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Local snowmelt and temperature – but not regional seaice – explain variation in spring phenology in coastal Arctic tundra

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3

4   **Title**

5   Local snowmelt and temperature – but not regional sea-ice – explain variation in spring

6   phenology in coastal Arctic tundra

7

8   **Running head**

9   Snowmelt and temp. predict tundra phenology

10

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32   **Paper type**

33   Primary Research Article

34

35   **Abstract**

36   The Arctic is undergoing dramatic environmental change with rapidly rising surface

37   temperatures, accelerating sea-ice decline and changing snow regimes, all of which influence

38   tundra plant phenology. Despite these changes, no globally consistent direction of trends in

39   spring phenology has been reported across the Arctic. While spring has advanced at some

40   sites, spring has delayed or not changed at other sites, highlighting substantial unexplained

41   variation. Here, we test the relative importance of local temperatures, local snowmelt date

42   and regional spring drop in sea-ice extent as controls of variation in spring phenology across

43   different sites and species. Trends in long-term time-series of spring leaf out and flowering

44   (average span: 18 years) were highly variable for the 14 tundra species monitored at our four

45   study sites on the Arctic coasts of Alaska, Canada and Greenland, ranging from advances of

46   10.06 days per decade to delays of 1.67 days per decade. Spring temperatures and the day of

47   spring drop in sea-ice extent advanced at all sites (average 1 °C per decade and 21 days per

48   decade respectively), but only those sites with advances in snowmelt (average 5 days advance

49   per decade) also had advancing phenology. Variation in spring plant phenology was best

50   explained by snowmelt date (mean effect: 0.45 days advance in phenology per day advance

51   snowmelt) and, to a lesser extent, by mean spring temperature (mean effect: 2.39 days

52   advance in phenology per °C). In contrast to previous studies examining sea ice and

53   phenology at different spatial scales, regional spring drop in sea-ice extent did not predict

54   spring phenology for any species or site in our analysis. Our findings highlight that tundra

55   vegetation responses to global change are more complex than a direct response to warming

56   and emphasize the importance of snowmelt as a local driver of tundra spring phenology.

57

58   **Introduction**

59   *The importance of phenology and global change*

60   Changing phenology is considered one of the most apparent effects of climate change on

61   natural systems world-wide (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; IPCC,

62   2014; Menzel et al., 2006; Parmesan & Yohe, 2003). Phenological processes control

63   ecosystem functions (Ernakovich et al., 2014; Richardson et al., 2013), are linked through

64   feedbacks to the climate system (Richardson et al., 2013) and contribute to structuring food

65   webs through trophic interactions (Kharouba et al., 2018; Visser & Both, 2005). In high-

66   latitude ecosystems, the onset of plant growth in spring and senescence in autumn are linked

67   with ecosystem net productivity (Forkel et al., 2016; Park et al., 2016; Piao et al., 2008; Xu et

68   al., 2013) and food availability for herbivores (Barboza, Van Someren, Gustine, & Bret-

69   Harte, 2018; Doiron, Gauthier, & Lévesque, 2015; Gustine et al., 2017; Kerby & Post, 2013b,

70   2013a; Post, Pedersen, Wilmers, & Forchhammer, 2008). Varying phenological responses to

71   environmental drivers among species or taxa, particularly in the highly-seasonal Arctic

72   tundra, yield a high potential for phenological mismatch (Doiron et al., 2015; Kerby & Post,

73   2013b; Post et al., 2008) and shorter flowering seasons with warming (Prevéy et al., 2018).

74   Tundra plants are temperature sensitive, especially at high latitudes (Prevéy et al., 2017), but

75   no net advance in leaf or flowering phenology has been observed across the biome

76   (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Oberbauer et al., 2013; Post,

77   Kerby, Pedersen, & Steltzer, 2016) despite Arctic surface temperatures rising at twice the

78   global average (IPCC, 2014; Winton, 2006). Instead a more complex picture is emerging,

79   highlighting a considerable amount of unexplained variation in phenology across sites,

80   species and phenological events (Bjorkman et al., 2015; Oberbauer et al., 2013; Post & Høye,

81   2013; Post et al., 2016; Prevéy et al., 2017).

82

83   *Variation in plant phenology – what controls it?*

84   A detailed understanding of which environmental variables serve as cues for Arctic spring

85   phenology is key for explaining the absence of an overall trend in phenology across sites

86   despite rapid warming, and is critical for predicting future responses of Arctic ecosystems to

87   the effects of climate and environmental change (Richardson et al., 2013). Interannual

88   variation in tundra phenology has been attributed to variation in temperature (Bjorkman et al.,

89   2015; Iler, Inouye, Schmidt, & Høye, 2017; Molau, Urban Nordenhäll, & Bente Eriksen,

90   2005; Oberbauer et al., 2013; Panchen & Gorelick, 2017; Prevéy et al., 2017; H. C. Wheeler,

91   Høye, Schmidt, Svenning, & Forchhammer, 2015), snowmelt (Bjorkman et al., 2015; Iler et

92   al., 2017; Semenchuk et al., 2016) and sea-ice (Kerby & Post, 2013a; Post et al., 2016). To

93   date, no study has combined all three environmental variables to test the degree to which

94   local snowmelt, temperature and regional sea-ice melt influence spring phenological events

95   (leaf-out and flowering time) in the Arctic tundra across multiple coastal sites.

96

97   *Temperature as a driver*

98   The environmental variable most widely used to explain variation in spring phenological

99   events across latitudes and seasons is temperature (Post, Steinman, & Mann, 2018; Thackeray

100   et al., 2016), including the phenology of both Arctic and alpine tundra plants (Bjorkman et

101   al., 2015; Huelber et al., 2006; Iler et al., 2017; Kuoo & Suzuki, 1999; Molau et al., 2005;

102   Oberbauer et al., 2013; Panchen & Gorelick, 2017; Prevéy et al., 2017; Thórhallsdóttir, 1998;

103   H. C. Wheeler et al., 2015). Temperature influences phenology through increasing plant

104   metabolism and development in response to warmer ambient temperatures (Jones, 2013).

105   Average temperatures over a predefined period (Bjorkman et al., 2015; Iler et al., 2017;

106   Panchen & Gorelick, 2017; Prevéy et al., 2017) as well as cumulative temperatures up to the

107   onset of a phenological event (Barrett, Hollister, Oberbauer, & Tweedie, 2015; Henry &

108   Molau, 1997; Huelber et al., 2006; Kuoo & Suzuki, 1999; Molau et al., 2005; Oberbauer et

109   al., 2013; H. C. Wheeler et al., 2015) have been shown to explain variation in Arctic and

110   alpine plant phenology. Species-specific minimum heat energy requirements for phenological

111   progress have been suggested for tundra plants (Huelber et al., 2006; Molau et al., 2005) and

112   the sensitivity of flowering to temperature has been shown to vary between sites and plots

113   within tundra plant species (Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013;

114   Prevéy et al., 2017). However, in highly seasonal tundra ecosystems, temperature is only one

115   factor determining spring plant phenology.

116

117   *Snowmelt as a driver*

118   Snowmelt timing has been recognised as early as the 1930s as a primary initiator of plant

119   phenological events in both Arctic and alpine tundra (Schwartz, 2013; see for example

120   Sørensen, 1941; Billings & Mooney, 1968; Wipf & Rixen, 2010) and many recent studies

121   have demonstrated that snowmelt date is a key driver explaining variation in spring

122   phenology in tundra ecosystems (Bjorkman et al., 2015; Cooper, Dullinger, & Semenchuk,

123   2011; Cortés et al., 2014; Iler et al., 2017; Semenchuk et al., 2016; Sherwood, Debinski,

124   Caragea, & Germino, 2017; Molau et al., 2005; Wipf, 2009; Wipf, Stoeckli, & Bebi, 2009;

125 but see Thórhallsdóttir, 1998). During snowmelt, tundra plants experience dramatic changes

126 in their immediate environment: light availability increases and plant and soil surfaces are

127 exposed to atmospheric temperatures and CO_2 concentrations (Starr & Oberbauer, 2003),

128 which in turn stimulate plant metabolic and developmental activity (Jones, 2013). In addition,

129 snowmelt may act as an indicator for suitable growing conditions to come as the growing

130 season advances (H. C. Wheeler et al., 2015). Prior to melt, the insulation of the snow layer

131 protects the plants from frost damage, desiccation, photoinhibition (Lundell, Saarinen, &

132 Hänninen, 2010; Mølgaard & Christensen, 2003; Sherwood et al., 2017; H. C. Wheeler et al.,

133 2015; Wipf & Rixen, 2010; Wipf et al., 2009) and reduces early-season herbivory (J. A.

