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RESEARCH ARTICLE

Towards rainy high Arctic winters: How experimental icing and summer warming affect tundra plant phenology, productivity and reproduction

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Abstract

1. The Arctic is warming rapidly and much faster in winter than in summer. Warm spells in winter lead to more frequent extreme rain-on-snow events that alter snowpack conditions and can encapsulate plants in 'basal ice' ('icing') for months. Yet, how icing affects plant communities, especially over multiple winters and under warmer summers, remains largely unstudied.
2. We investigated winter icing and summer warming effects on vascular plants' productivity, reproduction and phenology in mesic dwarf shrub heath, an important reindeer habitat in high Arctic Svalbard, where winter temperatures have been rising particularly fast. In a full-factorial field experiment, rain-on-snow and resultant icing were simulated in five consecutive winters, and each followed by experimentally increased summer temperatures. Vascular plant responses at the community level, with particular attention to the dominant dwarf shrub *Salix polaris*, were assessed throughout each subsequent growing season.
3. Icing alone increased community-level primary productivity, but only late in the growing season and reduced inflorescence production. Accordingly, *S. polaris* showed delayed early leaf phenophases, but accelerated subsequent development, resulting in smaller, thinner leaves. This compensatory growth response apparently occurred at the cost of delayed seed maturation. The phenological delay

was associated with icing-induced delays in spring soil warm-up, possibly favouring resource allocation to primary productivity over reproduction. Experimental summer warming (on average 0.8°C) largely counteracted the effects of icing, enhancing community productivity throughout the growing season, offsetting *S. polaris* leaf size reductions and turning around its delayed phenophases, including seed dispersal. Effect sizes of icing and warming combined could be larger than those under warming alone. Yet, summer warming did not negate the reduction in community inflorescence production caused by icing.

4. *Synthesis*. Extreme rain-on-snow events encapsulating plants in ice can influence high Arctic plant communities in mesic habitats to similar extents as—the better-studied—summer warming. Nevertheless, the absence of magnified icing effects over the years indicates community resistance to icing, particularly under warmer summers, which contrasts with earlier documented ice-induced die-offs in communities dominated by evergreen shrubs. As warm spells during winter become the rule rather than exception, we call for similar experiments in coordinated circumpolar monitoring programmes across the tundra biome.

KEYWORDS
basal ice, extreme events, multi-year tundra experiment, open top chamber, rain-on-snow, *Salix polaris*, seasonality, Svalbard

1 | INTRODUCTION

Global warming comes with stronger and more frequent extreme climate events, prompting research activity aimed at determining their ecological and evolutionary consequences for terrestrial biota (Harris et al., 2018; IPCC, 2021; Trisos et al., 2020). In the Arctic, warming occurs three times as fast as the global average, with marked climate variability, including for instance extreme droughts, floods, heat and cold waves (AMAP, 2021; Panchen et al., 2022; Van Beest et al., 2022; You et al., 2021). Arctic winter warming is even more pronounced—up to seven times faster than in summer in some regions, resulting in a drastic increase in the frequency of extreme warm spells affecting terrestrial ecosystem functioning (Bintanja & Andry, 2017; Graham et al., 2017; Lemaire et al., 2025; Serreze et al., 2021). Most studies, however, have primarily focused on rising summer temperatures and changes in snow depth (Bjorkman et al., 2020; Frei & Henry, 2022; Henry et al., 2022; Rixen et al., 2022), although winter temperatures are increasingly recognised as important drivers of fine-scale regional vegetation patterns (Bjorkman et al., 2018; Niittynen et al., 2020). Given the key role tundra ecosystems play in global carbon cycling and climate feedback (Maes et al., 2024; Zhang et al., 2020), it is now urgent to understand how the increased frequency of warm spells, combined with warmer summers, influences Arctic plant communities.

Warm spells during winter often come with 'rain-on-snow' events, transforming the snowpack (Bokhorst et al., 2016; Pan et al., 2018; Rasmus et al., 2018). The snowpack may completely melt, exposing plants to thaw–freeze cycles (Bokhorst et al., 2009, 2011) or—especially in the high Arctic—meltwater freezes to the ground, forming a layer of basal ice (hereafter referred to as 'icing') up to several decimetres thick (Langlois et al., 2017; Peeters et al., 2019; Putkonen & Roe, 2003). Low-growing Arctic plants can remain entirely encapsulated in such ice for months. Both winter warm spells and icing have been identified as the cause of regional Arctic vegetation 'browning' (i.e. a decrease in expected 'Arctic greening' under climate warming; Berner et al., 2020; Bjerke et al., 2017; Myers-Smith et al., 2020; Phoenix et al., 2025; Vickers et al., 2016). However, changes in winter conditions can also interact with summer warming (Frei & Henry, 2022; Kelsey et al., 2021), adding complexity and spatial variability to vegetation productivity trends, highlighting the need to consider the combined effect of winter and summer effects.

Icing has the potential for ecosystem-wide consequences by directly or indirectly affecting several trophic levels, for example by reducing soil arthropod abundance (Coulson et al., 2000), disrupting snow conditions critical for small mammals' survival and reproduction (Kausrud et al., 2008), and causing starvation-induced die-offs in large herbivores, which then affect predators and scavengers (Hansen et al., 2013; Serreze et al., 2021; Sokolov et al., 2016). However, the immediate and long-term effects of icing on high Arctic plant productivity, reproduction and phenology—fuelling the tundra food web—remain largely unknown.

Icing can directly damage vegetation through frost injury, especially after possible de-acclimatation ('de-hardening') to cold during a warm spell (Bokhorst et al., 2010, 2018) or through stress-induced anoxia from anaerobic respiration (Crawford et al., 1994; Preece & Phoenix, 2014). Indirect effects include altered soil thermal properties (Putkonen & Roe, 2003), delayed nutrient availability and possibly shifted phenology in ways similar to late snowmelt (Assmann et al., 2019; Darrouzet-Nardi et al., 2019; Frei & Henry, 2022; Semenchuk et al., 2016). Icing may also protect plants from winter herbivory. In response, plants may modify life-history trade-offs by altering resource allocation towards growth and survival (Bazzaz et al., 1987; Jónsdóttir, 2011) or leach nutrients into the soil for use by surviving plants and their microbial networks (Darrouzet-Nardi et al., 2019).

Experimental studies on icing effects are limited and all short-term so far, including only a limited number of species of vascular plants and lichens. They reveal impacts on both productivity and reproduction, likely through mechanisms that link the two. Evergreen shrubs and some lichen species seem particularly sensitive to icing (Bjerke, 2011; Bjerke et al., 2017; Finne et al., 2025; Milner et al., 2016; Preece & Phoenix, 2014). Shoot mortality and tissue damage can reduce primary productivity and photosynthetic efficiency, while surviving shoots may exhibit compensatory growth (Bjerke et al., 2018; Finne et al., 2025; Milner et al., 2016; Preece et al., 2012). Such reallocation of resources seems to come at the cost of reduced flowering (e.g. in *Cassiope tetragona*; Milner et al., 2016) or fruit production (e.g. reduced berry yield in *Empetrum nigrum* after repeated icing; Preece & Phoenix, 2014). However, responses vary and some deciduous shrub species such as *Vaccinium myrtillus* showed accelerated leaf emergence with unclear reproductive costs (Preece et al., 2012), while seedlings of *Salix polaris* and the woodrush *Luzula confusa* appeared relatively tolerant, despite some shoot damage (Bjerke et al., 2018).

Warmer summers may counteract some of the icing effects through enhanced growth of surviving shoots and advanced phenology, particularly of the reproductive phenophases of late-flowering species (Collins et al., 2021; Prevéy et al., 2019). Because Arctic plants commonly form flower buds the previous summer (Billings & Mooney, 1968), increased bud initiation under warmer summers could compensate for bud loss from icing. Detecting such effects requires multi-year studies.

