

Local snow melt and temperature—but not regional sea ice—explain variation in spring phenology in coastal Arctic tundra

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Abstract

The Arctic is undergoing dramatic environmental change with rapidly rising surface temperatures, accelerating sea ice decline and changing snow regimes, all of which influence tundra plant phenology. Despite these changes, no globally consistent direction of trends in spring phenology has been reported across the Arctic. While spring has advanced at some sites, spring has delayed or not changed at other sites, highlighting substantial unexplained variation. Here, we test the relative importance of local temperatures, local snow melt date and regional spring drop in sea ice extent as controls of variation in spring phenology across different sites and species. Trends in long-term time series of spring leaf-out and flowering (average span: 18 years) were highly variable for the 14 tundra species monitored at our four study sites on the Arctic coasts of Alaska, Canada and Greenland, ranging from advances of 10.06 days per decade to delays of 1.67 days per decade. Spring temperatures and the day of spring drop in sea ice extent advanced at all sites (average 1°C per decade and 21 days per decade, respectively), but only those sites with advances in snow melt (average 5 days advance per decade) also had advancing phenology. Variation in spring plant phenology was best explained by snow melt date (mean effect: 0.45 days advance in phenology per day advance snow melt) and, to a lesser extent, by mean spring temperature (mean effect: 2.39 days advance in phenology per °C). In contrast to previous studies examining sea ice and phenology at different spatial scales, regional spring drop in sea ice extent did not predict spring phenology for any species or site in our analysis. Our findings highlight that tundra vegetation responses to global change are more complex than a direct response to warming and emphasize the importance of snow melt as a local driver of tundra spring phenology.

KEYWORDS

Arctic tundra, climate change, phenology, sea ice, snow melt, spring, temperature, vegetation

1 | INTRODUCTION

1.1 | The importance of phenology and global change

Changing phenology is considered one of the most apparent effects of climate change on natural systems worldwide (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; IPCC, 2014; Menzel et al., 2006; Parmesan & Yohe, 2003). Phenological processes control ecosystem functions (Ernakovich et al., 2014; Richardson et al., 2013), are linked through feedbacks to the climate system (Richardson et al., 2013) and contribute to structuring food webs through trophic interactions (Kharouba et al., 2018; Visser & Both, 2005). In high-latitude ecosystems, the onset of plant growth in spring and senescence in autumn is linked with ecosystem net productivity (Forkel et al., 2016; Park et al., 2016; Piao et al., 2008; Xu et al., 2013) and food availability for herbivores (Barboza, Van Someren, Gustine, & Bret-Harte, 2018; Doiron, Gauthier, & Lévesque, 2015; Gustine et al., 2017; Kerby & Post, 2013a, 2013b; Post et al., 2008). Varying phenological responses to environmental drivers among species or taxa, particularly in the highly seasonal Arctic tundra, yield a high potential for phenological mismatch (Doiron et al., 2015; Kerby & Post, 2013b; Piao et al., 2008) and shorter flowering seasons with warming (Prevéy et al., 2019). Tundra plants are temperature sensitive, especially at high latitudes (Prevéy et al., 2017), but no net advance in leaf or flowering phenology has been observed across the biome (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Oberbauer et al., 2013; Post, Kerby, Pedersen, & Steltzer, 2016) despite Arctic surface temperatures rising at twice the global average (IPCC, 2014; Winton, 2006). Instead, a more complex picture is emerging, highlighting a considerable amount of unexplained variation in phenology across sites, species and phenological events (Bjorkman et al., 2015; Oberbauer et al., 2013; Post & Høye, 2013; Post et al., 2016; Prévéy et al., 2017).

1.2 | Variation in plant phenology—what controls it?

A detailed understanding of which environmental variables serve as cues for Arctic spring phenology is key for explaining the absence of an overall trend in phenology across sites despite rapid warming and is critical for predicting future responses of Arctic ecosystems to the effects of climate and environmental change (Richardson et al., 2013). Interannual variation in tundra phenology has been attributed to variation in temperature (Bjorkman et al., 2015; Iler, Inouye, Schmidt, & Høye, 2017; Molau, Nordenhäll, & Eriksen, 2005; Oberbauer et al., 2013; Panchen & Gorelick, 2017; Prévéy et al., 2017; Wheeler, Høye, Schmidt, Svenning, & Forchhammer, 2015), snow melt (Bjorkman et al., 2015; Iler et al., 2017; Semenchuk et al., 2016) and sea ice (Kerby & Post, 2013a; Post et al., 2016). To date, no study has combined all three environmental variables to test the degree to which local snow melt, temperature and regional sea ice melt influence spring phenological events (leaf-out and flowering time) in the Arctic tundra across multiple coastal sites.

1.3 | Temperature as a driver

The environmental variable most widely used to explain variation in spring phenological events across latitudes and seasons is temperature (Post, Steinman, & Mann, 2018; Thackeray et al., 2016), including the phenology of both Arctic and alpine tundra plants (Bjorkman et al., 2015; Huelber et al., 2006; Iler et al., 2017; Kuoo & Suzuki, 1999; Molau et al., 2005; Oberbauer et al., 2013; Panchen & Gorelick, 2017; Prévéy et al., 2017; Thórhallsdóttir, 1998; Wheeler et al., 2015). Temperature influences phenology through increasing plant metabolism and development in response to warmer ambient temperatures (Jones, 2013). Average temperatures over a pre-defined period (Bjorkman et al., 2015; Iler et al., 2017; Panchen & Gorelick, 2017; Prévéy et al., 2017) as well as cumulative temperatures up to the onset of a phenological event (Barrett, Hollister, Oberbauer, & Tweedie, 2015; Henry & Molau, 1997; Huelber et al., 2006; Kuoo & Suzuki, 1999; Molau et al., 2005; Oberbauer et al., 2013; Wheeler et al., 2015) have been shown to explain variation in Arctic and alpine plant phenology. Species-specific minimum heat energy requirements for phenological progress have been suggested for tundra plants (Huelber et al., 2006; Molau et al., 2005), and the sensitivity of flowering to temperature has been shown to vary between sites and plots within tundra plant species (Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Prévéy et al., 2017). However, in highly seasonal tundra ecosystems, temperature is only one factor determining spring plant phenology.

1.4 | Snow melt as a driver

Snow melt timing has been recognized as early as the 1930s as a primary initiator of plant phenological events in both Arctic and alpine tundra (Schwartz, 2013; see, e.g., Billings & Mooney, 1968; Sørensen, 1941; Wipf & Rixen, 2010), and many recent studies have demonstrated that snow melt date is a key driver explaining variation in spring phenology in tundra ecosystems (Bjorkman et al., 2015; Cooper, Dullinger, & Semenchuk, 2011; Cortés et al., 2014; Iler et al., 2017; Molau et al., 2005; Semenchuk et al., 2016; Sherwood, Debinski, Caragea, & Germino, 2017; Wipf, 2009; Wipf, Stoeckli, & Bebi, 2009; but see Thórhallsdóttir, 1998). During snow melt, tundra plants experience dramatic changes in their immediate environment: light availability increases and plant and soil surfaces are exposed to atmospheric temperatures and CO₂ concentrations (Starr & Oberbauer, 2003), which in turn stimulate plant metabolic and developmental activities (Jones, 2013). In addition, snow melt may act as an indicator for suitable growing conditions to come as the growing season advances (Wheeler et al., 2015). Prior to melt, the insulation of the snow layer protects the plants from frost damage, desiccation and photoinhibition (Lundell, Saarinen, & Hänninen, 2010; Mølgaard & Christensen, 2003; Sherwood et al., 2017; Wheeler et al., 2015; Wipf & Rixen, 2010; Wipf et al., 2009) and reduces early-season herbivory (Wheeler et al., 2016), while after snow melt, the availability of soil moisture and nutrients is increased (Wipf & Rixen, 2010). Plants may therefore experience

strong evolutionary pressure to adapt spring metabolic activity to coincide directly with the timing of snow melt (Cortés et al., 2014). In fact, some species can begin development once the snow pack is thin enough to allow sufficient light and diurnal temperature variations (Larsen, Ibrom, Jonasson, Michelsen, & Beier, 2007; Starr & Oberbauer, 2003). Although spring temperatures influence the snow melt process, snow melt timing is a complex function of winter precipitation, topography, prevailing wind conditions and radiative exposure across the landscape (Billings & Bliss, 1959; Bjorkman et al., 2015; Molau & Mølgaard, 1996; Vaganov, Hughes, Kiryanov, Schweingruber, & Silkin, 1999; Wheeler et al., 2016) and can therefore be partially decoupled from spring temperatures (Bjorkman et al., 2015; Hinkler, Hansen, Tamstorf, Sigsgaard, & Petersen, 2008; Wheeler et al., 2015). Localized variation in snow cover therefore causes heterogeneity in spring plant phenology across the tundra landscape with pronounced differences in timing observed between snow beds and areas with sparse snow cover (Cooper et al., 2011).