134 Wheeler et al., 2016), while after snowmelt the availability of soil moisture and nutrients is

135 increased (Wipf & Rixen, 2010). Plants may therefore experience strong evolutionary

136 pressure to adapt spring metabolic activity to coincide directly with the timing of snowmelt

137 (Cortés et al., 2014). In fact, some species can begin development once the snow pack is thin

138 enough to allow sufficient light and diurnal temperature variations (Larsen, Ibrom, Jonasson,

139 Michelsen, & Beier, 2007; Starr & Oberbauer, 2003). Although spring temperatures influence

140 the snowmelt process, snowmelt timing is a complex function of winter precipitation,

141 topography, prevailing wind conditions and radiative exposure across the landscape (Billings

142 & Bliss, 1959; Bjorkman et al., 2015; Molau & Mølgaard, 1996; Vaganov, Hughes,

143 Kirdyanov, Schweingruber, & Silkin, 1999; J. A. Wheeler et al., 2016), and can therefore be

144 partially decoupled from spring temperatures (Bjorkman et al., 2015; Hinkler, Hansen,

145 Tamstorf, Sigsgaard, & Petersen, 2008; H. C. Wheeler et al., 2015). Localised variation in

146 snow-cover therefore causes heterogeneity in spring plant phenology across the tundra

147 landscape with pronounced differences in timing observed between snow beds and areas with

148 sparse snow cover (Cooper et al., 2011).

149

150 *Sea ice as a driver*

151 Variation in tundra phenology and productivity has also been attributed to sea-ice conditions,

152 including the northern hemisphere annual minimum sea-ice extent and January mean extent

153 (Bhatt et al., 2010; Forchhammer, 2017; Kerby & Post, 2013a; Macias-Fauria, Karlsen, &

154 Forbes, 2017; Macias-Fauria & Post, 2018; Post et al., 2013, 2016). Macias-Fauria et al.

155 (2017) found linkages between regional sea-ice conditions and satellite derived early-season

156 vegetation productivity on eastern Svalbard and suggested that cool sea breeze off sea-ice

157 along the adjacent coast may influence land surface temperatures through cold air advection

158 (Haugen & Brown, 1980). The presence of sea ice in coastal environments could also

159 influence atmospheric humidity (Screen & Simmonds, 2010) and light availability through

160 cloud and fog formation during spring ice melt (Tjernström et al., 2015), thus providing a

161 plausible mechanism that could explain plant phenology at coastal tundra sites separately to

162 the influence of sea-ice on local temperatures via sea-breeze. Alternatively, sea ice conditions

163 could be an aggregate indicator of synoptic atmospheric circulation at regional to continental

164 scales (Kerby & Post, 2013a; Macias-Fauria & Post, 2018; Post et al., 2013) and may not

165 have a direct and localised mechanistic link as a control over tundra plant phenology.

166

167 In this study, we test the importance of temperature, snowmelt and the spring drop in regional

168 sea-ice extent as controls over variation in spring plant phenology using a dataset of plant

169 phenology observations on 14 species spanning up to 21 years at four coastal tundra sites.

170 Specifically, we address the following three questions: (1) To what extent do trends in plant

171 spring phenological events vary among sites and species? (2) How have the environmental

172 conditions changed at each site over the time-period of monitoring? (3) What is the relative

173 explanatory power of snowmelt date, spring temperatures and the date of spring drop in

174 regional sea-ice extent in a multi-predictor model of spring phenology at the study sites? Our

175 analysis therefore allows us to test the strength of the statistical relationships among the three

176 most commonly suggested cues for tundra spring plant phenology across tundra species and

177 sites: temperature, snowmelt and sea ice, and will contribute to improved predictions of the

178 response of tundra plant communities to changing growing conditions.

179

180 **Materials and methods**

181

182 *Phenological Observations*

183 The observations of phenology used in this paper are a subset of the most recent version of

184 the International Tundra Experiment (ITEX) (Henry & Molau, 1997; Webber & Walker,

185 1991) phenology control dataset (Prevéy et al., 2017). The dataset is openly available via the

186 Polar Data Catalogue (CCIN Reference Number 12722,

187 www.polardata.ca/pdcsearch/PDCSearchDOI.jsp?doi_id=12722) and was originally

188 compiled by Oberbauer et al. (2013). All observations were recorded according to methods

189 outlined in the ITEX Manual (Molau & Mølgaard, 1996). See also Oberbauer et al. (2013)

190 and Prevéy et al. (2017), as well as Bjorkman et al. (2015), Cooley et al. (2012), Hollister et

191 al. (2005) and Schmidt et al. (2016) for site-specific descriptions of methods. We obtained a

192 subset of the ITEX dataset for coastal sites by exclusion based on the following criteria: a)

193 coastal proximity (less than 3 km from the sea), b) data record spanning more than 10 years,

194 and c) snowmelt timing data available. Four sites met these criteria: Alexandra Fiord (NU,

195 Canada), Qikiqtaruk – Herschel Island (YT, Canada), Utqiaġvik – formerly Barrow (AK,

196 USA) and Zackenberg (Greenland). We have included additional 2016 data for the

197 Qikiqtaruk site and plot-level data for the Zackenberg site.

198

199 *Site descriptions*

200   The selected sites include mid-Arctic (Qikiqtaruk and Utqiaġvik) and high-Arctic (Alexandra

201   Fiord and Zackenberg) sites, and cover a wide geographical range (Figure 1) and diversity of

202   tundra types, climate, topography and soil properties (Table S1): Alexandra Fiord (75.92 W,

203   78.88 N) on Ellesmere Island has dwarf-shrub dominated tundra communities on glacio-

204   fluvial sediment composed of mixtures of granitic and carbonate rocks; Utqiaġvik (156.62 W,

205   71.317 N) consists of wet meadow and heath tundra on ice-rich permafrost; the vegetation at

206   Qikiqtaruk (138.91 W, 69.57 N) is dwarf shrub and forb-dominated tundra on ice-rich

207   permafrost; and the Zackenberg (20.56 W, 74.47 N) site is dwarf-shrub dominated tundra on

208   noncarbonated bedrock.
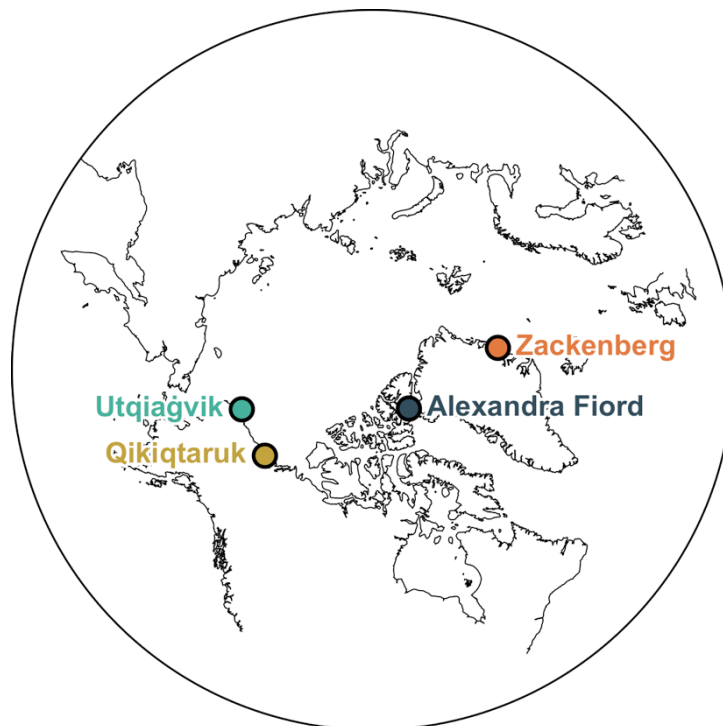
209

210   **Figure 1** Locations of the four sites included in this study: Alexandra Fiord (NU, Canada),