We assessed how year-on-year occurrence of icing and summer warming interact to shape high Arctic plant productivity, reproduction and phenology. To achieve this, we set up a full-factorial field experiment in which we simulated, for 5 years in a row, (i) plot-level rain-on-snow and basal ice formation in winter and (ii) warming using open top chambers during summer (treatment and control) following the protocol of the International Tundra Experiment (ITEX; Henry & Molau, 1997). Each growing season, we determined plant community responses and recorded phenology and leaf traits of the dominant species *S. polaris*. We expected icing to (1) delay early phenophases due to a slower soil warm-up; (2) reduce community productivity due to plant damage and shorter growing season; and (3) reduce flower production due to reallocation of resources to compensatory growth. We anticipated summer warming to offset some effects of icing, but with net outcomes to depend on species, plant part and phenophase.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was located in high Arctic Svalbard, in the valley of Adventdalen (78°17′ N, 16°02′ E), with measurements collected for five consecutive years (January 2016–August 2020). At Svalbard Airport, 15 km from the study site, the annual mean air temperature was −5.9°C for the reference period 1971–2000 (winter: −13.9°C, summer: 4.5°C; Hanssen-Bauer et al., 2019), rising to −2.2°C during the study period (https://seklima.met.no/). The average annual precipitation was 196 mm for the reference period (winter: 51 mm, summer: 52 mm; Hanssen-Bauer et al., 2019), increasing to 223 mm during the study period. RCP8.5 projections for Svalbard anticipate increases of 7°C–9°C for annual temperature and 20%–40% for annual precipitation by 2100 (Hanssen-Bauer et al., 2019), with winter warming rates five to seven times faster than in summer (Isaksen, Nordli, et al., 2022). The proportion of annual precipitation falling as snow has already dropped from 50% to 30% over 1975–2015 (Hanssen-Bauer et al., 2019), resulting in more frequent rain-on-snow events (Hansen et al., 2014; Peeters et al., 2019). The basal ice layer formed can reach an average thickness of 15 cm (Peeters et al., 2019). Svalbard currently experiences conditions already seen, or soon expected, across large parts of the Arctic (Bintanja & Andry, 2017; Lemaire et al., 2025; Serreze et al., 2021).

Soil thermal conditions are influenced by the underlying permafrost. At the permafrost monitoring site Janssonhaugen, about 6 km east of the study site, temperature at the permafrost table (2 m depth) warmed at a rate of 1.4°C per decade (2002–2018; Etzelmüller et al., 2020). At our study site, mean sub-surface soil temperatures (5 cm depth) were 4.7°C in June and 7.5°C in July (Table S1a), the two most important months for plant growth (Van der Wal & Stien, 2014). Volumetric water content (i.e. soil moisture) decreased from about 45% in early June to 25% by mid-August at 10 cm depth (Table S1a), with strong negative correlations between moisture and temperature (Table S1b).

The tundra plant growing season starts immediately upon the onset of soil thaw (Descals et al., 2020), around mid to late May at our site and lasts approximately 3 months (Table 1). Adventdalen lies in the bioclimatic subzone C 'middle Arctic tundra' (CAVM Team, 2003). The plant community studied here was a mesic grass and moss-rich dwarf shrub heath, dominated by the prostrate deciduous dwarf shrub *Salix polaris* and the grass *Alopecurus borealis*. Other abundant vascular plants were the horsetail *Equisetum arvense*, the woodrush *Luzula confusa*, the forb *Bistorta vivipara* and the grass *Poa arctica* (Figure S1). The most abundant bryophytes were *Sanionia uncinata*, *Tomentypnum nitens* and *Polytrichastrum* spp. Nomenclature follows http://panarcticflora.org/ for vascular plants and Frisvoll and Elvebakk (1996) for bryophytes.

2.2 | Experimental design

The experiment followed a full-factorial design with two treatments (winter icing and summer warming), each at two levels (present/

TABLE 1 Overview of annual mean biotic and abiotic measurements.

	2016	2017	2018	2019	2020
Soil thaw onset day (range) and DOY [CI]	13th May (8th–22rd May), 134 [129;143]	21th May (3rd May–1st June), 141 [123;152]	10th May (6th–14th May), 130 [126;134]	30th Apr (18th Apr–20th May), 120 [108;140]	18th May (16th–22th May), 139 [137;143]
Air T°C June (range)	5.0 (3.6–6.7)	4.6 (3.2–6.5)	4.0 (2.3–6)	4.8 (3.3–6.8)	4.5 (2.8–6.8)
July (range)	9.0 (7.4–11.1)	6.9 (5.4–8.9)	7.2 (5.6–9.5)	8.4 (6.5–10.6)	9.8 (7.7–12.2)
Time of max. NDVI date and DOY [CI]	16th July, 197 [189;205]	NA	19th July, 199 [191;207]	12th July, 192 [184;200]	15th July, 196 [188;204]
Max. NDVI [CI]	0.74 [0.72;0.77]	NA	0.76 [0.73;0.78]	0.76 [0.73;0.78]	0.79 [0.76;0.81]
Flower count m^2 [CI]	263 [181;345]	229 [151;288]	314 [218;409]	295 [204;386]	491 [341;642]

Note: The daily average air temperatures were recorded at the Svalbard Airport (available on https://eklima.met.no/), while the soil thaw onset day, maximum Normalised Difference Vegetation Index (max. NDVI) metrics and the community inflorescence counts (Flower count) were recorded in control plots. Predicted means are presented with their 95% confidence intervals (CI) or range of values. The 'time of max. NDVI' is interpreted as the peak growing season.

Abbreviation: DOY, day-of-year (i.e. Julian day, where 1 = 1 January).

absent), resulting in four treatment combinations: icing only (*I*), warming only (*W*), combined icing and warming (*IW*) and control (*C*). In summer 2015, we selected three blocks (150–780 m apart) of visually homogenous dry-to-mesic tundra. Within each block, we chose 12 plots of 60 × 60 cm with similar vegetation structure and composition of dominant species (listed above), and randomly assigned treatments to obtain three blocks of replicated treatment combinations (Figure 1). The 36 plots received their same respective treatment each year starting in January 2016 (Table S2). Resource constraints meant that not all traits and parameters were measured each year. A major field campaign in 2018, after the third consecutive winter with experimental icing, covered the entire growing season with weekly measurements.

2.2.1 | Winter icing

Icing was applied to *I* and *IW* plots over 2–3 days in January–February (Figure 1a). Snow was carefully removed from all plots to equalise disturbance, and natural ice occurrence was recorded. Natural ice was common in 2017, with partial ice coverage occurring in all plots (3 cm average thickness). Snow was immediately placed back on non-icing (*C* and *W*) plots. For *I* and *IW* treatments, a 13 cm high wooden frame (60 × 60 cm) was placed around the plot and gradually filled up with cold water until frozen solid (Figure 1a), following Milner et al. (2016). The resulting ice thickness was within the natural range after extreme rain-on-snow events (Peeters et al., 2019). In the 3 days after treatment application, sub-surface soil temperature increased on average by 2.9°C [2.3;3.5] compared to *C* plots (Figure S2). Frames did not influence snow accumulation pattern later in winter and were removed at the onset of snowmelt. Ice-covered plots (*I* and *IW*) melted almost simultaneously with snow-covered plots (*C* and *W*).

Permission to perform the experiment was accorded by Longyearbyen Lokalstyre (RiS ID: 10484).

2.2.2 | Summer warming

Immediately after snowmelt (Table S2), hexagonal open top chambers (1.4 m base diameter and 33 cm height) made of plexiglass were deployed over the *W* and *IW* plots following the ITEX protocol (Henry & Molau, 1997). Open top chambers were deployed and removed at the start and end of the growing season.

2.2.3 | Herbivore exclusion

Vertebrate herbivores were excluded from all plots during the snow-free season using metal net cages over *I* and *C* plots and nets on top of the open top chambers in *W* and *IW* plots (mesh-size 1.9 × 1.9 cm, Figure 1b). Nets were deployed and removed on the same day as the open top chambers.