1.5 | Sea ice as a driver

Variation in tundra phenology and productivity has also been attributed to sea ice conditions, including the Northern Hemisphere annual minimum sea ice extent and January mean extent (Bhatt et al., 2010; Forchhammer, 2017; Kerby & Post, 2013a; Macias-Fauria, Karlsen, & Forbes, 2017; Macias-Fauria & Post, 2018; Post et al., 2013, 2016). Macias-Fauria et al. (2017) found linkages between regional sea ice conditions and satellite-derived early-season vegetation productivity on eastern Svalbard and suggested that cool sea breeze off sea ice along the adjacent coast may influence land surface temperatures through cold air advection (Haugen & Brown, 1980). The presence of sea ice in coastal environments could also influence atmospheric humidity (Screen & Simmonds, 2010) and light availability through cloud and fog formation during spring ice melt (Tjernström et al., 2015), thus providing a plausible mechanism that could explain plant phenology at coastal tundra sites separately to the influence of sea ice on local temperatures via sea breeze. Alternatively, sea ice conditions could be an aggregate indicator of synoptic atmospheric circulation at regional to continental scales (Kerby & Post, 2013a; Macias-Fauria & Post, 2018; Post et al., 2013) and may not have a direct and localized mechanistic link as a control over tundra plant phenology.

In this study, we test the importance of temperature, snow melt and the spring drop in regional sea ice extent as controls over variation in spring plant phenology using a data set of plant phenology observations on 14 species spanning up to 21 years at four coastal tundra sites. Specifically, we address the following three questions: (a) To what extent do trends in plant spring phenological events vary among sites and species? (b) How have the environmental conditions changed at each site over the time period of monitoring? (c) What is the relative explanatory power of snow melt date, spring temperatures and the date of spring drop in regional sea ice extent in a multipredictor model of spring phenology at the study sites? Our analysis therefore allows us to test the strength of the statistical

relationships among the three most commonly suggested cues for tundra spring plant phenology across tundra species and sites: temperature, snow melt and sea ice, and will contribute to improved predictions of the response of tundra plant communities to changing growing conditions.

2 | MATERIALS AND METHODS

2.1 | Phenological observations

The observations of phenology used in this paper are a subset of the most recent version of the International Tundra Experiment (ITEX; Henry & Molau, 1997; Webber & Walker, 1991) phenology control data set (Prevéy et al., 2017). The data set is openly available via the Polar Data Catalogue (CCIN Reference Number 12722, www.polar-data.ca/pdcsearch/PDCSearchDOI.jsp?doi_xml:id=12722) and was originally compiled by Oberbauer et al. (2013). All observations were recorded according to methods outlined in the ITEX Manual (Molau & Mølgaard, 1996). See also Oberbauer et al. (2013) and Prévéy et al. (2017), as well as Bjorkman et al. (2015), Cooley, Eckert, and Gordon (2012), Hollister, Webber, and Tweedie (2005) and Schmidt, Mosbacher, et al. (2016) for site-specific descriptions of methods. We obtained a subset of the ITEX data set for coastal sites by exclusion based on the following criteria: (a) coastal proximity (<3 km from the sea), (b) data record spanning more than 10 years and (c) snow melt timing data available. Four sites met these criteria: Alexandra Fiord (NU, Canada), Qikiqtaruk—Herschel Island (YT, Canada), Utqiagvik—formerly Barrow (AK, USA) and Zackenberg (Greenland). We have included additional 2016 data for the Qikiqtaruk site and plot-level data for the Zackenberg site.

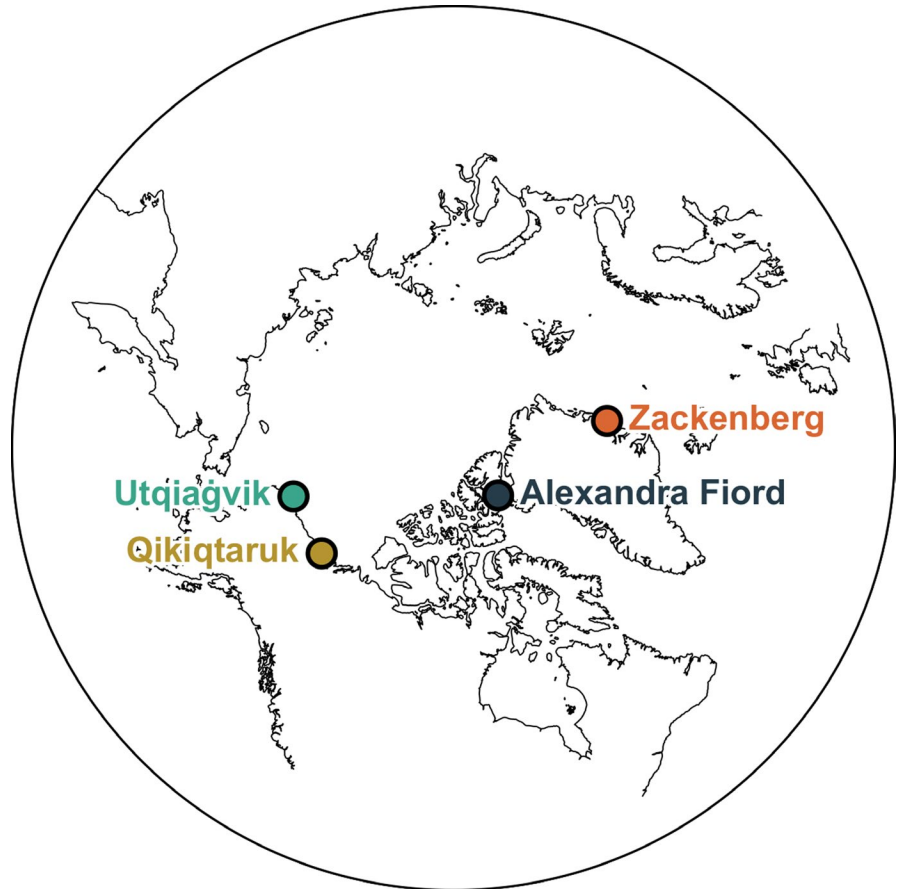
2.2 | Site descriptions

The selected sites include mid-Arctic (Qikiqtaruk and Utqiagvik) and high-Arctic (Alexandra Fiord and Zackenberg) sites and cover a wide geographical range (Figure 1) and diversity of tundra types, climate, topography and soil properties (Table S1): Alexandra Fiord (75.92 W, 78.88 N) on Ellesmere Island has dwarf shrub-dominated tundra communities on glacio-fluvial sediment composed of mixtures of granitic and carbonate rocks; Utqiagvik (156.62 W, 71.317 N) consists of wet meadow and heath tundra on ice-rich permafrost; the vegetation at Qikiqtaruk (138.91 W, 69.57 N) is dwarf shrub- and forb-dominated tundra on ice-rich permafrost; and the Zackenberg (20.56 W, 74.47 N) site is dwarf shrub-dominated tundra on noncarbonated bedrock.