211   Qikiqtaruk (YT, Canada), Utqiaġvik (AK, USA) and Zackenberg (Greenland).

212

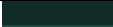213   *Selected species and phenological event*

214   Our final subset of the ITEX data contained 14 species (*Cassiope tetragona* D.Don, *Dupontia*

215   *psilosantha* Ruprecht, *Dryas integrifolia* Vahl, *Dryas octopetala* L., *Eriophorum vaginatum*

216   L., *Luzula arctica* Blytt, *Luzula confusa* Lindeb., *Oxyria digyna* Hill, *Papaver radicatum*

217   Rottb., *Poa arctica* R.Br., *Salix arctica* Pall., *Salix rotundifolia* Trautv., *Saxifraga*

218   *oppositifolia* L., *Silene acaulis* (L.) Jacq.), which represent the dominant plants in the

219   communities at the selected sites. We selected all species-phenological event combinations

220   that occurred in spring (mean phenological event occurring within 30 days of mean snowmelt

221   at each site). For Utqiaġvik and Qikiqtaruk, this selection resulted in 38 and 2 species-

222   phenological event combinations, respectively. To balance the sample size across sites, we

223   narrowed down the Utqiaġvik subset by selecting only species that make up at least 10% of

224   the ITEX community composition plots at the site and extended the Qikiqtaruk dataset by

225   one additional species with the next earliest mean phenological event in the record of the site.

226   The final subset contained a total of 8469 observations for 14 species and two phenological

227   events (spring green up and flowering), resulting in a total of 24 unique site-species-

228   phenological event combinations (Table 1). Phenological events were defined differently for

229   each plant species (Molau & Mølgaard, 1996), but recorded consistently over time (Prevéy et

230   al., 2017). Depending on the species, 'green up' was defined as the date of leaf emergence -

231   the date when the first leaf was visible or open, and 'flowering' was defined as the date when

232   either the first flower was open, the first pollen was visible or the first anthers were exposed

233   (Prevéy et al., 2017).

234

235   **Table 1:** Full species names, phenological event, start, end and length of time-series in years,

236   years with observations in the time-series and colours used for the site-species-phenological

237   event combinations in the dataset.

Site Name	Species	Phenological Event	Start Year	End Year	Time-Series Length (yrs)	Years with observ.	Colour
	Dryas integrifolia	flowering	1993	2013	21	15	
	Dryas integrifolia	green up	1993	2013	21	14	
	*Luzula spp.**	flowering	1992	2003	12	10	
Alexandra Fiord	*Oxyria digyna*	flowering	1992	2013	22	18	
	Oxyria digyna	green up	1992	2013	22	18	
	Papaver radicatum	flowering	1992	2013	22	18	
	Papaver radicatum	green up	1992	2013	22	18	

Site	Species	Phenophase	Start	End			
	Salix arctica	flowering	1995	2013	19	14	
Utqiaġvik	*Cassiope tetragona*	green up	1997	2014	18	12	
	Dupontia psilosantha	green up	1995	2014	20	14	
	Luzula arctica	flowering	1994	2014	21	14	
	Luzula arctica	green up	1994	2014	21	14	
	Poa arctica	green up	1994	2014	21	15	
	Salix rotundifolia	flowering	1994	2014	21	15	
	Salix rotundifolia	green up	1994	2014	21	15	
Qikiqtaruk	*Dryas integrifolia*	flowering	2001	2016	16	16	
	Eriophorum vaginatum	flowering	2002	2016	15	15	
	Salix arctica	green up	2001	2016	16	16	
Zackenberg	*Cassiope tetragona* *Dryas octopetala* *Papaver radicatum* *Salix arctica* *Saxifraga oppositifolia* *Silene acaulis*	flowering	1996	2011	16	16	

*includes *L. arctica* and *L. confusa*

238

239   *Snowmelt dates*

240   Snowmelt dates were determined at the plot or site level with site-specific protocols based on

241   guidelines in the ITEX manual (Molau & Mølgaard, 1996). Alexandra Fiord snowmelt dates

242   were recorded for each plot as the first day of year at which at least 90% of the plot was snow

243   free. Twenty percent of the snowmelt dates at Alexandra Fiord were unobserved. The missing

244   values were gap-filled as detailed in Bjorkman et al. (2015). Utqiaġvik snowmelt dates were

245   based on visual observations of when the plot was 100% snow free or soil surface

246   temperatures when snowmelt occurred in years prior to visual estimates. Snowmelt dates on

247   Qikiqtaruk were determined for each monitored plant individual or plot and recorded as the

248   first date in the year when the individual or plot area was >90% snow free (Cooley et al.,

249   2012). Zackenberg snowmelt dates were determined by multiple visits to the designated plant

250   phenology plots across the landscape. Snowmelt dates were defined as the day at which 50%

251   bare-ground was first visible at a given plot (Schmidt, Hansen, et al., 2016). As not all plant

252   phenology plots at Zackenberg were included in the snowmelt observations, we used the

253   mean snowmelt date of the monitored plots to predict spring phenology at the site. The

254   variation in methods for recording snowmelt are due to the use of different protocols for

255   long-term snowmelt monitoring across these sites.

256

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 temperature as the mean daily temperature within a calendar year from the earliest snowmelt 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 snowmelt to the day when 75% of phenological events occurred within the community across the record of the site.

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 hypothesised 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

281   including the months of May, June and July (Table S3) and found consistent results to the

282   model with spring drop in sea-ice extent.

283

284   The yearly spring drop in sea-ice extent was determined from the NOAA/NSIDC Climate

285   Data Record (CDR) v3 Passive Microwave Sea-Ice Concentrations (Meier et al., 2017; Peng,

286   Meier, Scott, & Savoie, 2013) projected in the NSIDC polar stereographic grid (NSIDC,

287   2018). We calculated daily regional sea-ice extent for each site within a bounding box of 21 x

288   21 grid cells (approximately 525 km x 525 km) centred on the cell containing the study site.

289   We used sea ice extent, rather than raw sea-ice concentrations as it provides a more reliable

290   measure during melt (Worby & Comiso, 2004). To avoid effects of land overspill (Cavalieri,

291   Parkinson, Gloersen, Comiso, & Zwally, 1999), we removed all cells that were directly

292   adjacent to the coastline, retaining only cells that were at least one cell removed from land.

293   Daily regional sea-ice extent was calculated as the total area of cells within the bounding box

294   with a sea-ice concentration of at least 15%. The day associated with the regional spring drop

295   in sea ice extent was then determined as the day of year (DOY) closest to the annual

296   minimum on which the sea-ice extent drops below 85% of the total area (Figure S4 and Table

297   S5). Our measure therefore only selects the final melt event leading up to the annual

298   minimum in the region and allows for fluctuations of the regional extent above and below

299   85% prior to the final melt event.

300

301   *Statistical analysis*

302   We estimated slope parameters for the temporal trends in plant phenological events and

303   environmental predictors using interval-censored and Gaussian-response Bayesian

304   hierarchical models (respectively) from the MCMCglmm package (Hadfield, 2010) in the R

305   Statistical Environment version 3.4.3 (R Core Team, 2018). We also used interval-censored

306   hierarchical models using to conduct variance partitioning of the environmental predictors on

307   spring phenology.