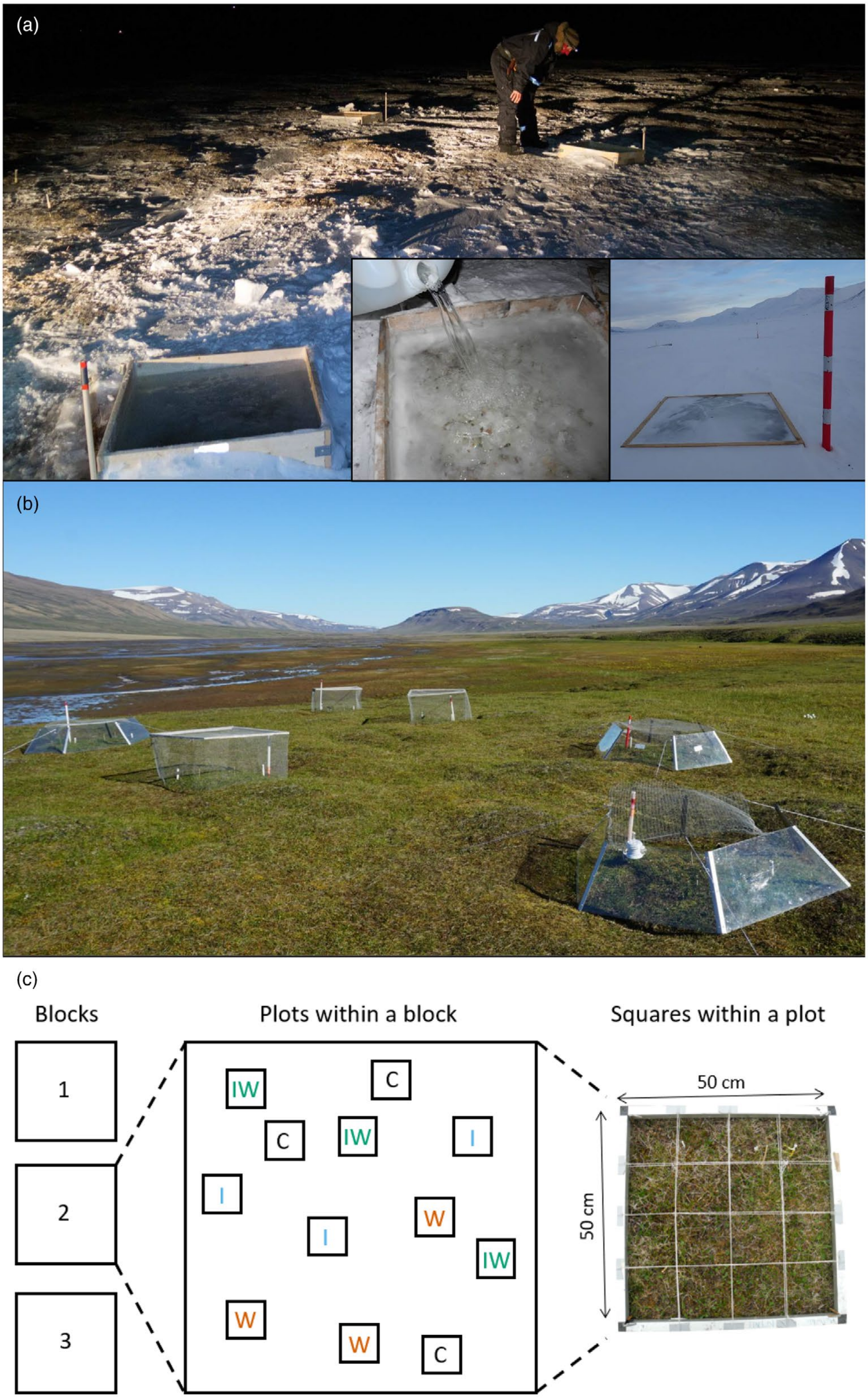


FIGURE 1 The experimental set up in the Adventdalen valley, Svalbard. Overview of the field site (a) in the polar night, when applying the icing treatment by filling a wooden frame with water and (b) in summer with the open top chambers (plexiglass hexagons of 1.4m base diameter and 33cm height) simulating warming and net cages to protect against herbivory. (c) Experimental nested design with the vegetation frame fitting the plot size. C = control, I = icing, IW = icing × warming, W = warming. Picture credits: Ø. Varpe and M. Le Moullec.

2.3 | Field measurements

Soil temperatures were recorded with iButton loggers (type DS1921G-F5, ±1.0°C accuracy, 0.5°C resolution) every 120 min in summer and 240 min in winter. Sub-surface loggers were placed in the soil layer 5 cm below the top of the 1–3 cm thick bryophyte layer (Table S1a) to investigate how treatments influenced the upper soil melt onset. In spring 2018, we also investigated treatment effects on soil temperatures at greater depth (20 cm depth, not in *IW* plots), placing loggers in mid-September 2017 using a standard soil core sampler (3 cm diameter cylinder) and delicately replacing the extracted soil columns. We estimated the onset of soil thaw for each plot as the first day when soil sub-surface temperatures were ≥0°C for at least 10 consecutive days. We also monitored surface air temperature every 30 min (5 cm above the bryophyte layer) with HOBO loggers (type U23-003/UA-001; ±0.2°C accuracy) in *C* and *W* (one pair per block) from 15 June to 1 September in the years 2016–2018 (Table S1a).

Above-ground plant productivity was monitored weekly during the growing season by measuring Normalised Difference Vegetation Index (NDVI, Pettorelli et al., 2005), at the central (30 cm diameter) part of each plot with a Skye SpectroSense2+ handheld device at 125 cm high (with integrated light sensor). We considered the peak growing season to be the average day control (*C*) plots reached maximum NDVI (Table 1). We also measured community-level vascular plant species abundance (hereafter referred to as 'abundance') shortly after peak growth (end of July) in 2016–2019 (Table 1; Table S2) using point intercept methodology (Bråthen & Hagberg, 2004). We used a 50 × 50 cm sampling frame elevated above the canopy (~20 cm high), with a double layer of strings creating 25 intersections. A pin of 3 mm diameter was then lowered onto the moss layer, at all intersections, recording all 'hits' of live vascular plant species and dead tissue classified as standing dead or litter.

We further investigated vegetative responses of the dominant vascular plant, *S. polaris*, by collecting leaves for trait measurements. Sampling design varied over years. In 2018, we randomly sampled entire shoots at five of the sampling frame's intersections and measured all leaves per shoot. Because of the high variability of leaf size and the time-consuming nature of this method, in 2019 and 2020 we targeted the upper tail of the size distribution, collecting the largest leaf from each of the 16 sub-squares of the 50 × 50 cm sampling frame (Figure 1c; Table S2). Leaves were kept moist until scanned for measuring their area, then oven-dried at 60°C for 4 days and weighed to the nearest 0.01 mg. Specific leaf area (SLA) was calculated as the ratio of leaf area to dry mass.

Flowering frequency was assessed in mid-July each year by counting inflorescences within the 50 × 50 cm area delineated by the recording frame, subdivided into 16 sub-squares, for the species *S. polaris* (males and females [catkins]), *B. vivipara*, *A. borealis*, *L. confusa* and *P. arctica* (Table S2).

Phenology of *S. polaris* was recorded for the most advanced vegetative and reproductive phenological stages ('phenophases') in each of the 16 sub-squares. Vegetative phenophases were: (1) leaves starting to unfurl, (2) leaves fully expanded, (3) start of senescence and (4) leaves fully senesced. Reproductive phenophases were: (1) distinct inflorescence buds visible, (2) buds recognisable as female or male, (3) receptive stigmas (female) and open anthers releasing pollen (male), (4) stigmas and anthers withered and (5) seed dispersal. Monitoring rounds were most frequent in 2018 and absent in 2020 (Table S2). We investigated different phenology parameters. Timing: the day-of-year when a sub-square reached a given phenophase. Duration: the number of days between two phenophases at the sub-square level. Proportion: the proportion of sub-squares within a plot that reached a given phenophase at specific time points.

2.4 | Statistical analysis

We quantified the effects of winter icing, summer warming and their combination, across and within years, on a range of response variables. These included measurements of vegetation productivity at the community level (i.e. NDVI metrics, vascular plants' abundance) and species level (i.e. leaf size traits, *S. polaris* phenophase [timing, duration, proportion]); reproduction at the community level (i.e. inflorescence counts) and species level (*S. polaris* reproductive phenophase [timing, duration, proportion]); and potential environmental drivers (i.e. air/soil temperature, onset of soil thaw).