2.3 | Selected species and phenological events

Our final subset of the ITEX data contained 14 species (*Cassiope tetragona* D.Don, *Dupontia psilosantha* Ruprecht, *Dryas integrifolia* Vahl, *Dryas octopetala* L., *Eriophorum vaginatum* L., *Luzula arctica* Blytt, *Luzula confusa* Lindeb., *Oxyria digyna* Hill, *Papaver radicum* Rottb., *Poa arctica* R.Br., *Salix arctica* Pall., *Salix rotundifolia* Trautv.,

FIGURE 1 Locations of the four sites included in this study: Alexandra Fiord (NU, Canada), Qikiqtaruk (YT, Canada), Utqiagvik (AK, USA) and Zackenberg (Greenland) [Colour figure can be viewed at wileyonlinelibrary.com]



Saxifraga oppositifolia L., *Silene acaulis* (L.) Jacq.), which represent the dominant plants in the communities at the selected sites. We selected all species-phenological event combinations that occurred in spring (mean phenological event occurring within 30 days of mean snow melt at each site). For Utqiagvik and Qikiqtaruk, this selection resulted in 38 and 2 species-phenological event combinations, respectively. To balance the sample size across sites, we narrowed down the Utqiagvik subset by selecting only species that make up at least 10% of the ITEX community composition plots at the site and extended the Qikiqtaruk data set by one additional species with the next earliest mean phenological event in the record of the site. The final subset contained a total of 8,469 observations for 14 species and two phenological events (spring green up and flowering), resulting in a total of 24 unique site-species-phenological event combinations (Table 1). Phenological events were defined differently for each plant species (Molau & Mølgaard, 1996), but recorded consistently over time (Prevéy et al., 2017). Depending on the species, “green up” was defined as the date of leaf emergence—the date when the first leaf was visible or open, and “flowering” was defined as the date when either the first flower was open, the first pollen was visible, or the first anthers were exposed (Prevéy et al., 2017).

2.4 | Snow melt dates

Snow melt dates were determined at the plot or site level with site-specific protocols based on guidelines in the ITEX manual (Molau &

Mølgaard, 1996). Alexandra Fiord snow melt dates were recorded for each plot as the first day of year (DOY) at which at least 90% of the plot was snow free. Twenty per cent of the snow melt dates at Alexandra Fiord were unobserved. The missing values were gap-filled as detailed in Bjorkman et al. (2015). Utqiagvik snow melt dates were based on visual observations of when the plot was 100% snow free or soil surface temperatures when snow melt occurred in years prior to visual estimates. Snow melt dates on Qikiqtaruk were determined for each monitored plant individual or plot and recorded as the first date in the year when the individual or plot area was >90% snow free (Cooley et al., 2012). Zackenberg snow melt dates were determined by multiple visits to the designated plant phenology plots across the landscape. Snow melt dates were defined as the day at which 50% bare ground was first visible at a given plot (Schmidt, Hansen, Hansen, Hansen, Berg, & Meltofte, 2016). As not all plant phenology plots at Zackenberg were included in the snow melt observations, we used the mean snow melt date of the monitored plots to predict spring phenology at the site. The variation in methods for recording snow melt is due to the use of different protocols for long-term snow melt monitoring across these sites.

2.5 | Spring temperatures

Daily average air temperatures were obtained from local weather stations (Table S2) and annual “spring” averages calculated for each site-species-phenological event time series. We defined spring average

TABLE 1 Full species names, phenological event, start, end and length of time series in years, years with observations in the time series and colours used for the site-species-phenological event combinations in the data set [Colour table can be viewed at wileyonlinelibrary.com]

Site name	Species	Phenological event	Start year	End year	Time-series length (years)	Years with observ.	Colour
Alexandra Fiord	<i>Dryas integrifolia</i>	Flowering	1993	2013	21	15	
	<i>Dryas integrifolia</i>	Green up	1993	2013	21	14	
	<i>Luzula</i> spp.*	Flowering	1992	2003	12	10	
	<i>Oxyria digyna</i>	Flowering	1992	2013	22	18	
	<i>Oxyria digyna</i>	Green up	1992	2013	22	18	
	<i>Papaver radiculatum</i>	Flowering	1992	2013	22	18	
	<i>Papaver radiculatum</i>	Green up	1992	2013	22	18	
	<i>Salix arctica</i>	Flowering	1995	2013	19	14	
Utqiagvik	<i>Cassiope tetragona</i>	Green up	1997	2014	18	12	
	<i>Dupontia psilosantha</i>	Green up	1995	2014	20	14	
	<i>Luzula arctica</i>	Flowering	1994	2014	21	14	
	<i>Luzula arctica</i>	Green up	1994	2014	21	14	
	<i>Poa arctica</i>	Green up	1994	2014	21	15	
	<i>Salix rotundifolia</i>	Flowering	1994	2014	21	15	
	<i>Salix rotundifolia</i>	Green up	1994	2014	21	15	
Qikiqtaruk	<i>Dryas integrifolia</i>	Flowering	2001	2016	16	16	
	<i>Eriophorum vaginatum</i>	Flowering	2002	2016	15	15	
	<i>Salix arctica</i>	Green up	2001	2016	16	16	
Zackenberg	<i>Cassiope tetragona</i>	Flowering	1996	2011	16	16	
	<i>Dryas octopetala</i>						
	<i>Papaver radiculatum</i>						
	<i>Salix arctica</i>						
	<i>Saxifraga oppositifolia</i>						
	<i>Silene acaulis</i>						

*Includes *L. arctica* and *L. confusa*.

temperature as the mean daily temperature within a calendar year from the earliest snow melt date on record to the day at which 75% of the phenological event had occurred across the whole length of the time series. Each time series therefore had its own specific time frame across which temperatures were averaged. The period was chosen to capture a static time window during which the plants are likely to strongly respond to ambient temperatures for each given phenological event. For cross-site comparison of spring temperature change, we calculated spring averages using the same approach but applied to the pooled phenology time-series data for each site. These site-specific spring temperatures therefore represent the yearly temperatures from the day of snow melt to the day when 75% of phenological events occurred within the community across the record of the site.

2.6 | Day of spring drop in regional sea ice extent

We decided to use the date of spring drop in regional sea ice extent as it represents the shift from ice-covered to “ice-free” ocean (the minimum sea ice extent in a given year) in the region surrounding the

study site, and hence a change in microclimatic conditions that may act as phenological cues to the tundra plants at our study sites. We hypothesized that, if sea ice influences plant phenology due to changing light and moisture availability, the time point at which the system shifts its state would carry the highest explanatory power for spring plant phenology at the sites. If air temperatures alone act as the proximate cue, any influence of sea ice on air temperatures would appear as an effect of temperature in our statistical analysis. We also tested the model using average regional sea ice extent for the period including the months of May, June and July (Table S3) and found consistent results to the model with spring drop in sea ice extent.

The yearly spring drop in sea ice extent was determined from the NOAA/NSIDC Climate Data Record (CDR) v3 Passive Microwave Sea Ice Concentrations (Meier et al., 2017; Peng, Meier, Scott, & Savoie, 2013) projected in the NSIDC polar stereographic grid (NSIDC, 2018). We calculated daily regional sea ice extent for each site within a bounding box of 21 × 21 grid cells (approximately 525 km × 525 km) centred on the cell containing the study site. We used sea ice extent, rather than raw sea ice concentrations, as

it provides a more reliable measure during melt (Worby & Comiso, 2004). To avoid effects of land overspill (Cavalieri, Parkinson, Gloersen, Comiso, & Zwally, 1999), we removed all cells that were directly adjacent to the coastline, retaining only cells that were at least one cell removed from land. Daily regional sea ice extent was calculated as the total area of cells within the bounding box with a sea ice concentration of at least 15%. The day associated with the regional spring drop in sea ice extent was then determined as the DOY closest to the annual minimum on which the sea ice extent drops below 85% of the total area (Figure S4 and Table S5). Our measure therefore only selects the final melt event leading up to the annual minimum in the region and allows for fluctuations of the regional extent above and below 85% prior to the final melt event.

2.7 | Statistical analysis

We estimated slope parameters for the temporal trends in plant phenological events and environmental predictors using interval-censored and Gaussian-response Bayesian hierarchical models, respectively, from the MCMCGLMM package (Hadfield, 2010) in the R Statistical Environment version 3.4.3 (R Core Team, 2018). We also used interval-censored hierarchical models using to conduct variance partitioning of the environmental predictors on spring phenology.