308

309   *Interval-censored phenology observations*

310   For the interval-censored models (Bjorkman et al., 2015; Hadfield, Heap, Bayer, Mittell, &

311   Crouch, 2013), we defined the upper interval bound as the day of year at which the

312   phenological event was first observed. Lower bounds were defined depending on whether

313   prior visits to the monitored individuals / plots were recorded or not. For Alexandra Fiord,

314   Utqiaġvik and Zackenberg, no record of prior visits was available and the lower bound was

315   set to the last day at which an observation was recorded at the site prior to the event. The

316   Qikiqtaruk dataset included records of all dates the plots were visited, independent of

317   whether a phenological event was observed or not. We used the last recorded visit prior to the

318   observed phenological event to define the lower bounds of the interval at this site. For

319   phenological observations at the beginning of the year, the lower bound was set as the

320   minimum snowmelt date recorded at the relevant site across the whole study period. The

321   mean interval length between observations were 3.2 days for Qikiqtaruk, 3.8 days for

322   Alexandra Fiord and Utqiaġvik, and 6.5 days for Zackenberg.

323

324   *Phenology trends*

325   Slope estimates for trends in phenological events were determined using a separate model for

326   each site-species-phenological event combination with the following structure:

327

328    $$unif\left[y_{lo}, y_{up}\right] = \mu + \beta_{year} + \alpha_{plot} + \alpha_{year} + \varepsilon$$

329

330   Where y_{lo} and y_{up} are the lower and upper bounds of the interval in which the phenological

331   event occurred, with a uniform likelihood of occurrence across the interval; μ is the global

332   intercept, β_{year} is the slope parameter for the trend across years; α_{plot} and α_{year} are the

333   random intercepts for plot and year respectively, and ε is the residual error. α_{plot} , α_{year} and

334   ε were normally distributed with a mean of zero and a variance estimated from the data. We

335   included plot and year as categorical random intercepts to account for the replication of

336   phenological observations at each plot over time and at each site in each year.

337

338   *Environmental predictor trends*

339   Trends in annual mean day of snowmelt, site-specific spring temperature and spring drop in

340   regional sea-ice extent were modelled individually for each site with the following model

341   formula:

342

343    $$y = \mu + \beta_{year} + \varepsilon$$

344

345   Where y is the value of the environmental predictor for a given year; μ is the global intercept

346   of the model; β_{year} is the slope parameter for the trend across years; and ε the residual error.

347   ε was distributed normally around zero with a variance estimated from the data. We did not

348   include a random intercept for year or plot, as there was no within-year replication of the site-

349   specific environmental variables.

350

351   We used weakly informative priors for all parameter estimates (inverse Wishart priors for

352   residual variances and normal priors for the fixed effects) when modelling the trends in

353   phenological events and environmental predictors (Hadfield, 2017). Convergence of these

354   models was assessed through examination of the trace plots.

355

356 *Prediction analysis*

357 We used a single global model for all site-species-phenological event combinations to

358 estimate the effect of the environmental predictors on spring phenological events. The

359 predictor variables were within-subject mean centred for each site-species-phenology event

360 combination (van de Pol & Wright, 2009) and scaled by the standard deviation to allow for

361 direct comparison between the effect sizes (Schielzeth, 2010). The model was structured as

362 follows:

363

$$unif[y_{lo,i}, y_{up,i}] = \bar{\mu} + \bar{\beta}_{snow} + \bar{\beta}_{temp} + \bar{\beta}_{ice} + \bar{\beta}_{year}$$

$$+ \beta_{snow,i} + \beta_{temp,i} + \beta_{ice,i} + \beta_{year,i}$$

$$+ \alpha_{site} + \alpha_{plot} + \alpha_{year} + \alpha_{site:year} + \varepsilon$$

367

368 Where $y_{lo,i}$ and $y_{up,i}$ are the upper and lower bounds of the interval in which a phenological

369 event of the site-species-phenological event combination i occurred, with a uniform

370 likelihood of occurrence across the interval; $\bar{\mu}$ the global intercept; $\bar{\beta}_{snow}$, $\bar{\beta}_{temp}$, $\bar{\beta}_{ice}$ and

371 $\bar{\beta}_{year}$ the mean slope parameters for snowmelt, spring temperature, day of spring drop in sea

372 ice extent and year respectively; $\beta_{snow,i}$, $\beta_{temp,i}$, $\beta_{ice,i}$ and $\beta_{year,i}$ the site-species-

373 phenological event specific slopes for snowmelt, spring temperature, spring drop in sea-ice

374 extent and year respectively; α_{site}, α_{plot}, α_{year} and $\alpha_{site:year}$ the random intercepts for site,

375 plot, year and site-year interaction; ε the residual error. The random intercepts and the

376 residual error were normally distributed around a mean of zero with variances estimated from

377 the data.

378

379   For each fixed effect x, the site-species-phenological event specific effects ($\beta_{x,i}$) were drawn

380   from a normal distribution with estimated variance around the mean slope $\bar{\beta}_x$ of the fixed

381   effect. We included year as a continuous predictor to account for the effects of variables that

382   have changed linearly over years and were not included in the analysis in addition to the

383   modelled fixed effects (Iler et al., 2017; Keogan et al., 2018). Furthermore, we added random

384   intercepts for plot and year to account for the nonindependence of plots measured repeatedly

385   over time as well as the nonindependence of observations conducted in the same year at a

386   given site. Finally, a year-site interaction was included to allow for the year effect to vary

387   among locations. Our model does not allow for: 1) a correlation of responses across species

388   at a site, 2) the correlation of species responses across sites, 3) the correlation of a species'

389   response across phenological events. We did not consider interactions between the

390   environmental predictors, as we had no a priori prediction of a consistent directional

391   interaction effect that would apply across species and locations.

392

393   The random slope and intercept parameters of the prediction analysis model were estimated

394   using an unstructured covariance matrix, which allowed for covariance between slopes and

395   the intercept (Hadfield, 2017). We used weakly informative priors for all coefficients

396   (parameter-expanded inverse Wishart priors for the variances and normal priors for the fixed

397   effects). The prediction analysis model was run with four chains and convergence was

398   confirmed through examination of the trace plots and Gelman-Rubin diagnostics (Gelman &

399   Rubin, 1992).

400

401   Environmental predictors were tested for multicollinearity with variance inflation factors

402   using the R package usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) prior to

403   execution of the model runs. The variance inflation factors for all three variables were below

404   1.27, suggesting no problems with multicollinearity. The highest correlation coefficient was

405   observed between spring temperatures and drop in sea ice extent (-0.38). We also ran reduced

406   models of the global model, only containing a single environmental predictor (Table S10),

407   which allowed us to test for indirect mechanisms linking two of the environmental predictors.

408

409   Due to the absence of plot-level snowmelt observations at Zackenberg the effect of snowmelt

410   at the Zackenberg site is solely due to among year variation, whereas at Alexandra Fiord,

411   Utqiaġvik and Qikiqtaruk the effect of snowmelt is affected by both among year and among

412   plot variation. Hence, our modelled estimates of the day of snowmelt effect at Zackenberg

413   may be biased earlier or later due to the loss of within site variation in snowmelt date. We

414   also ran the model with average annual snowmelt values for all sites and observed

415   comparable results to the original model with a slight reduction in the explanatory power for

416   snowmelt date (Table S3). Our original model may therefore be underestimating the effect of

417   snowmelt date at the Zackenberg site.

418

419   We refer to environmental predictors and trends as 'significant' when the 95% credible

420   interval (CI) for the corresponding parameter of the fitted models did not overlap zero. Code

421   and data are available at the following repository:

422   https://github.com/jakobjassmann/coastalphenology

423   **Results**

424   We observed strong variation in both the timing of annual mean spring phenological events

425   and their trends across the study periods for all species-phenological event combinations and

426   sites (Figure 2). While the trends indicate that spring is advancing overall at Qikiqtaruk and

427   Zackenberg, not all species or phenological events showed significant trends at the two sites.

428   In addition, we found little to no evidence for changes in the onset of spring at Alexandra

429   Fiord and Utqiaġvik. Estimated rates of change varied from an advance of 10.06 days per

430   decade (CI: -18.77 to -1.35 for *Cassiope tetragona* flowering at Zackenberg) to a delay of

431   1.67 days per decade (CI: -2.61 to 5.86 for *Oxyria digyna* flowering at Alexandra Fiord), with

432   five site-species-phenological event combinations advancing significantly and 19

433   combinations showing no significant change (Table S6).