We used (generalised) linear mixed-effect models as the main analytical tool, to account for unbalanced data with spatial and temporal hierarchical structures defined by our study design and did so by using the 'lmer' and 'glmer' functions from the lme4 package (Bates et al., 2015) in software R-3.6.3 (R Core Team, 2020). We built four separate models for each response variable to: (1) estimate treatment effect sizes and predicted means per year (treatment [categorical] × year [factor] as main and interaction fixed effects), (2) estimate treatment effect sizes and predicted means over years (treatment [categorical] as fixed effect, year as a random intercept), (3) test for icing-warming interaction per year (icing [binary] × warming [binary] × year [factor] as main, two- and three-way interaction fixed effects), (4) test for icing-warming interaction over years (icing [binary] × warming [binary] as main and interaction fixed effects, year as a random intercept). Treatment estimates were identical in models 1 and 3, and models 2 and 4, but the variance of *IW* level (model 1 and 3) depends only on its sample size and residual variance, shared across the other levels (*C*, *I* and *W*), thereby avoiding the additional variance introduced by the higher-order interaction (models 3 and 4). For response variables spanning a period (i.e. phenophase proportion, soil temperature), we fitted (5) a model with treatment [categorical] × day-of-year [as factor for predictions per day, as numeric for predicted curves] as main and interaction fixed effects, separately for each year. In these models, we did not test for three-way interactions.

The random intercept structure (i.e. variation in means between replicated units) always included plot ($n = 36$) nested within block ($n = 3$), with day-of-year nested within year for repeated measurements. It also included sub-square nested within plot (16 sub-squares per plot, $n = 576$) for inflorescence count and phenology.

For NDVI data specifically, we first derived different metrics from repeated measurements by fitting a generalised additive model (GAM) to each plot-year combination. This approach was chosen because NDVI changes nonlinearly during the growing season. We used the R function 'gam' from the mgvc package (Wood et al., 2015), fitted with restricted maximum likelihood. Model fit was good (visual evaluation of model residuals and k-indices >1), except for summer 2017 when measurements stopped before the peak growing season (Table S2). Therefore, we predicted daily NDVI values for each plot, each year, except 2017. We then computed five NDVI metrics: (1) maximum NDVI value; (2) day-of-the-year of maximum NDVI; (3) early-season cumulative NDVI (hereafter 'cumulative start') by integrating daily predicted NDVI values from the first day of measurements to the day when *C* plots, on average, reached maximum NDVI; (4) late-season cumulative NDVI (hereafter 'cumulative end') by integrating daily values from the day when *C* plot, on average, reached the maximum NDVI to the last measurement day of the season; and (5) cumulative NDVI across the growing season (hereafter 'cumulative total') by integrating daily values from the first to the last day of measurements.

Response distributions were matched to data properties: air/soil temperature data and NDVI metrics were best summarised by a normal distribution; count data of plant abundance, phenophase timing and duration by a Poisson distribution; inflorescences number were square-root transformed and leaf size and weight were log-transformed before modelling. For analysis of phenophase proportion, each phenophase was converted to a binary data format to fit a logistic regression from a binomial distribution. This analytical method best reflects the way the data were collected: by recording whether a sampling unit (i.e. sub-square) was in a certain phenophase (yes/no), regardless of the calendar day. Percentage differences between treatments and controls were calculated from back-transformed predicted means. We interpreted that there was an effect when the 95% confidence interval (CI) of the estimates did not overlap with 0 (i.e. the predicted mean of C); a tendency when it marginally overlapped with 0 but showed a clear direction; and as no effect if it largely overlapped with 0.

3 | RESULTS

3.1 | Summer soil temperature

Our icing (*I*) treatment consistently delayed soil thaw, while warming (*W*) increased soil temperature, and the combination of icing + warming (*IW*) produced intermediary effects. Following snowmelt and associated spring meltwater floods, *I* extended the period soils remained frozen, even though the experimental ice on top of these plots melted almost simultaneously with the snow on top of the control (C) plots (Figure 2a; Table S1a). The onset of sub-surface soil thaw was delayed by 6.0 [2.2;9.9] days in *I* plots and 4.4 [0.4;8.5] days in *IW* plots, while *W* plots remained unaffected (−0.9 [−5.0;3.1] days) relative to *C* plots (hereafter, results are reported as mean effect sizes [95% CI] in comparison to controls [C] over 2016–2020, unless specified differently). These icing-induced delays were longer at greater depth. At 20 cm depth (data only from 2018), thaw was delayed by 9.0 [1.3;16.7] days in *I* plots, staying for about 2 weeks at −0.5°C (i.e. 'the zero curtain period'; Outcalt et al., 1990; Figure 2b), resulting in lagged soil warming throughout June (Figure 2b).

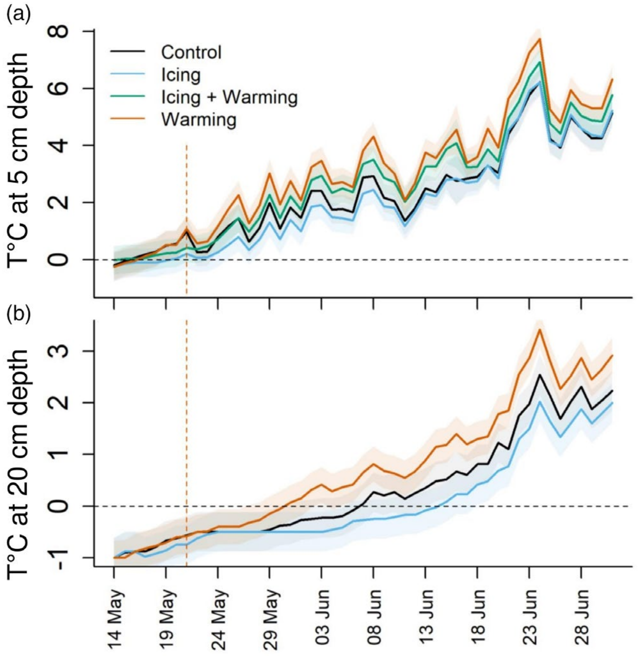


FIGURE 2 Daily predicted means of soil temperatures during the soil-thawing period from mid-May to end of June 2018, at (a) 5 cm depth (i.e. sub-surface) and (b) 20 cm depth. Shaded areas represent 95% CIs and the orange vertical dashed lines show the day the warming treatments started.

Open top chambers increased soil sub-surface temperatures by 0.6 [0.3;1]°C in *W* plots and 0.4 [0.1;0.7]°C in *IW* plots (in 2016, 2018 and 2019) and surface air temperature by 0.8 [0.7;0.9]°C in *W* plots (June–August, 2016–2018; Table S1a). Soil moisture varied between years but not treatments (Table S1a).

3.2 | Community-level vegetative responses: NDVI metrics and live vascular plant abundance

Icing delayed the onset of peak NDVI but enhanced late-season NDVI, while *IW* showed greatest seasonal increase. Maximum NDVI occurred on average on 15 July in *C* plots (Figure 3a; Table 1). It was reached 4 [2;7] days later in *I* plots, and consistently so over the years (Figure 3i). This delay was reduced in *IW* plots (2 [−1;4] days) and reversed in *W* plots (−3 [−5;0] days; Figure 3i, Table S3). Maximum NDVI was higher in *I* and *IW* plots in 2016, but this effect vanished in subsequent years as all treatments, including *C* plots, reached the saturation value of 0.8 (Figure 3b,j; Figure S3; Table S3; Myers-Smith et al., 2020). Cumulative NDVI metrics captured treatment differences in seasonal curve shape (Figure S3). In early-season, only *IW* increased 'cumulative start' NDVI; NDVI thereafter ('cumulative end') remained high, resulting in an overall increased 'cumulative total' NDVI (Figure 3k–m; Table S3). Icing plots caught up in late season with *IW* plots (NDVI 'cumulative end') exceeding *C* plots. Warming alone did not affect NDVI metrics (Figure 3i–m; Table S3). There were no significant interaction effects between *I* and *W* in NDVI metrics (Table S3).

Vascular plant abundance was unchanged under *I* (3% [−11;19]), but increased by 26% [9;46] under *IW*, with the largest effect in 2016 (69% [43;99]; Figure 3n; Table S4). These patterns were driven by the two most abundant vascular plants, the shrub *S. polaris* and the grass *A. borealis* (Table S4), whose abundances determine NDVI values (based on among-plot correlations; Table S5). Under *W*, vascular plant abundance tended to increase by 13% [−2;31] (Table S4). There were no interaction effects between *I* and *W* (Table S4).

