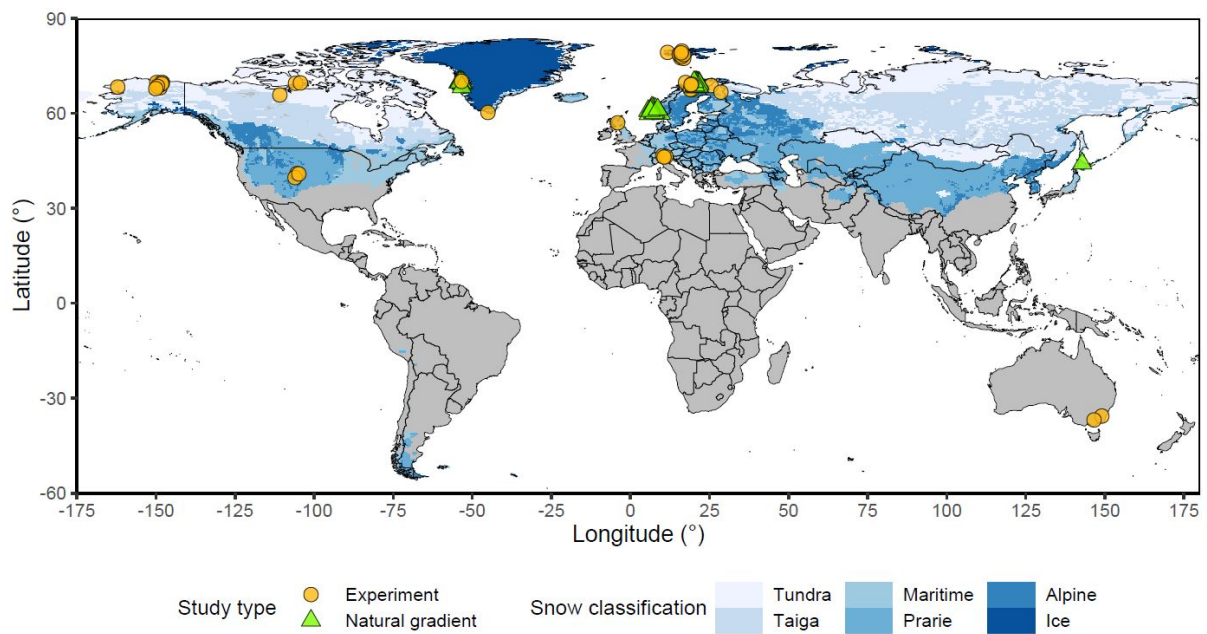
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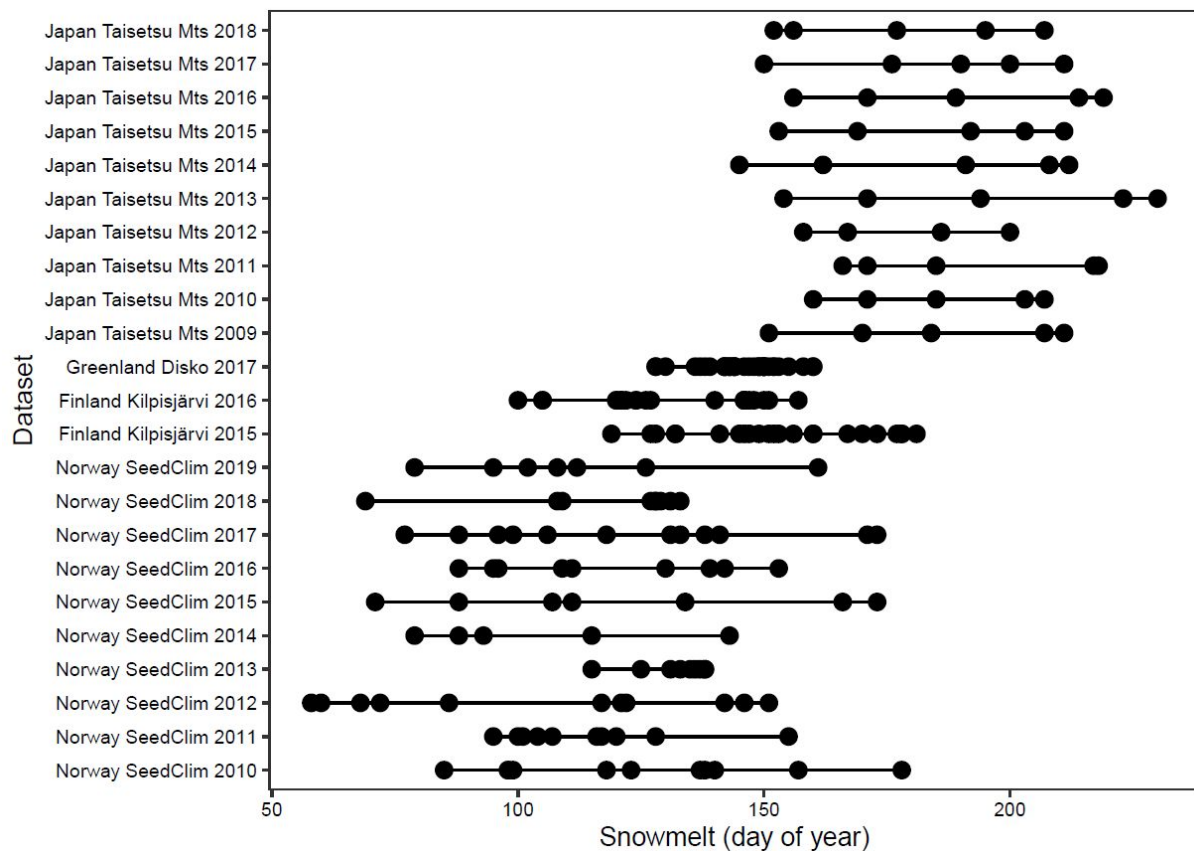
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Fig. 1. Map of studies used in our analysis. Yellow dots indicate a snow manipulation experiment, green triangles indicate studies along a natural snow gradient (i.e. plots within a given region with

2233 different abouts of snow due to topography). The snow classification and the shape files for
 2234 projecting these layers follows Sturm et al. (1995) and the Atlas of the Cryosphere (Maurer 2007),
 2235 where darkest blue to lightest blue colours in order represent ice, alpine, prairie, maritime, taiga, and
 2236 tundra. Some regions with seasonal snow, primarily in the Southern Hemisphere, do not have a
 2237 classification according to the system of Sturm et al. (1995). The base map was produced in R using
 2238 the 'ggplot2' R package (Wickham 2016) to project a 2013 world map that is freely available from