2.8 | Interval-censored phenology observations

For the interval-censored models (Bjorkman et al., 2015; Hadfield, Heap, Bayer, Mittell, & Crouch, 2013), we defined the upper interval bound as the DOY at which the phenological event was first observed. Lower bounds were defined depending on whether prior visits to the monitored individuals/plots were recorded or not. For Alexandra Fiord, Utqiagvik and Zackenberg, no record of prior visits was available and the lower bound was set to the last day at which an observation was recorded at the site prior to the event. The Qikiqtaruk data set included records of all dates the plots were visited, independent of whether a phenological event was observed or not. We used the last recorded visit prior to the observed phenological event to define the lower bounds of the interval at this site. For phenological observations at the beginning of the year, the lower bound was set as the minimum snow melt date recorded at the relevant site across the whole study period. The mean interval length between observations was 3.2 days for Qikiqtaruk, 3.8 days for Alexandra Fiord and Utqiagvik and 6.5 days for Zackenberg.

2.9 | Phenology trends

Slope estimates for trends in phenological events were determined using a separate model for each site-species-phenological event combination with the following structure:

$$\text{unif}[y_{\text{lo}}, y_{\text{up}}] = \mu + \beta_{\text{year}} + \alpha_{\text{plot}} + \alpha_{\text{year}} + \epsilon$$

where y_{lo} and y_{up} are the lower and upper bounds of the interval in which the phenological event occurred, with a uniform likelihood of occurrence across the interval; μ is the global intercept; β_{year} is the slope parameter for the trend across years; α_{plot} and α_{year} are the random intercepts for plot and year, respectively; and ϵ is the residual error. α_{plot} , α_{year} and ϵ were normally distributed with a mean of zero and a variance estimated from the data. We included plot and year as categorical random intercepts to account for the replication of phenological observations at each plot over time and at each site in each year.

2.10 | Environmental predictor trends

Trends in annual mean day of snow melt, site-specific spring temperature and spring drop in regional sea ice extent were modelled individually for each site with the following model formula:

$$y = \mu + \beta_{\text{year}} + \epsilon$$

where y is the value of the environmental predictor for a given year; μ is the global intercept of the model; β_{year} is the slope parameter for the trend across years; and ϵ is the residual error. ϵ was distributed normally around zero with a variance estimated from the data. We did not include a random intercept for year or plot, as there was no within-year replication of the site-specific environmental variables.

We used weakly informative priors for all parameter estimates (inverse Wishart priors for residual variances and normal priors for the fixed effects) when modelling the trends in phenological events and environmental predictors (Hadfield, 2017). Convergence of these models was assessed through examination of the trace plots.

2.11 | Prediction analysis

We used a single global model for all site-species-phenological event combinations to estimate the effect of the environmental predictors on spring phenological events. The predictor variables were within-subject mean centred for each site-species-phenological event combination (van de Pol & Wright, 2009) and scaled by the standard deviation to allow for direct comparison between the effect sizes (Schielzeth, 2010). The model was structured as follows:

$$\begin{aligned} \text{unif}[y_{\text{lo},i}, y_{\text{up},i}] = & \bar{\mu} + \bar{\beta}_{\text{snow}} + \bar{\beta}_{\text{temp}} + \bar{\beta}_{\text{ice}} + \bar{\beta}_{\text{year}} + \beta_{\text{snow},i} + \beta_{\text{temp},i} + \beta_{\text{ice},i} \\ & + \beta_{\text{year},i} + \alpha_{\text{site}} + \alpha_{\text{plot}} + \alpha_{\text{year}} + \alpha_{\text{site:year}} + \epsilon \end{aligned}$$

where $y_{\text{lo},i}$ and $y_{\text{up},i}$ are the upper and lower bounds of the interval in which a phenological event of the site-species-phenological event combination i occurred, with a uniform likelihood of occurrence across the interval; $\bar{\mu}$, the global intercept; $\bar{\beta}_{\text{snow}}$, $\bar{\beta}_{\text{temp}}$, $\bar{\beta}_{\text{ice}}$ and $\bar{\beta}_{\text{year}}$, the mean slope parameters for snow melt, spring temperature, day of spring drop in sea ice extent and year, respectively; $\beta_{\text{snow},i}$, $\beta_{\text{temp},i}$, $\beta_{\text{ice},i}$ and $\beta_{\text{year},i}$, the site-species-phenological event-specific slopes for snow melt, spring temperature, spring drop in sea ice extent and year, respectively; α_{site} , α_{plot} , α_{year} and $\alpha_{\text{site:year}}$, the random intercepts for site, plot, year and site-year interaction; and ϵ , the residual error. The

random intercepts and the residual error were normally distributed around a mean of zero with variances estimated from the data.

For each fixed effect x , the site-species-phenological event-specific effects ($\beta_{x,i}$) were drawn from a normal distribution with estimated variance around the mean slope $\bar{\beta}_x$ of the fixed effect. We included year as a continuous predictor to account for the effects of variables that have changed linearly over years and were not included in the analysis in addition to the modelled fixed effects (Iler et al., 2017; Keogan et al., 2018). Furthermore, we added random intercepts for plot and year to account for the nonindependence of plots measured repeatedly over time as well as the nonindependence of observations conducted in the same year at a given site. Finally, a year-site interaction was included to allow for the year effect to vary among locations. Our model does not allow for: (a) a correlation of responses across species at a site, (b) the correlation of species responses across sites and (c) the correlation of a species' response across phenological events. We did not consider interactions between the environmental predictors, as we had no a priori prediction of a consistent directional interaction effect that would apply across species and locations.

The random slope and intercept parameters of the prediction analysis model were estimated using an unstructured covariance matrix, which allowed for covariance between slopes and the intercept (Hadfield, 2017). We used weakly informative priors for all coefficients (parameter-expanded inverse Wishart priors for the variances and normal priors for the fixed effects). The prediction analysis model was run with four chains, and convergence was confirmed through examination of the trace plots and Gelman–Rubin diagnostics (Gelman & Rubin, 1992).

Environmental predictors were tested for multicollinearity with variance inflation factors using the R package *usdm* (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) prior to execution of the model runs. The variance inflation factors for all three variables were below 1.27, suggesting no problems with multicollinearity. The highest correlation coefficient was observed between spring temperatures and drop in sea ice extent (−0.38). We also ran reduced models of the global model, only containing a single environmental predictor (Table S10), which allowed us to test for indirect mechanisms linking two of the environmental predictors.

Due to the absence of plot-level snow melt observations at Zackenberg, the effect of snow melt at the Zackenberg site is solely due to among-year variation, whereas at Alexandra Fiord, Utqiagvik and Qikiqtaruk, the effect of snow melt is affected by both among-year and among-plot variation. Hence, our modelled estimates of the day of snow melt effect at Zackenberg may be biased earlier or later due to the loss of within-site variation in snow melt date. We also ran the model with average annual snow melt values for all sites and observed comparable results to the original model with a slight reduction in the explanatory power for snow melt date (Table S3). Our original model may therefore be underestimating the effect of snow melt date at the Zackenberg site.

We refer to environmental predictors and trends as “significant” when the 95% credible interval (CI) for the corresponding parameter of the fitted models did not overlap zero. Code and data are available

at the following repository: <https://github.com/jakobjassmann/coastalphenology>.

3 | RESULTS

We observed strong variation in both the timing of annual mean spring phenological events and their trends across the study periods for all species-phenological event combinations and sites (Figure 2). While the trends indicate that spring is advancing overall at Qikiqtaruk and Zackenberg, not all species or phenological events showed significant trends at the two sites. In addition, we found little to no evidence for changes in the onset of spring at Alexandra Fiord and Utqiagvik. Estimated rates of change varied from an advance of 10.06 days per decade (CI: −18.77, −1.35 for *Cassiope tetragona* flowering at Zackenberg) to a delay of 1.67 days per decade (CI: −2.61, 5.86 for *Oxyria digyna* flowering at Alexandra Fiord), with five site-species-phenological event combinations advancing significantly and 19 combinations showing no significant change (Table S6).