3.3 | Species-level vegetative responses: leaf size traits and phenology of *S. polaris*

Leaf dry mass and leaf area of *S. polaris* tended to be reduced under *I*, but not under *IW* and *W*. Because dry mass decreased more than leaf area, SLA increased substantially under *I* (Figure 4; Table S6). SLA of *W* plots also tended to increase, but not *IW* plots, resulting in a negative interaction effect (Table S6).

The timing of early leaf phenophases was delayed in *I* plots, but advanced in *IW* and *W* plots. Leaves unfurled 4 [1;8] days later in *I* plots and by a similar number of days earlier in *IW* and *W* plots (−4 [−8;−1] days; Figure 5a,b; Table S7). The duration to unfold leaves (from unfurled to fully expanded) was, however, one-third shorter in *I* plots (−3 [−4;−1] days; Figure S4a; Table S8), offsetting much of the initial delay. In contrast, leaves from *IW* and *W* plots remained fully expanded 20% longer (6 [2;8] days; Table S8) before senescing. Onset of senescence happened almost simultaneously across treatments (Figure 5c,d; Figure S4a), but its rate was 30% faster in *IW* and *W* plots (−2 [−3;−1] days; Figure S4a; Table S8).

3.4 | Community-level reproductive response: inflorescence production

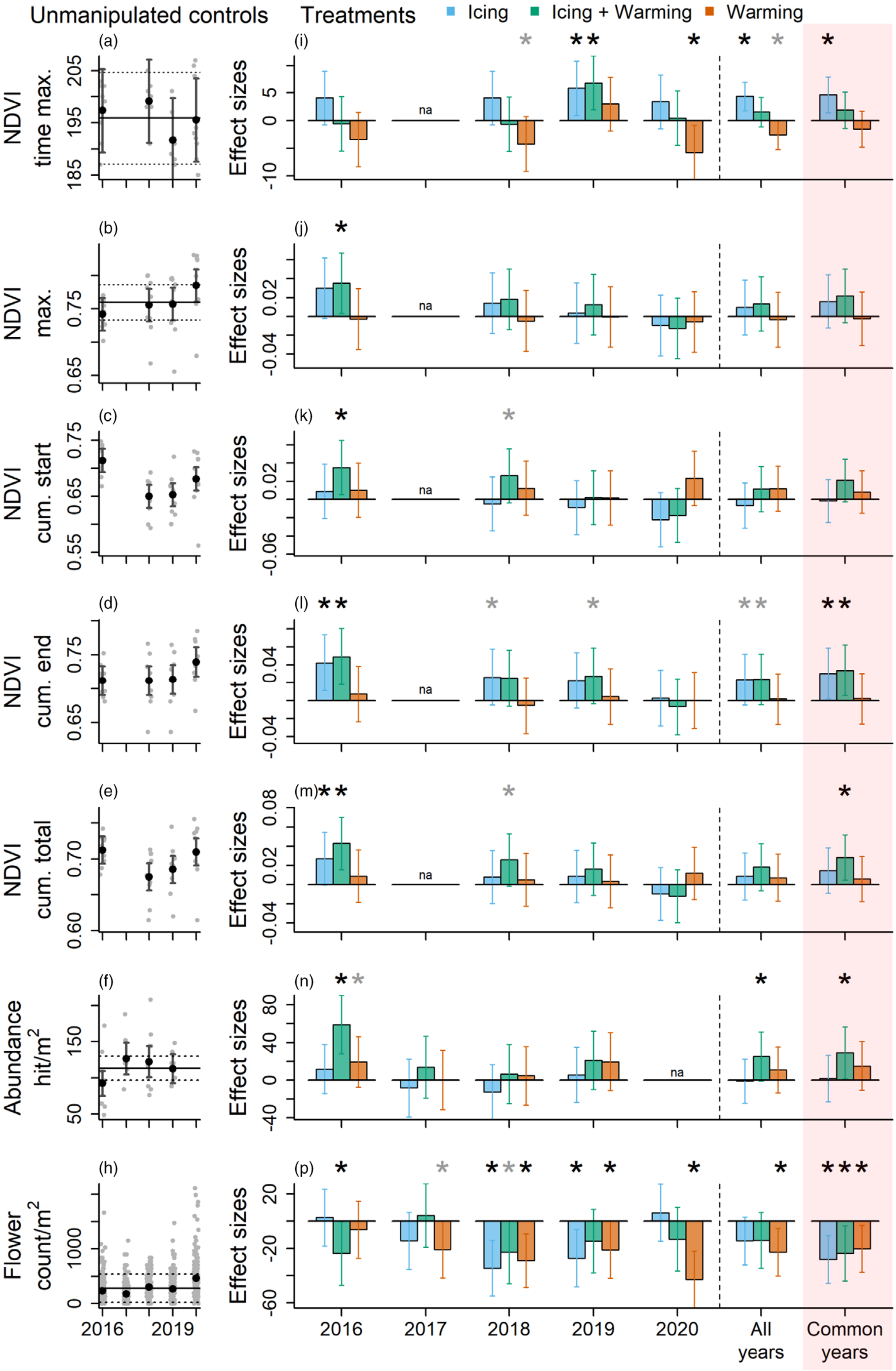
The total number of vascular plant inflorescences was reduced by one-third across all treatments, with variable year effects (Figure 3h; Table S9). Icing had no effect in the first and last treatment years, while *W* effects tended to increase over time (Figure 3p; Table S9). There were more inflorescences under *IW* than expected from *I* and *W* effects being additive (i.e. interaction effect; Table S9). Although *S. polaris* produced the highest number of inflorescences (male and female catkins) and drove the observed inter-annual variability, inflorescences of the forb *B. vivipara* and graminoids were also reduced by *I* (and *IW*) in all years (respectively by −52% [−72;−27] and −67% [−95;−11]; Table S7). Under *W*, *S. polaris* inflorescences were strongly reduced (−70% [−81;−56]), while graminoid inflorescences increased in number (146% [46;225]). Note that in 2020, a summer with rapid soil thaw onset followed by a 'heat wave' in July, the number of inflorescences in *C* plots reached more than twice the amount of any other year (Figure 3h; Table 1; Table S9). For instance, even with the greatest relative reduction under *W* (Figure 3p), 2020 was still the year with the greatest inflorescence production under this treatment (Table S9).

3.5 | Species-level reproductive responses: phenology of *S. polaris*

Reproductive phenophases of *S. polaris* were generally delayed under *I* but advanced under *IW* and *W*, with such effects occurring in all years and strongest in 2017 (Figure 5f–l; Figure S4b,c). Interaction effects were largest for seed dispersal: in 2018, when dispersal occurred slightly later in *I* plots (5 [−2;12] days), but markedly earlier in *IW* and, to some extent, *W* plots (−11 [−17;−6] and −5 [−12;2] days, respectively; Figure 5m; Table S7). This advanced seed dispersal in *IW* plots coincided with a 30% shorter duration for seeds to mature (−8 [−14;−1] days; Table S8), while the phase of stigmas being receptive to pollen was extended by 50% (2 [0;5] days; Table S8).

Male flower development followed similar patterns. The timing of anthers being visible and pollen release tended to be later in *I* plots (2 [−3;7] days in 2018; Figure 5j,k, but see Figure S4c for stronger delays in other years such as 2017), earlier in *IW* plots (−5 [−10;−0.4] days) and, to some extent, in *W* plots (−4 [−10;2] days; Figure 5j,k; Table S7). Because anther senescence was rather synchronous across treatments (Figure 5l), the duration of pollen release was twice as long in *IW* plots (5 [1;10] days) but 40% shorter in *I* plots (−2 [−3;0] days; Table S8).