434
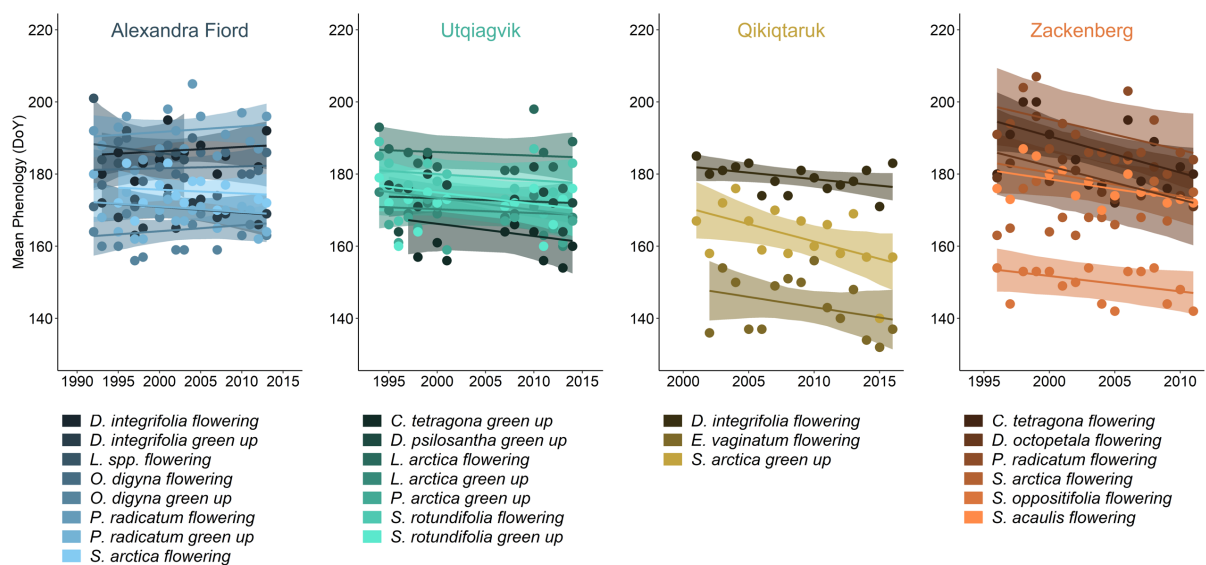
435   **Figure 2** Advancing phenology trends were observed for some but not all species and sites.

436   Annual mean spring phenology and trends for the species-phenological event combinations at

437   Alexandra Fiord, Utqiaġvik, Qikiqtaruk and Zackenberg. Trend lines were fitted with

438   Bayesian interval-censored models and shaded areas indicate 95% credible intervals. For a

439   detailed list of the phenological event and species combinations monitored see Table 1. For

440   graphical clarity, the credible intervals for the *Silene acaulis* flowering time-series at

441   Zackenberg are not shown. A low number of plot-level estimates with high variation in trends

442   resulted in high uncertainties of the model estimates for this time-series. See Figure S7 for a

443   plot including the credible intervals for the *S. acaulis* time-series.

444

445   The observed trends in environmental predictors indicate notable changes in spring climate

446   and environment at all sites across the study periods (Figure 3). Snowmelt dates advanced by

447   8.15 days per decade (CI: -16.19 to 0.31) at Qikiqtaruk and by 10.22 days per decade (CI: -

448   22.51 to 2.06) at Zackenberg, but the trends were marginally non-significant. No change was

449   observed at Alexandra Fiord (-0.61 days per decade; CI: -4.19 to 2.98) and Utqiaġvik (-1.41

450   days per decade; CI: -6.24 to 3.46) (Table S8). Average spring temperatures across the site-

451   specific spring periods increased significantly at all sites during the years monitored

452   respectively, with Qikiqtaruk experiencing the strongest trend of 2.30 °C warming per decade

453   (CI: 0.78, 3.83) and Alexandra Fiord experiencing the weakest trend of 0.63 °C warming per

454   decade (CI: 0.01, 1.24) (Table S8). The date of spring drop in sea-ice advanced for all sites,

455   roughly mirroring the trends in temperature with onset dates becoming earlier by -10.28 days

456   per decade (CI: -56.07; 34.36 at Zackenberg) to -46.39 days per decade (CI: -73.21, -19.40; at

457   Qikiqtaruk) (Table S8). However, the variation in onset of sea-ice melt among years was

458   substantial for all sites and particularly high for Zackenberg, and only the declining trend at

459   Qikiqtaruk was statistically significant (Figure 3, Table S8).

460
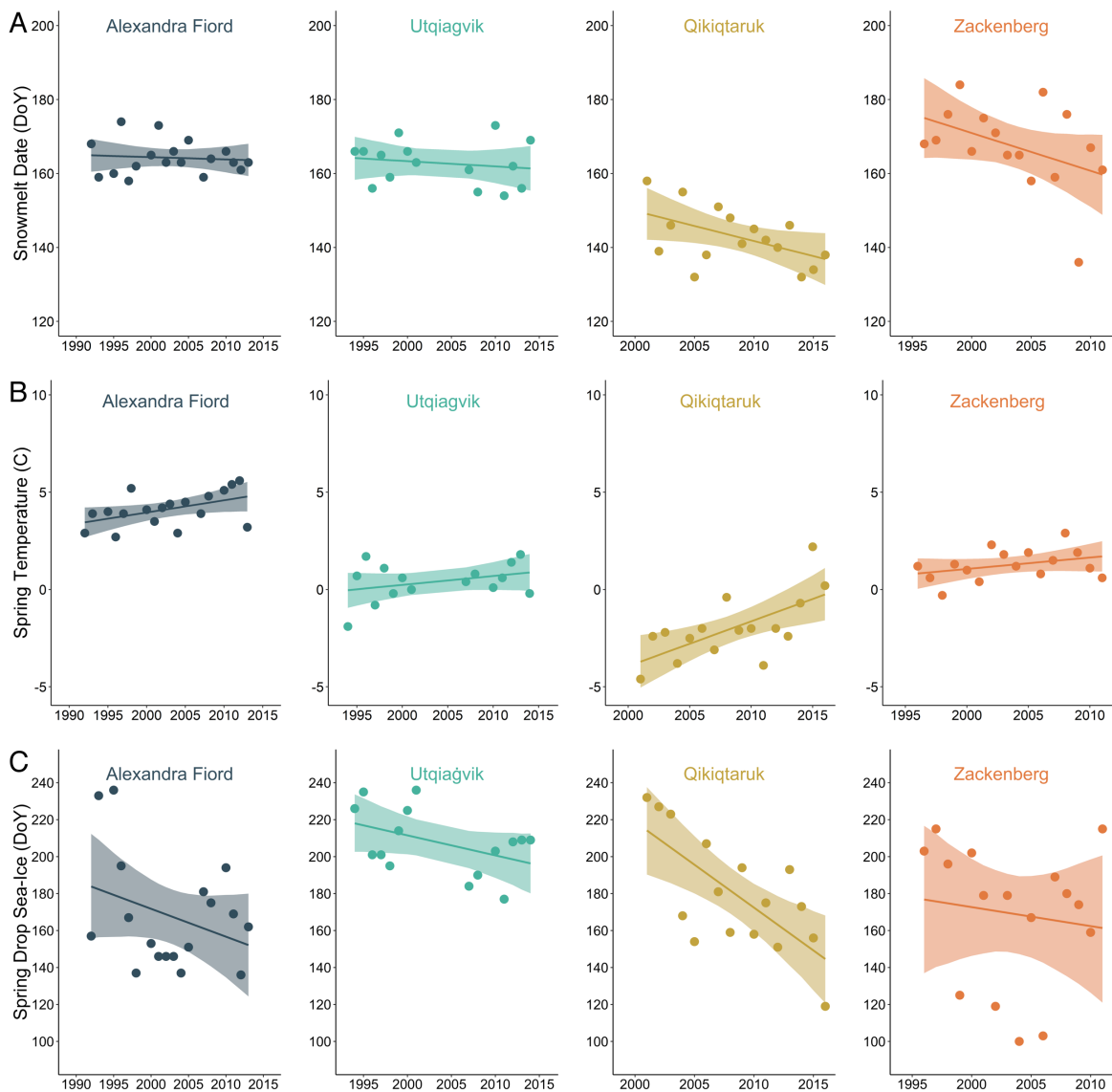
Figure 3 While spring drop in regional sea-ice extent advanced and temperatures increased across sites and study periods, snowmelt only advanced at some sites. Trends in site averages for snowmelt date (A), 'spring' temperature (B) and onset of regional sea-ice melt (C) for Alexandra Fiord, Utqiaġvik, 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 snowmelt on record to the day of year where 70% of the spring phenological events occurred in the pooled

469   community record of a given site. Due to these site-specific time-frames Alexandra Fiord

470   represents the 'warmest' spring temperatures despite being the northernmost site.