The observed trends in environmental predictors indicate notable changes in spring climate and environment at all sites across the study periods (Figure 3). Snow melt dates advanced by 8.15 days per decade (CI: −16.19, 0.31) at Qikiqtaruk and by 10.22 days per decade (CI: −22.51, 2.06) at Zackenberg, but the trends were marginally non-significant. No change was observed at Alexandra Fiord (−0.61 days per decade; CI: −4.19, 2.98) and Utqiagvik (−1.41 days per decade; CI: −6.24, 3.46; Table S8). Average spring temperatures across the site-specific spring periods increased significantly at all sites during the years monitored, respectively, with Qikiqtaruk experiencing the strongest trend of 2.30°C warming per decade (CI: 0.78, 3.83) and Alexandra Fiord experiencing the weakest trend of 0.63°C warming per decade (CI: 0.01, 1.24; Table S8). The date of spring drop in sea ice advanced for all sites, roughly mirroring the trends in temperature with onset dates becoming earlier by −10.28 days per decade (CI: −56.07, 34.36; at Zackenberg) to −46.39 days per decade (CI: −73.21, −19.40; at Qikiqtaruk; Table S8). However, the variation in onset of sea ice melt among years was substantial for all sites and particularly high for Zackenberg, and only the declining trend at Qikiqtaruk was statistically significant (Figure 3, Table S8).

Snow melt date consistently predicted phenology (Figures 4 and S9) with a mean scaled effect size of 3.26 (CI: 2.63, 3.91), corresponding to 0.45 days advance in phenology per day advance in snow melt. The variance in snow melt date slopes among site-species-phenological event combinations was 1.82 (CI: 0.89, 3.55), with 95% of the site-species-phenological event combinations predicted to fall in the range of 0.09–0.82 days advance in phenology per day advance in snow melt. Temperature explained variation in spring phenology for some, but not all, species-phenological event combinations with a mean scaled effect size of −2.21 (CI: −3.04, −1.39) and associated slope variance of 3.15 (CI: 1.51, 6.10). This result corresponds to 2.39 days advance in phenology per °C increase and 95% of the site-species-phenological event combinations fell between

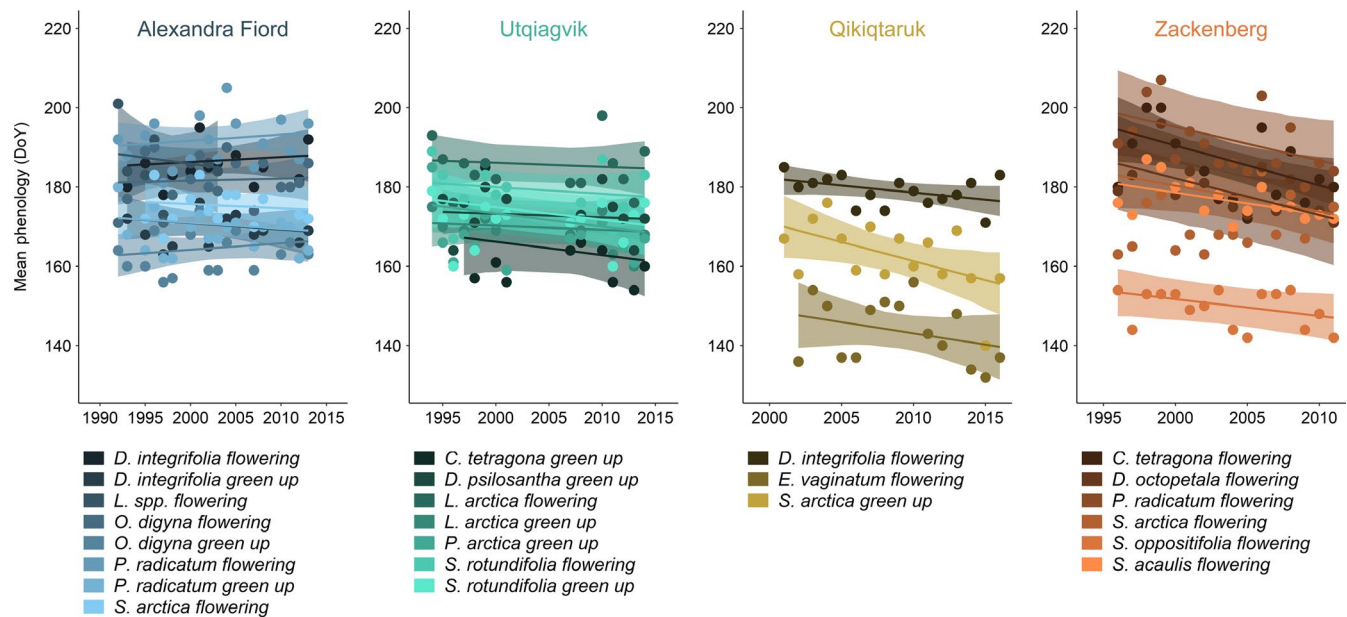


FIGURE 2 Advancing phenology trends were observed for some but not all species and sites. Annual mean spring phenology and trends for the species-phenological event combinations at Alexandra Fiord, Utqiagvik, Qikiqtaruk and Zackenberg. Trend lines were fitted with Bayesian interval-censored models, and shaded areas indicate 95% credible intervals. For a detailed list of the phenological event and species combinations monitored, see Table 1. For graphical clarity, the credible intervals for the *Silene acaulis* flowering time series at Zackenberg are not shown. A low number of plot-level estimates with high variation in trends resulted in high uncertainties of the model estimates for this time series. See Figure S7 for a plot including the credible intervals for the *S. acaulis* time series [Colour figure can be viewed at wileyonlinelibrary.com]

6.16 days advance and 1.38 days delay in phenology per °C increase. The spring drop in regional sea ice extent was a poor predictor of phenological timing in all cases with a mean scaled effect size of -0.01 (CI: $-0.94, 0.91$) and associated slope variance of 0.81 (CI: $0.28, 1.83$). This result corresponds to <0.01 days advance per day delay in regional drop in sea ice extent and 95% of the site-species-phenological event combinations fell between 0.07 days advance and 0.07 days delay per day delay in regional drop in sea ice extent. These findings are in broad agreement with the coefficients from the reduced models that tested each environmental predictor separately (Table S10).

Variation in phenological events of only one species-phenological event combination (*Dryas integrifolia* flowering at Qikiqtaruk) was not significantly explained by snow melt date, with the 95% confidence intervals overlapping zero for the posterior distributions for all three slope parameters (Figure 4 and Table S11). Eleven out of the twenty-four species-phenological event combinations were significantly explained by temperature: all Alexandra Fiord species-phenological event combinations, *Salix arctica* green up at Qikiqtaruk, *Cassiope tetragona* and *Salix arctica* flowering at Zackenberg (Table S11). Finally, the analysis highlighted high unexplained variance among unique site-year combinations (9.40, CI: 5.58, 14.72), which corresponds to 95% of site-year combinations being in the range of ± 6.01 days from the predicted values.

The multipredictor model indicated pronounced differences in the relative importance of the environmental predictors across plant communities at the different study sites and also within individual species found among different study sites. The differences were particularly

apparent for temperature, which predicted spring phenology for all species-phenological event combinations at Alexandra Fiord, but did not explain any variation in spring phenology at Utqiagvik and for some but not all species-phenological event combinations at Qikiqtaruk and Zackenberg (Figure 4). For the few species-phenological event combinations that overlapped across sites, some showed consistent responses to the environmental predictors, whereas others showed notable differences in the relative importance of the predictors across the study sites. For example, *Salix arctica* phenological events (flowering and green up) were consistently predicted by snow melt and temperature across the three sites where the species was monitored (Alexandra Fiord, Qikiqtaruk and Zackenberg), whereas *Dryas integrifolia* flowering showed contrasting responses between sites (Table S11). While *D. integrifolia* flowering was predicted by temperature and snow melt at Alexandra Fiord, neither of the two environmental factors was a significant predictor at Qikiqtaruk. Furthermore, the closely related *Dryas octopetala* at Zackenberg was predicted to respond to snow melt only (Table S11). Thus, substantial heterogeneity in controls on phenology between species and sites was highlighted by our study.