FIGURE 3 Effects of experimental treatments on Normalised Difference Vegetation Index (NDVI) metrics, vascular plant abundance and the community inflorescence counts (flower count). Left panel (a–h): Model predicted means of unmanipulated control plots (black dots) and their 95% confidence intervals (CIs), represented separately for each year. Horizontal full and dashed lines represent among-year model predictions and their 95% CIs, displayed only for variables comparable between years (i.e. with comparable sampling periods and/or design). Background dots show raw data at the plot ($n=9$) or sub-square (n range = 109–214) level, jittered for display. Model predictions and their CIs were back-transformed on the response scale. Right panel (i–p): Effect sizes of treatments and their 95% CIs, displayed separately for each year, across all five years and across 'common years' having all parameters measured (i.e. 2016, 2018 and 2019). The reference level at 0 corresponds to the predicted means of controls (presented in the left panel). Asterisks indicate CIs not overlapping zero (black = 95% CI, grey = 90% CI). NDVI cum. end, NDVI cumulative end; NDVI cum. start, NDVI cumulative start; NDVI cum. total, NDVI cumulative total; NDVI max., Maximum NDVI values from −1 to 1; NDVI Time max., Time of maximum NDVI as day-of-year.


Unmanipulated controls
Treatments
Icing
Icing + Warming
Warming
(a)
NDVI time max.
185
195
205
(i)
Effect sizes
-10
0
5
na
(b)
NDVI max.
0.65
0.75
(j)
-0.04
0.02
(c)
NDVI cum. start
0.55
0.65
0.75
(k)
-0.06
0.02
(d)
NDVI cum. end
0.65
0.75
(l)
-0.04
0.04
(e)
NDVI cum. total
0.60
0.70
(m)
-0.04
0.02
0.08
(f)
Abundance hit/m^2
50
150
(n)
-40
0
40
80
(h)
Flower count/m^2
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All years
Common years

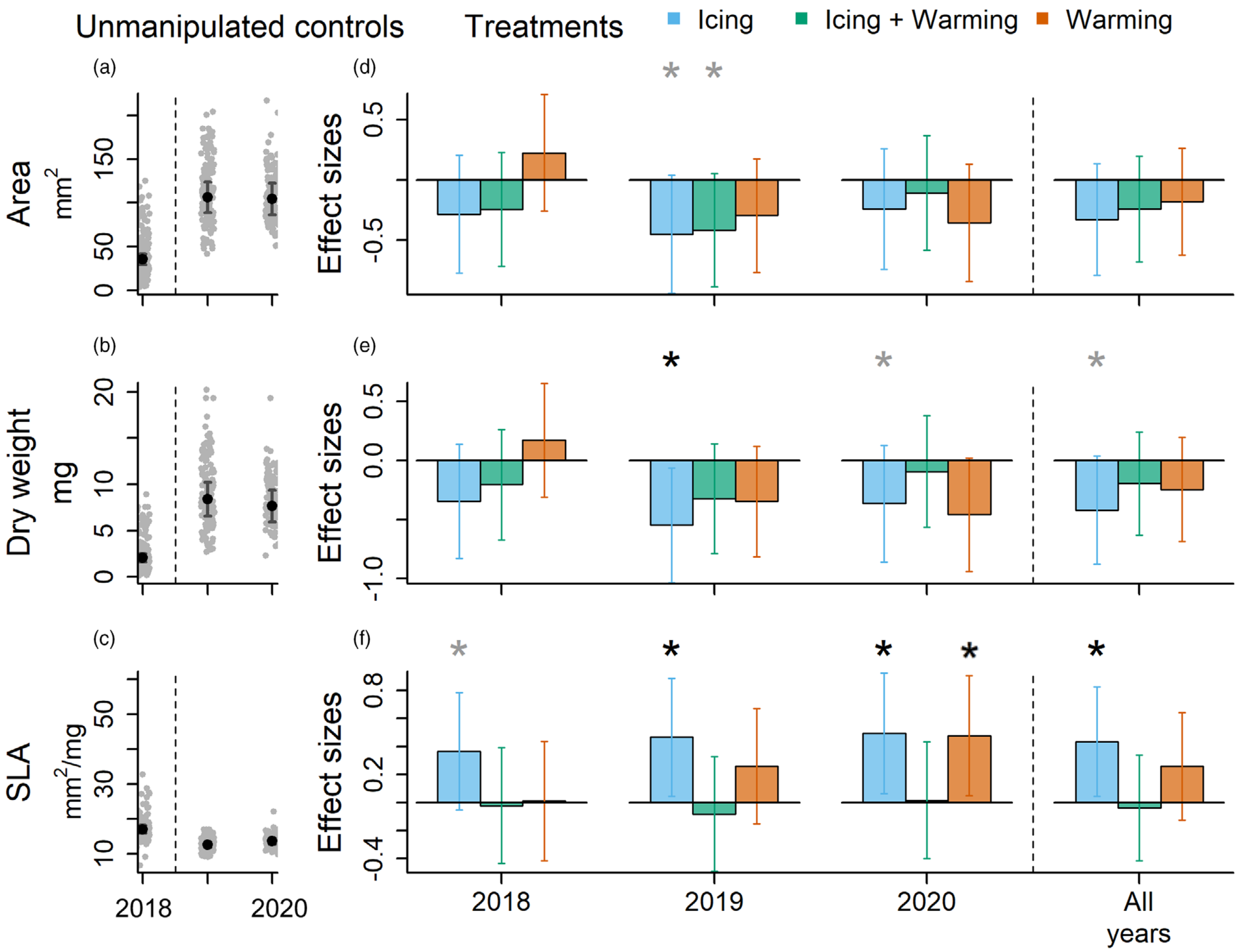

FIGURE 4 Effects of experimental treatments on leaf size measurements of *Salis polaris*. Left panel (a, c, e): Predicted means of control plots (black dots) and their 95% confidence intervals (CIs), with raw data (grey dots in the background) jittered for display. In 2018, shoots were selected at random and all leaves per shoot measured. In 2019 and 2020, the largest leaf per sub-plot was measured ($n=16$). Model predictions and their CIs were back-transformed on the response scale. Right panel (b, d, f): Effect sizes of treatments and their 95% CIs. The reference level at 0 corresponds to the predicted means of controls (presented in the left panels). Asterisks indicate CIs not overlapping zero (black = 95% CI, grey = 90% CI). SLA = Specific leaf area, the ratio of leaf area to dry weight.

4 | DISCUSSION

This field experiment simulating consecutive winters of extreme ice encapsulation of a high Arctic plant community revealed effects with an extent comparable to those of the much better-studied summer warming. Yet, we also found that the observed effects of winter icing could be more than counteracted by subsequent summer warming—supporting the need to account for net effects across seasons to predict climate change impacts. Icing initially delayed spring soil thaw, with a month-long lag in soil warming in the upper active layer, delaying early leaf phenophases of the dominant shrub, *S. polaris*. However, subsequent evidence showed a 'catching up' through accelerated leaf development resulting in smaller and thinner leaves and increased community-level primary productivity, reaching similar or even greater levels later in the growing season. This compensatory growth and productivity seem to happen at the expense of reproduction with species-specific lag-effects. The community-level inflorescence production was reduced and *S. polaris* seed maturation delayed. Summer warming largely counteracted effects of icing, enhancing primary productivity across the entire growing season and offsetting icing-induced reductions in plant leaf size and weight. It also turned around phenophase delays, including the timing of seed dispersal by advancing it even more than under warming alone. Yet, it did not negate the considerable reduction in inflorescence production caused by icing, perhaps because warming was similarly suppressive, suggesting a complex interplay of seasonal effects. Still, given the absence of dramatic die-off or magnified treatment effects over the years, this first multi-year tundra icing experiment reveals