471

472   Snowmelt date consistently predicted phenology (Figure 4 and Figure S9) with a mean scaled

473   effect size of 3.26 (CI: 2.63 to 3.91), corresponding to 0.45 days advance in phenology per

474   day advance in snowmelt. The variance in snowmelt date slopes among site-species-

475   phenology event combinations was 1.82 (CI: 0.89 to 3.55), with 95% of the site-species-

476   phenology event combinations predicted to fall in the range of 0.09 to 0.82 days advance in

477   phenology per day advance in snowmelt. Temperature explained variation in spring

478   phenology for some, but not all, species-phenological event combinations with a mean scaled

479   effect size of -2.21 (CI -3.04 to -1.39) and associated slope variance of 3.15 (CI: 1.51 to

480   6.10). This result corresponds to 2.39 days advance in phenology per °C increase and 95% of

481   the site-species-phenological event combinations fell between 6.16 days advance to 1.38 days

482   delay in phenology per °C increase. The spring drop in regional sea-ice extent was a poor

483   predictor of phenological timing in all cases with a mean scaled effect size of -0.01 (CI: -0.94

484   to 0.91) and associated slope variance of 0.81 (CI: 0.28 to 1.83). This result corresponds to

485   less than 0.01 days advance per day delay in regional drop in sea ice extent and 95% of the

486   site-species-phenological event combinations fell between 0.07 days advance to 0.07 days

487   delay per day delay in regional drop in sea ice extent. These findings are in broad agreement

488   with the coefficients from the reduced models that tested each environmental predictor

489   separately (Table S10).

490

491   Variation in phenological events of only one species-phenological event combination (*Dryas*

492   *integrifolia* flowering at Qikiqtaruk) was not significantly explained by snowmelt date, with

493   the 95% confidence intervals overlapping zero for the posterior distributions for all three

494 slope parameters (Figure 4 and Table S11). Eleven out of the twenty-four species-

495 phenological event combinations were significantly explained by temperature: all Alexandra

496 Fiord species-phenological event combinations, *Salix arctica* green up at Qikiqtaruk,

497 *Cassiope tetragona* and *Salix arctica* flowering at Zackenberg (Table S11). Finally, the

498 analysis highlighted high unexplained variance among unique site-year combinations (9.40,

499 CI: 5.58 to 14.72), which corresponds to 95% of site-year combinations being in the range of

500 +/- 6.01 days from the predicted values.

501
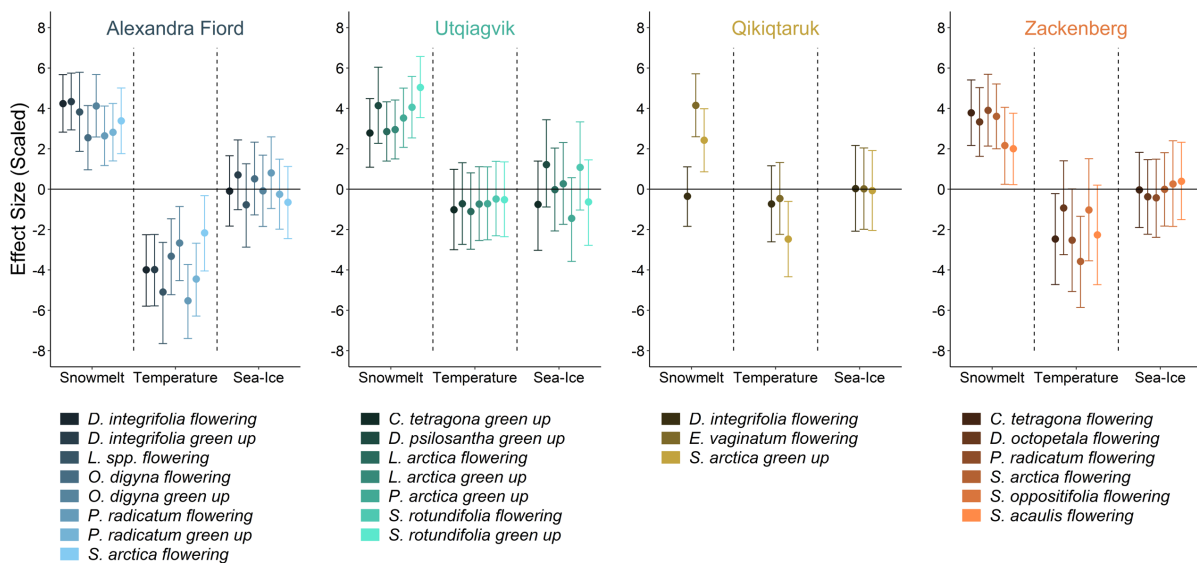
502

503 **Figure 4** Snowmelt date and temperature, but not the spring drop in regional sea-ice extent

504 explained variation in phenology across species and sites. Scaled effect sizes, grouped by the

505 environmental predictors (date of snowmelt, average spring temperature and date of spring

506 drop in regional sea-ice extent), for all species-phenological event combinations at Alexandra

507 Fiord, Utqiaġvik, Qikiqtaruk and Zackenberg. Error bars represent 95% credible intervals.

508 Effect sizes and credible intervals were estimated using a Bayesian hierarchical model.

509 Environmental predictors were within-subject mean centred and scaled by the standard

510   deviation (date of snowmelt: 7.20, spring temperature: 0.92 and spring drop in regional sea-

511   ice extent: 26.90).

512

513   The multi-predictor model indicated pronounced differences in the relative importance of the

514   environmental predictors across plant communities at the different study sites and also within

515   individual species found among different study sites. The differences were particularly

516   apparent for temperature, which predicted spring phenology for all species-phenology event

517   combinations at Alexandra Fiord, but did not explain any variation in spring phenology at

518   Utqiaġvik and for some but not all species-phenology event combinations at Qikiqtaruk and

519   Zackenberg (Figure 4). For the few species-phenology event combinations that overlapped

520   across sites, some showed consistent responses to the environmental predictors, whereas

521   others showed notable differences in the relative importance of the predictors across the study

522   sites. For example, *Salix arctica* phenology events (flowering and green up) were

523   consistently predicted by snowmelt and temperature across the three sites where the species

524   was monitored (Alexandra Fiord, Qikiqtaruk and Zackenberg), whereas *Dryas integrifolia*

525   flowering showed contrasting responses between sites (Table S11). While *D. integrifolia*

526   flowering was predicted by temperature and snowmelt at Alexandra Fiord, neither of the two

527   environmental factors was a significant predictor at Qikiqtaruk. Furthermore, the closely

528   related *Dryas octopetala* at Zackenberg was predicted to respond to snowmelt only (Table

529   S11). Thus, substantial heterogeneity in controls on phenology between species and sites

530   were highlighted by our study.

531

532   **Discussion**

533   Our test of the importance of temperature, snowmelt and drop in spring sea ice extent as

534   controls over coastal Arctic tundra plant phenology highlight three main findings: 1) Trends

535   in spring phenology were highly variable among species across these four sites emphasizing

536   the substantial heterogeneity in plant phenological response across tundra plant communities.

537   2) While all sites experienced pronounced advances in spring temperatures and onset of

538   regional sea-ice melt, spring phenology did not advance for all species and at all sites. Instead

539   spring phenology advanced only at sites with advancing snowmelt (Qikiqtaruk and

540   Zackenberg) and only for some species-phenological event combinations. 3) Localised

541   snowmelt best explained variation in spring phenology among these coastal Arctic sites,

542   suggesting that it is a key cue for spring leaf-out and early season flowering in coastal tundra

543   plant communities. Our findings confirm that timing of snowmelt (Bjorkman et al., 2015;

544   Cooper et al., 2011; Cortés et al., 2014; Iler et al., 2017; Kankaanpää et al., 2018; Molau et

545   al., 2005; Semenchuk et al., 2016; Sherwood et al., 2017; Thórhallsdóttir, 1998; Wipf, 2009;

546   Wipf et al., 2009), rather than a localised influence of sea ice, has important control over

547   spring plant phenology in coastal tundra ecosystems. Furthermore, our results indicate that

548   temperature, despite being the primary driver of spring plant phenology in temperate regions

549   (Cleland et al., 2007; Thackeray et al., 2016; Wolkovich et al., 2012), holds less explanatory

550   power for predicting spring phenology than snow in coastal tundra ecosystems of the Arctic.