4 | DISCUSSION

Our test of the importance of temperature, snow melt and drop in spring sea ice extent as controls over coastal Arctic tundra plant phenology highlights three main findings: (a) trends in spring phenology were highly variable among species across these four sites

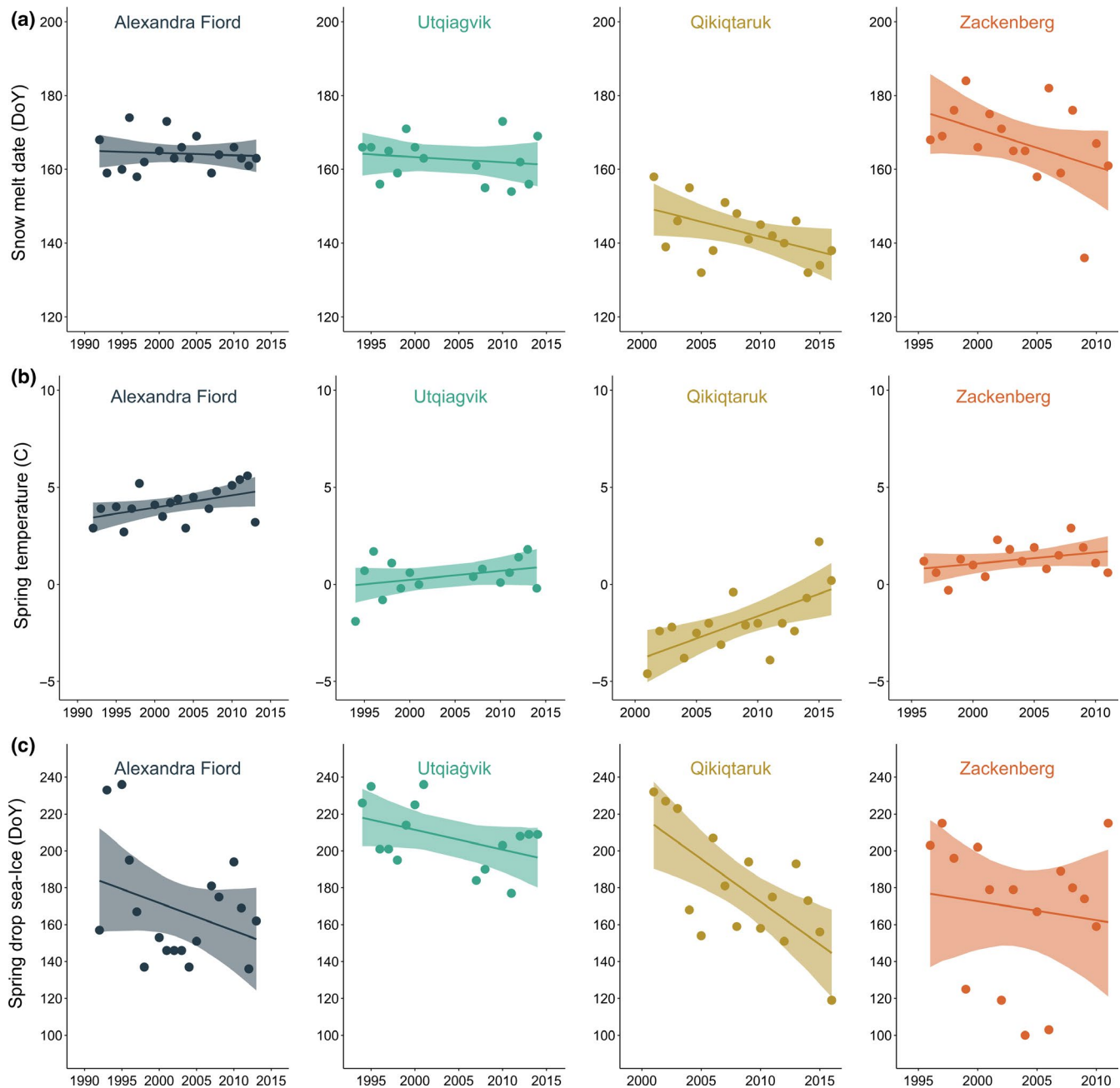


FIGURE 3 While spring drop in regional sea ice extent advanced and temperatures increased across sites and study periods, snow melt only advanced at some sites. Trends in site averages for snow melt date (a), “spring” temperature (b) and onset of regional sea ice melt (c) for Alexandra Fiord, Utqiagvik, Qikiqtaruk and Zackenberg for the years in the phenological records. Trend lines were fitted using Bayesian linear models, and shaded areas represent 95% credible intervals. “Spring” temperatures represent yearly averages of daily temperatures within the site-specific time frames from the earliest day of year of snow melt on record to the day of year where 70% of the spring phenological events occurred in the pooled community record of a given site. Due to these site-specific time frames, Alexandra Fiord represents the “warmest” spring temperatures despite being the northernmost site [Colour figure can be viewed at wileyonlinelibrary.com]

emphasizing the substantial heterogeneity in plant phenological response across tundra plant communities. (b) While all sites experienced pronounced advances in spring temperatures and onset of regional sea ice melt, spring phenology did not advance for all species and at all sites. Instead, spring phenology advanced only at sites with advancing snow melt (Qikiqtaruk and Zackenberg) and only for some species-phenological event combinations. (c) Localized

snow melt best explained variation in spring phenology among these coastal Arctic sites, suggesting that it is a key cue for spring leaf-out and early-season flowering in coastal tundra plant communities. Our findings confirm that timing of snow melt (Bjorkman et al., 2015; Cooper et al., 2011; Cortés et al., 2014; Iler et al., 2017; Kankaanpää et al., 2018; Molau et al., 2005; Semenchuk et al., 2016; Sherwood et al., 2017; Thórhallsdóttir, 1998; Wipf, 2009; Wipf et al.,

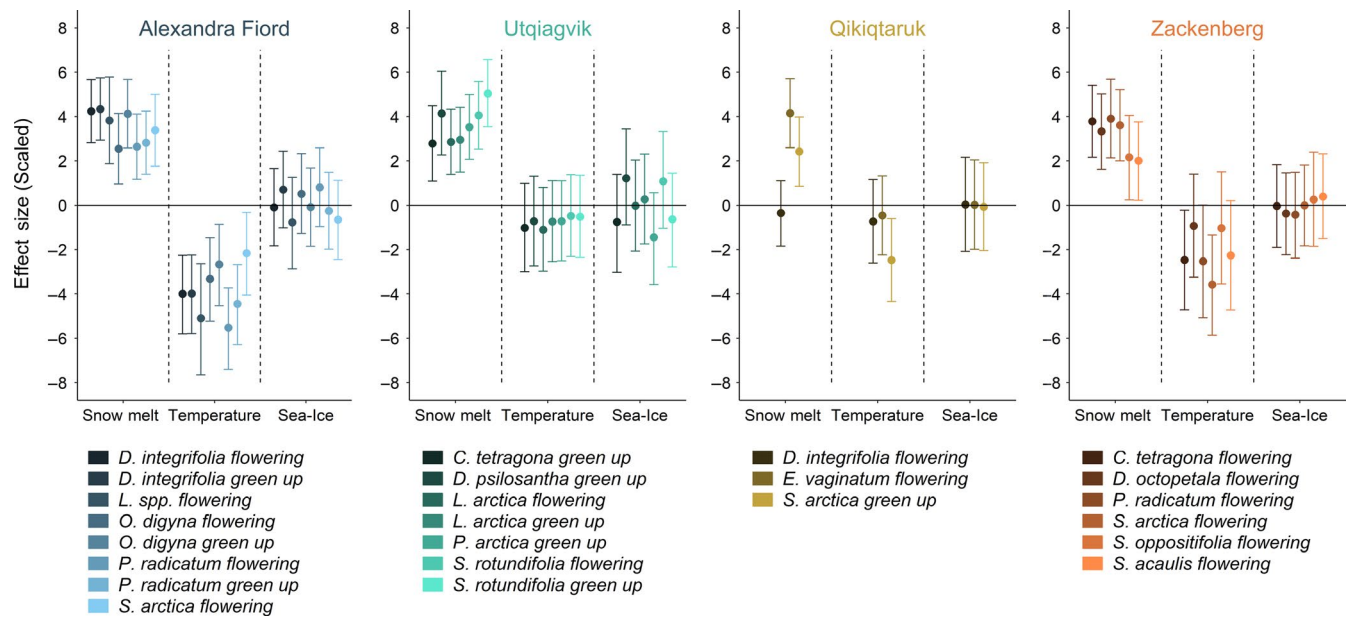


FIGURE 4 Snow melt date and temperature, but not the spring drop in regional sea ice extent, explained variation in phenology across species and sites. Scaled effect sizes, grouped by the environmental predictors (date of snow melt, average spring temperature and date of spring drop in regional sea ice extent), for all species-phenological event combinations at Alexandra Fiord, Utqiagvik, Qikiqtaruk and Zackenberg. Error bars represent 95% credible intervals. Effect sizes and credible intervals were estimated using a Bayesian hierarchical model. Environmental predictors were within-subject mean centred and scaled by the standard deviation (date of snow melt: 7.20, spring temperature: 0.92 and spring drop in regional sea ice extent: 26.90) [Colour figure can be viewed at wileyonlinelibrary.com]