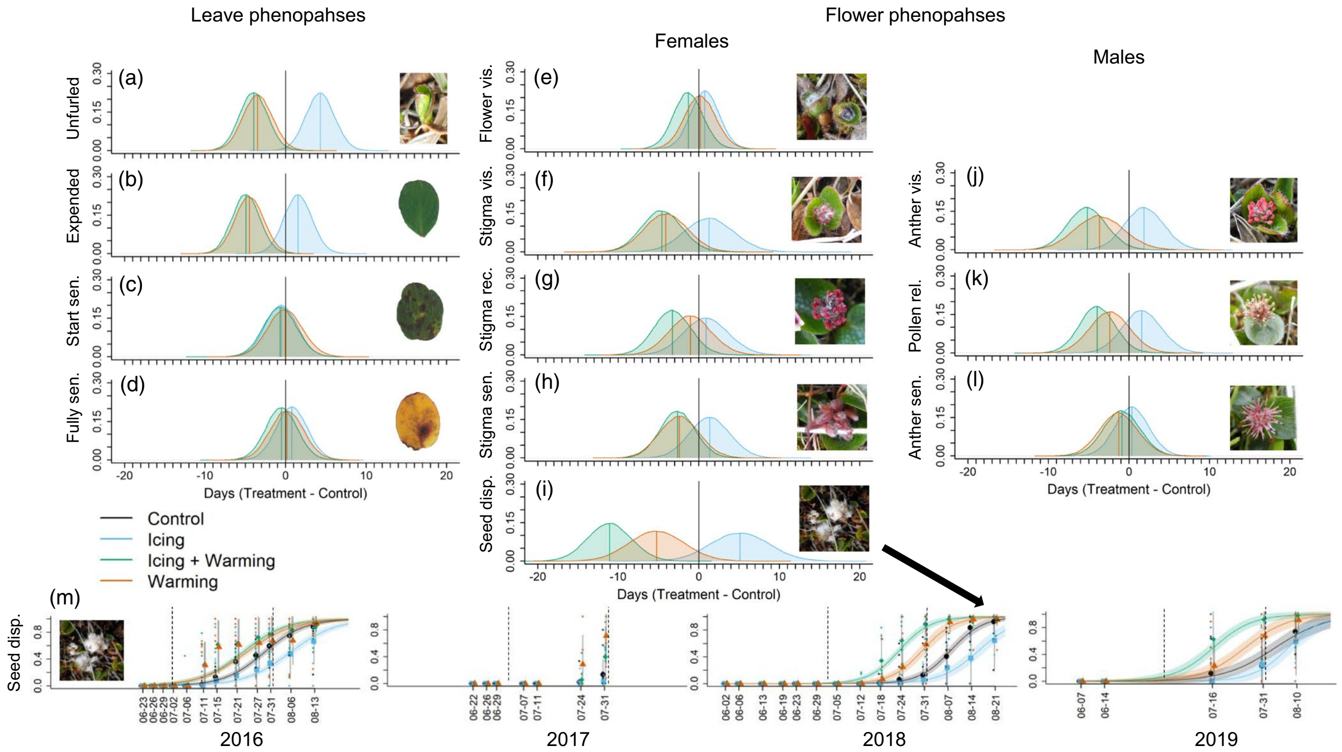

FIGURE 5 Treatment effects on *Salix polaris* phenophases. (a–l) Differential distributions of the day-of-year each phenophase is reached in 2018 (treatment—controls). Normal distributions were drawn for display from simulations using predicted means and standard-errors obtained from generalised linear mixed-effect models (GLMMs, Poisson distribution; Table S8). The vertical black line at 0 corresponds to the predicted means of controls. Coloured vertical lines represents treatment predicted means. (m) Proportion of sub-squares reaching seed dispersal at each monitoring time-step from 2016 to 2019, with probability curves for each summer (except for 2017 due to insufficient monitoring in late-season). Probability curves for other phenophases and years are presented in Figure S8. The predicted mean at each time-step (symbols) and curves were computed with binomial GLMMs. Grey bars and shaded areas represent 95% CIs; small dots show the raw data at the plot level; the arrow indicates when seed dispersal was reached (i.e. proportion of 1; marking the correspondence between graph i and m for 2018); vertical dashed lines represent 1 July and 1 August. Vegetative phenophases: (a) leaves unfurled, (b) leaves fully expanded, (c) leaves started senescing, (d) leaves fully senesced; reproductive female phenophases: (e) inflorescence visible (female or male catkin), (f) stigmas visible, (g) stigmas receptive, (h) stigmas senesced, (i and m) seed dispersed; reproductive male phenophases: (j) anthers visible, (k) pollen released and (l) anthers senesced.

a rather high level of plant tolerance to icing, particularly when followed by warm summers offsetting some effects of icing.

4.1 | Delayed growth but increased productivity: evidence of compensatory growth?

The apparent absence of major plant die-off due to icing, and even evidence of increased community-level primary productivity under combined icing + summer warming, contrasts with the documented 'Arctic browning' following extreme winter warm spells, a phenomenon in part related to damage in evergreen shrubs and reduced primary production (Bjerke et al., 2017; Phoenix & Bjerke, 2016). Evergreen shrubs, virtually lacking in our study plots, maintain long-lived leaves and dormant buds well above-ground, making them more vulnerable to icing than deciduous shrubs (Givnish, 2002). Dead shoots of evergreen shrubs will remain visible for several years, lowering spectral indices such as NDVI, even if growth may be enhanced in remaining surviving shoots (Bjerke et al., 2017; Milner et al., 2016; Treharne et al., 2020). In contrast, in our experiment dominated by the deciduous shrub *S. polaris*, with large parts of shoots nested into the ground (Le Moullec et al., 2019), had no evident above-ground signs of damage, likely allowing compensatory productivity and growth later in the season, reflected by the enhanced NDVI. Thus, despite severe treatments, the plant community seemed able to withstand repeated icing, possibly even contributing to a further 'Arctic greening'. The latter may also be a landscape-scale response to increased icing, allowing for a further expansion of deciduous shrubs and graminoids at the expense of icing-sensitive evergreen shrubs responsible for much of the observed 'Arctic browning'.

Icing delayed thawing and warming of the upper soil active layer, despite an almost simultaneous melting of basal ice and snow across treatments, shortening the time window for processes enabling plant nutrient acquisition and growth (Darrouzet-Nardi et al., 2019; Frei & Henry, 2022). This can be explained by infiltration and refreezing of meltwater in the underlying soil, increasing ice content in near-surface soils. Ice-rich or wet soils require more energy to warm, especially over permafrost (Isaksen, Lutz, et al., 2022). Summer warming shortened this lag.

In the 'race' for maximising primary production within the short Arctic growing season, *S. polaris* appears to compensate for initial delays in leaf phenology in icing plots by accelerating later leaf development, producing smaller and thinner leaves with resultant greater SLA (i.e. reflecting faster growth rate; Pérez-Harguindeguy et al., 2013). A laboratory icing experiment on *S. polaris* supports this, finding reduced leaf sizes but increased leaf numbers and unchanged photosynthetic capacity (Bjerke et al., 2018). This deciduous shrub has the ability to activate dormant buds to compensate for damage, as also seen in response to herbivory (Skarpe & Van der Wal, 2002). However, allocation of resources to primary growth may come at the expense of secondary growth (e.g. ring growth), which icing has been found to reduce in *S. polaris* (Le Moullec et al., 2020). Icing may alter the otherwise strong correlation between primary and secondary growth in this species (Le Moullec et al., 2019).

As we expected, summer warming partly counteracted icing effects. Furthermore, our results provided evidence of such effects being stronger than just additive. For instance, warming turned an icing-induced delay in leaf phenology of *S. polaris* into a phenology advance. In the low Arctic, where summers are warmer and could be comparable to our warming treatment, an icing experiment matched our findings with advanced shrubs' early leaf emergence explained by compensatory growth of frost-damaged ramets (Preece et al., 2012; Preece & Phoenix, 2014). Accordingly, in our plots, primary productivity increased early in the growing season under icing + warming and remained high, with leaves from *S. polaris* in fully expanded phase for 20% longer, its leaf size and mass sustained. In addition, the dominant graminoid *A. borealis* also increased in abundance in some years, and together the abundances of *S. polaris* and *A. borealis* shaped community-level productivity (i.e. NDVI; Table S5). Mechanisms may include: (1) damaged plants (e.g. roots or buds) from icing could leach nutrients into the local soil which, with warmer summers, may be available earlier for surviving plants, particularly in drier tundra (Bardgett et al., 2007); (2) earlier activation of growth hormones and internal reallocation of nutrients and carbohydrates to growth and repair of potential icing-induced stress or damage (Chapin III, 1991); (3) increased soil nutrient mineralisation under icing, leading to greater availability to plants after snowmelt (Rixen et al., 2022), although ice, unlike snow, does not insulate the soil and may restrict microbial respiration. Such possible responses need further investigation.