551

552   *Snowmelt needs to be included when studying tundra phenology in a global change context*

553   Our results highlight the importance of local snow conditions in addition to temperature for

554   the prediction of tundra plant phenological responses to global climate change. Despite snow

555   melt being long considered an important driver of tundra plant phenology (Schwartz, 2013),

556   to date, snowmelt has yet to be incorporated into syntheses investigating plant phenology in

557   response to global change across the tundra biome (Oberbauer et al., 2013; Prevéy et al.,

558   2017) nor in cross-biome studies that include phenological observations from both tundra and

559   temperate regions (Post et al., 2018; Wolkovich et al., 2012; Xu et al., 2013). Considering

560　just spring temperature as predictor for tundra plant phenology will not capture key tundra

561　ecosystem dynamics. Even though temperature is a primary driver of snowmelt (Hinkler et

562　al., 2008; Rango & Martinec, 1995), the timing of when Arctic and alpine tundra become

563　snow free is a complex function of winter and spring atmospheric temperatures, precipitation,

564　topography, solar radiation, wind velocity and the water vapour deficit that drives

565　sublimation (Billings & Bliss, 1959; Cortés et al., 2014; Liston, Mcfadden, Sturm, & Pielke,

566　2008; MacDonald, Pomeroy, & Pietroniro, 2010; Molau et al., 2005; Pomeroy, Marsh, &

567　Gray, 1997; Sturm et al., 2001; Vaganov et al., 1999; H. C. Wheeler et al., 2015). See also

568　Hinkler et al. (2008) and Bjorkman et al. (2015) who discuss this partial decoupling of

569　snowmelt timing from temperature at the Zackenberg and Alexandra Fiord in more detail. It

570　follows that excluding snowmelt timing from any analysis that includes tundra spring plant

571　phenology, may therefore lead to unreliable predictions of phenological responses to global

572　change in tundra ecosystems.

573

574　*Influence of snowmelt highlights importance of landscape-level heterogeneity in phenology*

575　The high explanatory power of snowmelt date in this study and its inherently high spatial

576　variability highlight the need to consider landscape heterogeneity in tundra phenology

577　analyses (Kankaanpää et al., 2018). Landscape heterogeneity in phenology integrates a

578　diversity of plant phenological responses and environmental controls (Armstrong, Takimoto,

579　Schindler, Hayes, & Kauffman, 2016). Different plant species, populations and individuals

580　differ in their phenology, and as communities change across the landscape, so too does

581　community-level phenology (CaraDonna, Iler, & Inouye, 2014; Cleland et al., 2007; Høye et

582　al., 2013; Klosterman et al., 2018; Prevéy et al., 2019; Wolkovich, Cook, & Davies, 2014).

583　The environmental controls on phenology may vary substantially across the landscape with

584　topography and microclimate and so may the phenological responses of the plants to climate

585   (Høye et al., 2013). In particular, snowmelt timing can vary at plot and even sub-plot scales

586   due to the localised interplay of micro-topography, radiation and wind (Cortés et al., 2014;

587   Sturm et al., 2001). The multitude of effects of melting snow cover on plant phenology

588   through frost protection (Sherwood, Debinski, Caragea, & Germino, 2017; Wheeler, Høye,

589   Schmidt, Svenning, & Forchhammer, 2015; Wipf & Rixen, 2010), modification of water

590   availability (Wipf & Rixen, 2010) and temperature in the microclimate (Starr & Oberbauer,

591   2003) likely further contributes to landscape dynamics in tundra spring phenology. These

592   localised dynamic effects may hold the key to understanding the high relative importance of

593   snowmelt as a driver of tundra spring phenology.

594

595   Individuals and populations of the same species may not only experience differences in the

596   localised environmental cues, but may also show variation in the relative strength of their

597   phenological responses to these cues, adding to the variation in phenology across the

598   landscape (Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Post et al., 2009). The

599   locality and distribution of phenological monitoring plots and observations of environmental

600   variables therefore need to encompass landscape-level variation, to obtain representative

601   estimates of species and community spring phenological events and drivers at any given site.

602   Emerging technologies such as phenocams (Andresen, Tweedie, & Lougheed, 2018;

603   Linkosalmi et al., 2016; Richardson et al., 2018), fine-scale aerial imagery from drones

604   (Klosterman et al., 2018) and spatiotemporal modelling of snow properties (Pedersen, Liston,

605   Tamstorf, Westergaard-Nielsen, & Schmidt, 2015) may help facilitate phenological and

606   snowmelt monitoring at the spatial grains, temporal frequencies and extents required to

607   understand landscape and community-level phenological change.

608

609   *Site-specific importance of temperature*

610 Our findings suggest that the relative importance of the environmental predictors for coastal

611 spring phenology can differ between sites, plant communities and species. Cross-site level

612 differences were particularly evident for temperature. The Alexandra Fiord site was the only

613 site where phenology was consistently predicted by temperature. Prevéy et al (2017) found

614 that temperature explained tundra phenology better at sites with colder versus warmer

615 summers and suggested that this might be due to different evolutionary strategies required at

616 colder sites. For example, a higher temperature sensitivity might be beneficial in optimising

617 rapid flower and seed development to facilitate the colonisation of bare ground at higher

618 latitude sites, where bare ground is often more common (Prevéy et al., 2017). On the other

619 hand, CaraDonna et al. (2015) found no evidence for a phylogenetic signal for the strength in

620 the responses of flowering to snowmelt and temperature in a subalpine plant community.

621 Høye et al. (2013) observed plot-specific responses of flowering to temperature within

622 individual species at the Zackenberg site and proposed that variation in localised snow depth

623 and below-ground conditions such as soil moisture and soil temperature could modify the

624 plant's responses to air temperatures in contrast to evolutionary processes. As Alexandra

625 Fiord is the northernmost site and a "warm oasis" in an otherwise harshly cold polar desert

626 (Freedman, Svoboda, & Henry, 1994), the effects of climate interactions may be reduced

627 compared to warmer and wetter sites further south. However, the low number of sites in our

628 study does not provide the statistical power to test the importance of cross-site differences.

629 Therefore, further investigation is required to test whether localised adaptation or interactions

630 with additional environmental factors are the cause of the variation in the relative importance

631 of the environmental predictors of tundra spring plant phenology across the tundra biome.

632

633 *Spring drop in sea ice extent did not explain variation in phenology*

634   The spring drop in sea ice extent did not explain spring phenology at the coastal tundra sites

635   in our analysis. This was the case for the models that included spring drop in sea-ice as the

636   only environmental predictor (Table S10) as well as for the model containing all three

637   environmental predictors. Thus, our findings suggest that there is neither a direct or indirect

638   regional mechanism linking spring drop in sea-ice to spring phenology at our study sites apart

639   from via temperatures. Due to limited localised data availability, we were not able to directly

640   test whether the sea-breeze mechanism proposed by Haugen & Brown (1980) and observed

641   by Macias-Fauria et al. (2017) or other indirect sea ice drivers have a significant impact on

642   plant spring phenology across our study sites. Thus, our study alone was not able to capture

643   all of the potential complexities suggested by other studies of sea ice at regional to

644   continental scales (Kerby & Post, 2013a; Macias-Fauria et al., 2017; Post et al., 2016).

645

646   The majority of previous studies that have attributed spring phenology variation and plant

647   productivity to sea-ice used large-scale integrative measures such as annual minimum global

648   sea-ice extent (Bhatt et al., 2010; Forchhammer, 2017; Kerby & Post, 2013a; Post et al.,

649   2013, 2016). Phenology has previously also been linked to other integrative global measures

650   such as ENSO or the North Atlantic Oscillation (NAO) (Chmielewski & Rötzer, 2001;

651   D'Odorico, Yoo, & Jaeger, 2002; Forchhammer, Post, & Stenseth, 1998; Scheifinger,

652   Menzel, Koch, Peter, & Ahas, 2002). Although the integrative measures may correlate well

653   with plant phenology, our findings highlight the value of directly testing interannual variation

654   of localised ecological mechanisms. New datasets of winds, fog, and other variables (Macias-

655   Fauria et al., 2017; Tjernström et al., 2015) and analyses that can incorporate additional direct

656   and indirect interactions among drivers will contribute to disentangling the complexity of

657   patterns and trends in plant phenology observed in the tundra biome and beyond.