2009), rather than a localized influence of sea ice, has important control over spring plant phenology in coastal tundra ecosystems. Furthermore, our results indicate that temperature, despite being the primary driver of spring plant phenology in temperate regions (Cleland et al., 2007; Thackeray et al., 2016; Wolkovich et al., 2012), holds less explanatory power for predicting spring phenology than snow in coastal tundra ecosystems of the Arctic.

4.1 | Snow melt needs to be included when studying tundra phenology in a global change context

Our results highlight the importance of local snow conditions in addition to temperature for the prediction of tundra plant phenological responses to global climate change. Despite snow melt being long considered an important driver of tundra plant phenology (Schwartz, 2013), to date, snow melt has yet to be incorporated into syntheses investigating plant phenology in response to global change across the tundra biome (Oberbauer et al., 2013; Prev  y et al., 2017) nor in cross-biome studies that include phenological observations from both tundra and temperate regions (Post et al., 2018; Wolkovich et al., 2012; Xu et al., 2013). Considering just spring temperature as predictor for tundra plant phenology will not capture key tundra ecosystem dynamics. Even though temperature is a primary driver of snow melt (Hinkler et al., 2008; Rango & Martinec, 1995), the timing of when Arctic and alpine tundra become snow free is a complex function of winter and spring atmospheric temperatures, precipitation, topography, solar radiation, wind velocity and the water vapour deficit that drives sublimation (Billings & Bliss, 1959; Cort  s

et al., 2014; Liston, Mcfadden, Sturm, & Pielke, 2008; MacDonald, Pomeroy, & Pietroniro, 2010; Molau et al., 2005; Pomeroy, Marsh, & Gray, 1997; Sturm et al., 2001; Vaganov et al., 1999; Wheeler et al., 2015). See also Bjorkman et al. (2015) and Hinkler et al. (2008) who discuss this partial decoupling of snow melt timing from temperature at the Zackenberg and Alexandra Fiord in more detail. It follows that excluding snow melt timing from any analysis that includes tundra spring plant phenology may therefore lead to unreliable predictions of phenological responses to global change in tundra ecosystems.

4.2 | Influence of snow melt highlights importance of landscape-level heterogeneity in phenology

The high explanatory power of snow melt date in this study and its inherently high spatial variability highlight the need to consider landscape heterogeneity in tundra phenology analyses (Kankaanp    et al., 2018). Landscape heterogeneity in phenology integrates a diversity of plant phenological responses and environmental controls (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016). Different plant species, populations and individuals differ in their phenology, and as communities change across the landscape, so too does community-level phenology (CaraDonna, Iler, & Inouye, 2014; Cleland et al., 2007; H  ye et al., 2013; Klosterman et al., 2018; Prev  y et al., 2019; Wolkovich, Cook, & Davies, 2014). The environmental controls on phenology may vary substantially across the landscape with topography and microclimate and so may the phenological responses of the plants to climate (H  ye et al., 2013). In

particular, snow melt timing can vary at plot and even subplot scales due to the localized interplay of microtopography, radiation and wind (Cortés et al., 2014; Sturm et al., 2001). The multitude of effects of melting snow cover on plant phenology through frost protection (Sherwood et al., 2017; Wheeler et al., 2015; Wipf & Rixen, 2010), modification of water availability (Wipf & Rixen, 2010) and temperature in the microclimate (Starr & Oberbauer, 2003) likely further contribute to landscape dynamics in tundra spring phenology. These localized dynamic effects may hold the key to understanding the high relative importance of snow melt as a driver of tundra spring phenology.

Individuals and populations of the same species may not only experience differences in the localized environmental cues, but may also show variation in the relative strength of their phenological responses to these cues, adding to the variation in phenology across the landscape (Høye et al., 2013; Post et al., 2009). The locality and distribution of phenological monitoring plots and observations of environmental variables therefore need to encompass landscape-level variation, to obtain representative estimates of species and community spring phenological events and drivers at any given site. Emerging technologies such as phenocams (Andresen, Tweedie, & Lougheed, 2018; Linkosalmi et al., 2016; Richardson et al., 2018), fine-scale aerial imagery from drones (Klosterman et al., 2018) and spatiotemporal modelling of snow properties (Pedersen, Liston, Tamstorf, Westergaard-Nielsen, & Schmidt, 2015) may help facilitate phenological and snow melt monitoring at the spatial grains, temporal frequencies and extents required to understand landscape- and community-level phenological change.

4.3 | Site-specific importance of temperature

Our findings suggest that the relative importance of the environmental predictors for coastal spring phenology can differ between sites, plant communities and species. Cross-site-level differences were particularly evident for temperature. The Alexandra Fiord site was the only site where phenology was consistently predicted by temperature. Prevéy et al. (2017) found that temperature explained tundra phenology better at sites with colder vs. warmer summers and suggested that this might be due to different evolutionary strategies required at colder sites. For example, a higher temperature sensitivity might be beneficial in optimizing rapid flower and seed development to facilitate the colonization of bare ground at higher latitude sites, where bare ground is often more common (Prevéy et al., 2017). On the other hand, CaraDonna and Inouye (2015) found no evidence for a phylogenetic signal for the strength in the responses of flowering to snow melt and temperature in a subalpine plant community. Høye et al. (2013) observed plot-specific responses of flowering to temperature within individual species at the Zackenberg site and proposed that variation in localized snow depth and below-ground conditions such as soil moisture and soil temperature could modify the plant's responses to air temperatures in contrast to evolutionary processes. As Alexandra Fiord is the northernmost site and a "warm oasis" in an otherwise harshly cold polar desert (Freedman, Svoboda,

& Henry, 1994), the effects of climate interactions may be reduced compared to warmer and wetter sites further south. However, the low number of sites in our study does not provide the statistical power to test the importance of cross-site differences. Therefore, further investigation is required to test whether localized adaptation or interactions with additional environmental factors are the cause of the variation in the relative importance of the environmental predictors of tundra spring plant phenology across the tundra biome.

4.4 | Spring drop in sea ice extent did not explain variation in phenology

The spring drop in sea ice extent did not explain spring phenology at the coastal tundra sites in our analysis. This was the case for the models that included spring drop in sea ice as the only environmental predictor (Table S10) as well as for the model containing all three environmental predictors. Thus, our findings suggest that there is neither a direct nor an indirect regional mechanism linking spring drop in sea ice to spring phenology at our study sites apart from via temperatures. Due to limited localized data availability, we were not able to directly test whether the sea-breeze mechanism proposed by Haugen and Brown (1980) and observed by Macias-Fauria et al. (2017) or other indirect sea ice drivers have a significant impact on plant spring phenology across our study sites. Thus, our study alone was not able to capture all of the potential complexities suggested by other studies of sea ice at regional to continental scales (Kerby & Post, 2013a; Macias-Fauria et al., 2017; Post et al., 2016).