 2239 the Natural Earth project (<https://www.naturalearthdata.com/>, 1:50m scale, no permission for reuse
 2240 required). The map and the snow classification layers were projected using a WGS84 geographic
 2241 coordinate system from the 'raster' R package (Hijmans 2021), which aligned coordinates from the
 2242 map and snow layers with the GPS coordinates of the study locations.



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2247 Fig. 2. Snowmelt timing along natural snow gradients (caused by topography, wind etc.) varies
2248 considerably at individual sites (multiple sites across western Norway in the SeedClim data) and
2249 between years (see methods for site selection, calculations etc.). The X axis represents the day of the
2250 year (DOY) on which snowmelt occurs. Different dots represent plots within one studied gradient in
2251 a given year. Site-year combinations are ordered first by mean snowmelt date of sites (across years
2252 per site) and then by year. Different site-year combinations can be from the same study. Most
2253 studies include only small elevation differences (except Norway), hence the snow differences are
2254 caused by micro-topography, wind drift and other factors. Japan: 43.67°N, 142.91°E, 1800 m asl
2255 (Kudo 2016); Greenland: 69.27°N 53.50°E, 90 m asl; Finland: 69.06°N 20.81°E, 697-768 m asl;
2256 Norway: 60.54-61.09°N 5.96-8.70°E, 346-1213 m asl.

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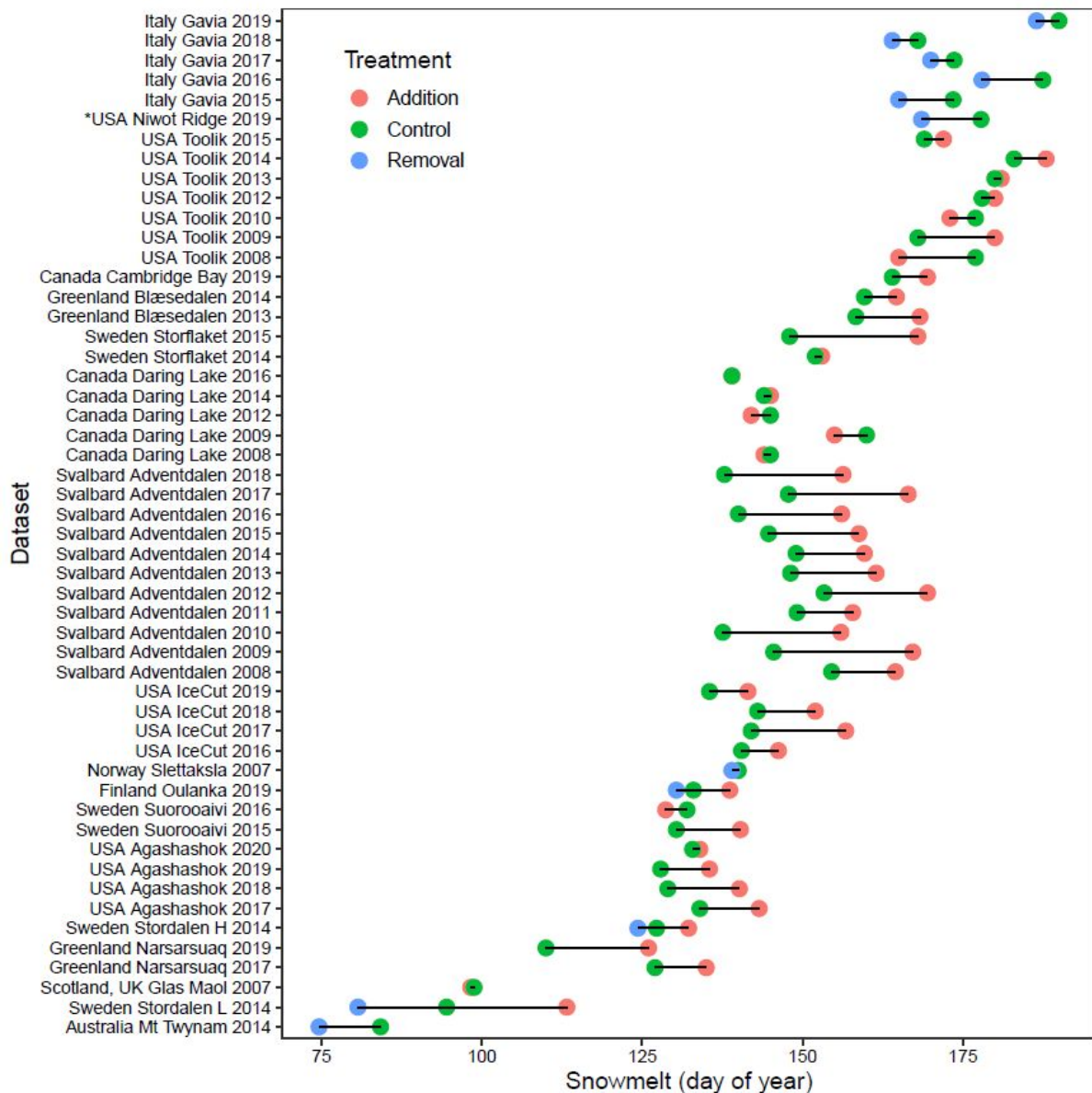
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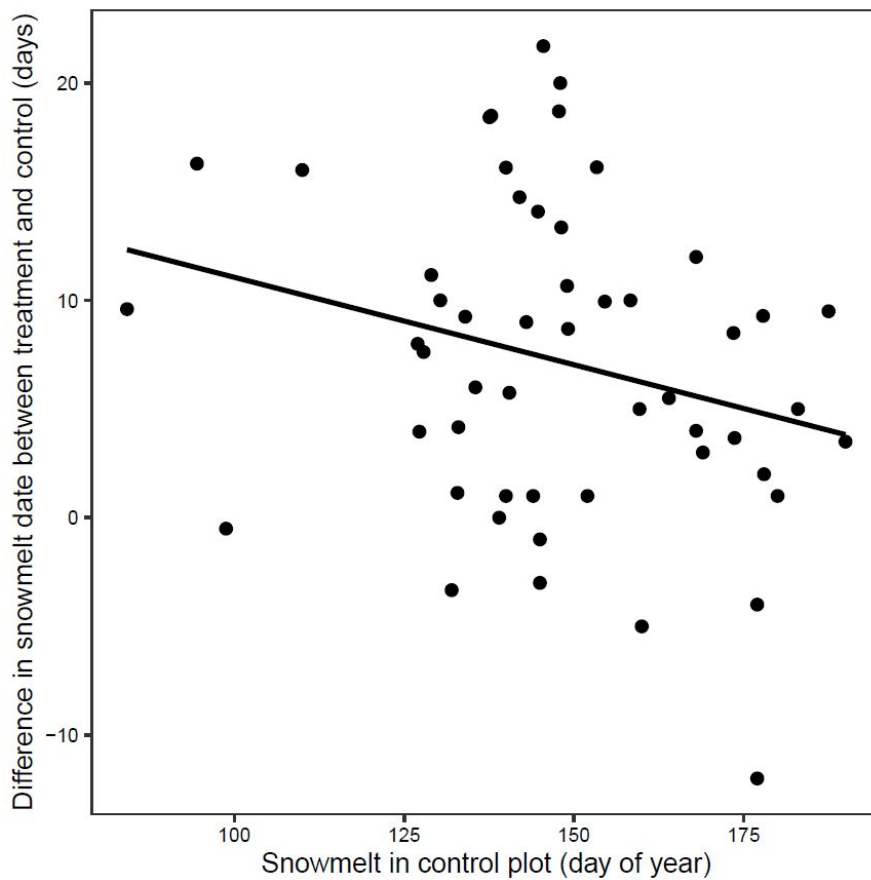
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Fig. 3. Most snow manipulation experiments change the snowmelt date by less than what can be observed due to variation in space or time (Fig. 2). Treatment x year combinations are ordered by site day of snowmelt (i.e. day of year for sites from the 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 (exception USA Niwot Ridge, marked with *, were black sand was used to advance snowmelt).

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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.).