658

659   *The challenges of measuring localised sea ice conditions*

660   Determining regional and interannual variation in the onset of sea ice melt can be challenging

661   due to the lack of locally collected data. Globally available satellite products such as the

662   passive microwave data set used in this study (Peng et al., 2013) struggle to detect the ice

663   edge during the melt period (Comiso & Nishio, 2008; Worby & Comiso, 2004) and suffer

664   from land spill-over in cells adjacent to the coast-line (Cavalieri et al., 1999). More accurate

665   manually interpreted datasets based on a mixture of data sources (including optical satellite

666   data) such as those developed by national agencies for navigational purposes could be used,

667   but are often available only for recent years (Canadian Ice Service, 2009) and/or are limited

668   to specific geographic regions (http://polarview.met.no). We chose the passive microwave

669   satellite data to estimate the timing of drop in spring sea-ice extent as no other data were

670   available for the entire time-period and geographical extent of our study at a daily resolution.

671   Due to our cautious pre-processing procedure, our measure of onset of sea-ice melt from the

672   NOAA/NSIDC climate data record likely is a conservative estimate and might mask out

673   some of the fine-scale temporal and spatial variation in the sea-ice conditions in the different

674   study regions. Thus, we caution that the interannual variation in regional sea-ice extent may

675   not be entirely comparable to higher-resolution temperature (site level) and snowmelt

676   estimates (site to plot level) used in this study. With advances in technology and growing

677   interest in the northern maritime regions, higher quality sea-ice data are becoming

678   increasingly available in certain geographic regions (see for example Macias-Fauria et al.,

679   2017), and we encourage future studies to repeat our analyses using these data products when

680   available.

681

682   *Photoperiod as a control on spring phenology*

683 Our study was not able to address the separate effect of photoperiod as a control on spring

684 phenology because of the lack of temporal variation required for an analysis such as we have

685 employed here. Arctic and alpine plant phenology can be sensitive to photoperiod as

686 suggested by common garden experiments (Bennington et al., 2012; Bjorkman, Vellend, Frei,

687 & Henry, 2017; Parker, Tang, Clark, Moody, & Fetcher, 2017) and demonstrated in growth

688 chamber experiments (Heide, 1989, 1992; Keller & Körner, 2003). Keller and Körner (2003)

689 found day-length cues for flowering in 54% of the 20 studied alpine plant species and

690 estimated a minimum day length requirement of about 15 h for plants adapted to their study

691 site in the central Alps in Europe. It is therefore likely that minimum daylight requirements

692 were met at all our study sites prior to snowmelt: Alexandra Fiord, Barrow and Zackenberg

693 already experienced 24 hours of daylight two weeks prior to the minimum snowmelt date on

694 record, and Qikiqtaruk experienced 14.5 hours of daylight with no night and only

695 astronomical twilight during spring. However, increases in day length beyond the minimum

696 requirement may accelerate development and phenology of Arctic and alpine plants (Keller

697 & Körner, 2003) and dual requirements based on interactions of temperature and photoperiod

698 have been documented in other studies (Heide, 1989). Thus, understanding the interactive

699 nature of photoperiod and environmental cues on phenology, particularly in the context of

700 lengthening growing seasons and range expansions with warming from lower latitudes with

701 stronger diurnal light variation to high latitudes, remains a future challenge for tundra plant

702 ecology.

703

704 *Phenology, trophic interactions and ecosystem change*

705 Tundra plant phenology impacts ecosystem functions such as net primary productivity

706 (Forkel et al., 2016; Piao et al., 2008; Xu et al., 2013) thereby creating feedbacks to the

707 global climate system (Richardson et al., 2013). Our study underlines the importance of

708   localised snowmelt dates for spring plant phenology in coastal tundra ecosystems. Snow

709   cover is projected to decrease across the Arctic (AMAP, 2017), but predicted changes in

710   snow conditions differ in direction and magnitude amongst regions and seasons (AMAP,

711   2017). While high declines in snow cover are expected for warmer coastal areas and during

712   spring, high Arctic sites, such as Alexandra Fiord, are predicted to experience increases in the

713   annual accumulation of snow (AMAP, 2017). Locally reduced spring snow cover could

714   increase the susceptibility of plants to freezing events and damage due to photoinhibition

715   (Lundell et al., 2010), affecting plant productivity, community composition and evolution

716   through plant health and mortality (Bokhorst, Bjerke, Street, Callaghan, & Phoenix, 2011;

717   Cortés et al., 2014; Jonas, Rixen, Sturm, & Stoeckli, 2008; Phoenix & Bjerke, 2016; J. A.

718   Wheeler et al., 2016; Wipf & Rixen, 2010). Thus, quantifying the impact of plant phenology

719   on productivity change over time is a key element to improved projections of tundra carbon

720   storage and energy flux feedbacks to the global climate system (Park et al., 2016).

721

722   Tundra plant phenology influences resource availability for secondary consumers (Barboza et

723   al., 2018; Doiron et al., 2015; Gustine et al., 2017; Kerby & Post, 2013b) and asynchronous

724   shifts between interacting species due to climate change could result in trophic mismatches

725   (Doiron et al., 2015; Kerby & Post, 2013b, 2013a; Schmidt, Mosbacher, et al., 2016). Locally

726   reduced spring snow cover could decrease spatial variation in snowmelt timing and thus

727   lessen the extent of landscape-scale heterogeneity in plant phenology and shorten flowering

728   duration (Prevéy et al., 2018), with potentially detrimental impacts on consumers, as these

729   may rely on temporal and spatial variation in their food sources to maximise energy intake

730   across the season (Armstrong et al., 2016; Moorter et al., 2013). This interaction between

731   spatial and temporal patterning and trends in trophic mismatches has only rarely been

732   explored in the tundra and other ecosystems (Bischof et al., 2012; Burgess et al., 2018;

733   Sawyer & Kauffman, 2011). A comprehensive understanding of the mechanistic drivers of

734   plant phenology, and how these drivers are changing over time, is therefore key to our ability

735   to predict and manage the consequences of future environmental change in tundra ecosystems

736   and beyond (Kharouba et al., 2018; Richardson et al., 2013; Thackeray, 2016; Thackeray et

737   al., 2016; Wolkovich et al., 2014)

738

739   *Conclusions*

740   The Arctic is warming more rapidly than any other region of the planet (IPCC, 2014), with

741   well documented consequences for tundra plant communities, including changes in

742   community composition (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012;

743   Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Elmendorf et al., 2015;

744   Ernakovich et al., 2014), trophic mismatch (Doiron et al., 2015; Gustine et al., 2017; Kerby

745   & Post, 2013b, 2013a; Post et al., 2008) and altered plant phenology (Høye, Post, Meltofte,

746   Schmidt, & Forchhammer, 2007; Post et al., 2018). Our findings suggest that snowmelt and

747   temperature, but not spring drop in sea-ice extent are the dominant cues for spring phenology

748   in coastal Arctic plant communities that experience short growing seasons and persistent

749   snow cover. Later snowmelt therefore can delay phenology, even when air temperatures are

750   warming over time. Our findings further suggest that the relative importance of snowmelt

751   timing and temperature as predictors of tundra spring plant phenology may differ among

752   communities, species and populations across the tundra biome. Together, these results

753   highlight the growing evidence that tundra vegetation responses to rapid environmental

754   change are more complex than a simple response to increasing temperatures and help explain

755   the variation in phenological trends seen among tundra sites. Thus, to understand and better

756   predict future tundra vegetation change and associated feedbacks on the global climate

757   system, we require localised tests of the specific influences of mechanistic drivers of change.

758   Our study illustrates the value of long-term monitoring programmes (sensu Post & Høye,

759   2013; Hobbie et al., 2017; Schmidt, Christensen, & Roslin, 2017; Myers-Smith et al., 2019)

760   and cross-site data syntheses for quantifying site- and species-specific responses to

761   environmental change. Only with quantitative tests carried out on comprehensive cross-site

762   datasets, can we attribute variation in plant phenology to localised environmental cues and

763   improve our predictions of tundra ecosystem responses to global change.

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