The majority of previous studies that have attributed spring phenology variation and plant productivity to sea ice used large-scale integrative measures such as annual minimum global sea ice extent (Bhatt et al., 2010; Forchhammer, 2017; Kerby & Post, 2013a; Post et al., 2013, 2016). Phenology has previously also been linked to other integrative global measures such as ENSO or the North Atlantic Oscillation (NAO; Chmielewski & Rötzer, 2001; D'Odorico, Yoo, & Jaeger, 2002; Forchhammer, Post, & Stenseth, 1998; Scheifinger, Menzel, Koch, Peter, & Ahas, 2002). Although the integrative measures may correlate well with plant phenology, our findings highlight the value of directly testing interannual variation of localized ecological mechanisms. New data sets of winds, fog and other variables (Macias-Fauria et al., 2017; Tjernström et al., 2015) and analyses that can incorporate additional direct and indirect interactions among drivers will contribute to disentangling the complexity of patterns and trends in plant phenology observed in the tundra biome and beyond.

4.5 | The challenges of measuring localized sea ice conditions

Determining regional and interannual variation in the onset of sea ice melt can be challenging due to the lack of locally collected data. Globally available satellite products such as the passive microwave data set used in this study (Peng et al., 2013) struggle to detect the ice edge during the melt period (Comiso & Nishio, 2008; Worby &

Comiso, 2004) and suffer from land spillover in cells adjacent to the coastline (Cavalieri et al., 1999). More accurate manually interpreted data sets based on a mixture of data sources (including optical satellite data) such as those developed by national agencies for navigational purposes could be used, but are often available only for recent years (Canadian Ice Service, 2009) and/or are limited to specific geographical regions (<http://polarview.met.no>). We chose the passive microwave satellite data to estimate the timing of drop in spring sea ice extent as no other data were available for the entire time period and geographical extent of our study at a daily resolution. Due to our cautious preprocessing procedure, our measure of onset of sea ice melt from the NOAA/NSIDC CDR likely is a conservative estimate and might mask out some of the fine-scale temporal and spatial variations in the sea ice conditions in the different study regions. Thus, we caution that the interannual variation in regional sea ice extent may not be entirely comparable to higher-resolution temperature (site level) and snow melt estimates (site to plot level) used in this study. With advances in technology and growing interest in the northern maritime regions, higher quality sea ice data are becoming increasingly available in certain geographical regions (see, e.g., Macias-Fauria et al., 2017), and we encourage future studies to repeat our analyses using these data products when available.

4.6 | Photoperiod as a control on spring phenology

Our study was not able to address the separate effect of photoperiod as a control on spring phenology because of the lack of temporal variation required for an analysis such as we have employed here. Arctic and alpine plant phenology can be sensitive to photoperiod as suggested by common garden experiments (Bennington et al., 2012; Bjorkman, Vellend, Frei, & Henry, 2017; Parker, Tang, Clark, Moody, & Fetcher, 2017) and demonstrated in growth chamber experiments (Heide, 1989, 1992; Keller & Körner, 2003). Keller and Körner (2003) found day-length cues for flowering in 54% of the 20 studied alpine plant species and estimated a minimum day-length requirement of about 15 hr for plants adapted to their study site in the central Alps in Europe. It is therefore likely that minimum daylight requirements were met at all our study sites prior to snow melt: Alexandra Fiord, Barrow and Zackenberg already experienced 24 hr of daylight two weeks prior to the minimum snow melt date on record, and Qikiqtaruk experienced 14.5 hr of daylight with no night and only astronomical twilight during spring. However, increases in day length beyond the minimum requirement may accelerate development and phenology of Arctic and alpine plants (Keller & Körner, 2003) and dual requirements based on interactions of temperature and photoperiod have been documented in other studies (Heide, 1989). Thus, understanding the interactive nature of photoperiod and environmental cues on phenology, particularly in the context of lengthening growing seasons and range expansions with warming from lower latitudes with stronger diurnal light variation to high latitudes, remains a future challenge for tundra plant ecology.

4.7 | Phenology, trophic interactions and ecosystem change

Tundra plant phenology impacts ecosystem functions such as net primary productivity (Forkel et al., 2016; Piao et al., 2008; Xu et al., 2013), thereby creating feedbacks to the global climate system (Richardson et al., 2013). Our study underlines the importance of localized snow melt dates for spring plant phenology in coastal tundra ecosystems. Snow cover is projected to decrease across the Arctic (AMAP, 2017), but predicted changes in snow conditions differ in direction and magnitude among regions and seasons (AMAP, 2017). While high declines in snow cover are expected for warmer coastal areas and during spring, high-Arctic sites, such as Alexandra Fiord, are predicted to experience increases in the annual accumulation of snow (AMAP, 2017). Locally reduced spring snow cover could increase the susceptibility of plants to freezing events and damage due to photoinhibition (Lundell et al., 2010), affecting plant productivity, community composition and evolution through plant health and mortality (Bokhorst, Bjerke, Street, Callaghan, & Phoenix, 2011; Cortés et al., 2014; Jonas, Rixen, Sturm, & Stoeckli, 2008; Phoenix & Bjerke, 2016; Wheeler et al., 2016; Wipf & Rixen, 2010). Thus, quantifying the impact of plant phenology on productivity change over time is a key element to improved projections of tundra carbon storage and energy flux feedbacks to the global climate system (Park et al., 2016).

Tundra plant phenology influences resource availability for secondary consumers (Barboza et al., 2018; Doiron et al., 2015; Gustine et al., 2017; Kerby & Post, 2013b), and asynchronous shifts between interacting species due to climate change could result in trophic mismatches (Doiron et al., 2015; Kerby & Post, 2013a, 2013b; Schmidt, Mosbacher, et al., 2016). Locally reduced spring snow cover could decrease spatial variation in snow melt timing and thus lessen the extent of landscape-scale heterogeneity in plant phenology and shorten flowering duration (Prevéy et al., 2019), with potentially detrimental impacts on consumers, as these may rely on temporal and spatial variations in their food sources to maximize energy intake across the season (Armstrong et al., 2016; Moorter et al., 2013). This interaction between spatial and temporal patterning and trends in trophic mismatches has only rarely been explored in the tundra and other ecosystems (Bischof et al., 2012; Burgess et al., 2018; Sawyer & Kauffman, 2011). A comprehensive understanding of the mechanistic drivers of plant phenology, and how these drivers are changing over time, is therefore key to our ability to predict and manage the consequences of future environmental change in tundra ecosystems and beyond (Kharouba et al., 2018; Richardson et al., 2013; Thackeray, 2016; Thackeray et al., 2016; Wolkovich et al., 2014).

5 | CONCLUSIONS

The Arctic is warming more rapidly than any other region of the planet (IPCC, 2014), with well-documented consequences for tundra plant communities, including changes in community composition (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Elmendorf

et al., 2015; Ernakovich et al., 2014), trophic mismatch (Doiron et al., 2015; Gustine et al., 2017; Kerby & Post, 2013a, 2013b; Post, Pedersen, Wilms, & Forchhammer, 2008) and altered plant phenology (Høye, Post, Meltofte, Schmidt, & Forchhammer, 2007; Post et al., 2018). Our findings suggest that snow melt and temperature, but not spring drop in sea ice extent, are the dominant cues for spring phenology in coastal Arctic plant communities that experience short growing seasons and persistent snow cover. Later snow melt therefore can delay phenology, even when air temperatures are warming over time. Our findings further suggest that the relative importance of snow melt timing and temperature as predictors of tundra spring plant phenology may differ among communities, species and populations across the tundra biome. Together, these results highlight the growing evidence that tundra vegetation responses to rapid environmental change are more complex than a simple response to increasing temperatures and help explain the variation in phenological trends seen among tundra sites. Thus, to understand and better predict future tundra vegetation change and associated feedbacks on the global climate system, we require localized tests of the specific influences of mechanistic drivers of change. Our study illustrates the value of long-term monitoring programmes (sensu Hobbie et al., 2017; Myers-Smith et al., 2019; Post & Høye, 2013; Schmidt, Christensen, & Roslin, 2017) and cross-site data syntheses for quantifying site- and species-specific responses to environmental change. Only with quantitative tests carried out on comprehensive cross-site data sets, can we attribute variation in plant phenology to localized environmental cues and improve our predictions of tundra ecosystem responses to global change.

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