Despite the greater primary productivity in late-season under icing and icing + warming, leaf senescence occurred synchronously across treatments, most likely driven by cues such as photoperiod. However, the timing of leaf senescence in control plots varied among years by more than 10 days (Figure S4a), suggesting interactions with other variables shared across treatments, for example timing of snow or ice-melt (Bjorkman et al., 2015; Cooper et al., 2011; Kelsey et al., 2021; Wipf & Rixen, 2010). Under warming, however, leaf senescence was slightly delayed (Figure S4a), which agrees with previous syntheses (Bjorkman et al., 2020; Collins et al., 2021).

4.2 | Reduced reproduction: Result of trade-offs?

Compensatory growth may come at the cost of reproduction, as observed after thaw–freeze cycles (Bokhorst et al., 2011), snow manipulation (Cooper et al., 2011), nutrient addition (Petraglia et al., 2013), colder summers (Johnstone & Henry, 1997) and icing in evergreen shrubs (Milner et al., 2016). In our study, icing reduced the number of inflorescences (in some years by half) possibly due to increased vegetative sink strength, direct winter damage to reproductive buds and a subsequent shift in resource allocation from reproduction to growth, or a shorter time between green-up and flowering (i.e. green-up being more delayed than flowering), which can reduce investment in flowering (Collins et al., 2021; Gougherty & Gougherty, 2018). In the first experimental year, *S. polaris* showed no reduction of inflorescences, suggesting that inflorescence buds formed the previous summer survived a winter of icing. In contrast, other species, for example *B. vivipara* and *A. borealis*, exhibited a strong reduction without a lag. In the same valley, extreme natural rain-on-snow events in the winter of 2012 were suggested to cause a record low number of inflorescences in the community (Semenchuk et al., 2013).

While summer warming suppressed community-level inflorescence abundance without adding to the negative effect of icing, it clearly reduced the icing-induced delay in reproductive phenophases of *S. polaris*, and to a level beyond that obtained by warming alone. Advancing flowering and fruiting under warming are consistent with results of circumpolar warming experiments (Arft et al., 1999; Bjorkman et al., 2020; Collins et al., 2021; Prevéy et al., 2019). Like Collins et al. (2021), we found larger shifts in reproductive than vegetative phenophases, considerably shortening the period between leaf emergence and seed dispersal. Interestingly, the duration of reproductive phenophases was not fixed, which contradicts the overall findings from a neighbouring snow manipulation experiment (Semenchuk et al., 2016). For example, the periods of inflorescence and seed development were both shortened under summer warming (regardless of icing), while those of pollen release and stigmas receptive to pollen doubled in duration under icing + warming. Such phenological flexibility can be adaptive in variable environments. Phenology studies rarely distinguish these short, but critical stages for reproduction from the overall flowering time (Song & Saavedra, 2018).

4.3 | Evolutionary implications

Evolutionary consequences can be expected from changing trade-offs influencing sexual reproductive effort and success. However, most Arctic plant species are clonal perennials that can delay sexual reproduction until favourable years (Bazzaz et al., 1987; Jónsdóttir, 2011). In addition, Arctic plants show relatively large intraspecific functional trait variability (Thomas et al., 2020), which further contributes to the community-level resistance to environmental changes (Jónsdóttir et al., 2023). Consequently, we can expect slow evolutionary responses to icing and summer warming. The lack of accentuated effects after five consecutive years of icing indicates that species of the mesic community studied here have evolved strategies to cope with such extreme events.

In the oceanic climate of Svalbard, winter rain-on-snow events have occurred for decades, although their frequency and extent have increased dramatically in recent years (Hansen et al., 2014; Peeters et al., 2019). Selection acting upon life-history traits might change when acute stress episodes from occasional icy winters become 'chronic', as projected for the Arctic (Bintanja & Andry, 2017). In regions that have more rarely encountered widespread icing events than Svalbard (e.g. the Canadian high Arctic), effects may be more severe, particularly where there would be no possible introgression of adapted genes from nearby habitat (Bjorkman et al., 2017). Such limits to adaptation could lead to tipping points and irreversible ecosystem change. Comparative studies among Arctic regions with different frequencies of rain-on-snow events could shed light on plants' adaptive capacities to icing.

4.4 | Ecological implications

The effect sizes of winter icing versus summer warming were of similar magnitude and within the range of natural inter-annual variation of controls. Although the use of open top chambers only increased summer surface air and sub-surface soil temperatures by 0.8°C and 0.9°C, respectively, this increase was similar to the decadal trend found in this region (Etzelmüller et al., 2020; Isaksen, Nordli, et al., 2022) and to other high Arctic ITEX sites, where low irradiance restricts warming (Bokhorst et al., 2013; Hollister et al., 2023; Jónsdóttir et al., 2023). As for other decadal-scale warming experiments, there was no evidence of exacerbated treatment effects over the years, and increases in primary productivity were therefore limited (Barrett & Hollister, 2016; Jónsdóttir et al., 2023). Similar or larger effect sizes from treatments concerning winter rather than summer conditions have been found in other tundra studies, notably those manipulating snow accumulation (Cooper et al., 2011; Frei & Henry, 2022; Niittynen et al., 2020), underscoring that conditions during the 'dormant season' should not be overlooked.

In contrast to evergreen shrub communities, the mesic community studied here represents an important resource for Arctic herbivores (Chapin III et al., 1996). Widespread icing may thus affect plant-herbivore interactions in opposite ways: directly by limiting food accessibility during winter (Hansen et al., 2013; Langlois et al., 2017) but also indirectly by shifting phenology (e.g. phenological mismatches; Doiron et al., 2015; Post et al., 2009) and subsequently increasing summer forage availability.

Although our pioneer multi-year experiment revealed measurable effects, their magnitude remained moderate, highlighting the relatively high tolerance of the plants to icing and summer warming, which contributes to community resistance to these potential drivers of change (Finne et al., 2025; Hudson & Henry, 2010; Jónsdóttir et al., 2023). However, our 60×60 cm basal ice plots may not fully capture processes during large-scale icing events. For instance, anoxia could be more severe without edge effects, potentially causing asphyxiation of plants, arthropods and microorganisms (Coulson et al., 2000; Crawford et al., 1994). Likewise, effects on soil thermal properties might be stronger in natural conditions, potentially amplifying the responses observed here.

5 | CONCLUSIONS

High Arctic environments are naturally variable, and plants have developed elaborate strategies to persist under these extreme conditions, resulting in communities that are highly resistant to climate change, despite measurable impacts (Jónsdóttir et al., 2023). This study has shown that the impact of winter rain-on-snow and associated tundra icing can be of similar extent as summer warming, but without causing dramatic die-off. Following up on over 30 years of ITEX experimentation across the tundra biome, providing critical knowledge on tundra responses to summer warming (Henry et al., 2022; Hollister et al., 2023), we call for the implementation of similar coordinated, distributed experiments investigating effects of winter warming and rain-on-snow events in particular.

AUTHOR CONTRIBUTIONS

Brage Bremset Hansen, Øystein Varpe, Ingibjörg Svala Jónsdóttir, René Van der Wal, Mathilde Le Moullec and Matteo Petit Bon conceived the ideas and designed methodology; Mathilde Le Moullec, with the help of all authors, collected the data; Mathilde Le Moullec, with the help of Anna-Lena Hendel analysed the data; Mathilde Le Moullec led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data deposited in the open access Dryad Digital Repository at https://doi.org/10.5061/dryad.9ghx3ffxx (Le Moullec et al., 2025).

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SUPPORTING INFORMATION

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

Table S1: Summary statistics of summer soil temperature and volumetric water content.

Table S2: Sampling dates and number of repeated measurements.

Table S3: Summary statistics of NDVI metrics.

Table S4: Summary statistics of the abundance of vascular plants.

Table S5: Correlation coefficients between maximum NDVI and abundance.

Table S6: Summary of leaf trait statistics for *Salix polaris*.

Table S7: Summary statistics of the day-of-year a certain phenophase is reached ('timing').

Table S8: Summary statistics of time spent in a certain phenophase ('duration').

Table S9: Summary statistics of flower counts.

Figure S1: Mesic habitat species composition.

Figure S2: Immediate icing treatment effect on soil temperature.

Figure S3: Estimated NDVI curves across treatments and years.

Figure S4: Salix *polaris* phenology.

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