Edinburgh Research Explorer

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

1   **Draft Manuscript "Coastal Phenology"**

2   **Primary research article for submission to Global Change Biology**

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

11   **List of Authors**

12   Jakob J. Assmann[1*], Isla H. Myers-Smith[1], Albert B. Phillimore[1], Anne D. Bjorkman[2],

13   Richard E. Ennos[1], Janet S. Prevéy[3], Greg H.R. Henry[4], Niels M. Schmidt[5], Robert D.

14   Hollister[6]

15

16   **Institute(s) of origin**

17   [1]The University of Edinburgh, Edinburgh, Scotland, United Kingdom

18   [2]Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany

19   [3]Pacific Northwest Research Station, United States Department of Agriculture - Forest Service,

20   Olympia, WA, United States

21   [4]University of British Columbia, Vancouver, Canada

22   [5]Arctic Research Centre, Aarhus University, Roskilde, Denmark

23   [6]Grand Valley State University, Allendale, MI, USA

24

25   *Corresponding author: Jakob J Assmann, email: j.assmann@ed.ac.uk, phone +44 7542 455

26   770

27

28   **Keywords**

31

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.
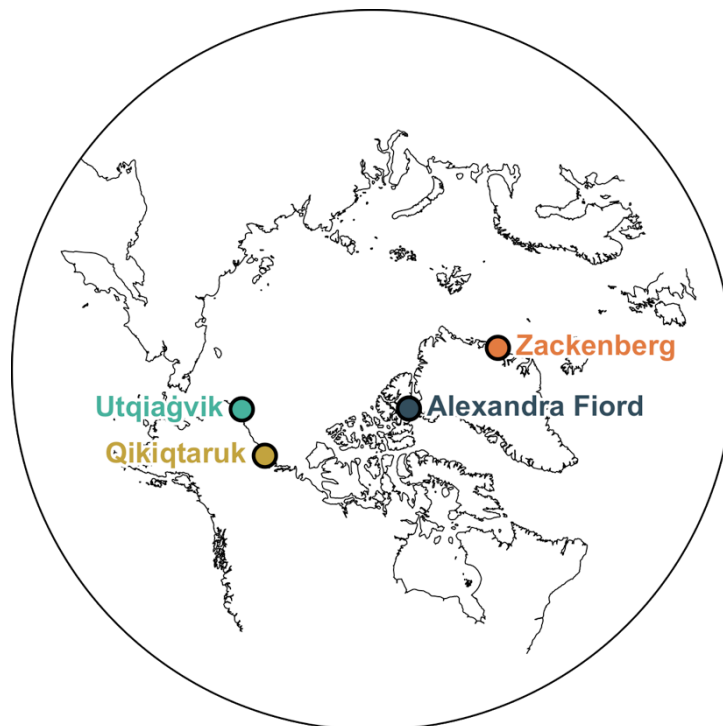
209

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						
	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

Snowmelt dates

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

256

257 *Spring Temperatures*

258 Daily average air temperatures were obtained from local weather stations (Table S2) and

259 annual 'spring' averages calculated for each site-species-phenological event time-series. We

260 defined spring average temperature as the mean daily temperature within a calendar year

261 from the earliest snowmelt date on record to the day at which 75% of the phenological event

262 had occurred across the whole length of the time-series. Each time-series therefore had its

263 own specific time-frame across which temperatures were averaged. The period was chosen to

264 capture a static time-window during which the plants are likely to strongly respond to

265 ambient temperatures for each given phenological event. For cross-site comparison of spring

266 temperature change, we calculated spring averages using the same approach but applied to

267 the pooled phenology time-series data for each site. These site-specific spring temperatures

268 therefore represent the yearly temperatures from the day of snowmelt to the day when 75% of

269 phenological events occurred within the community across the record of the site.

270

271 *Day of spring drop in regional sea ice extent*

272 We decided to use the date of spring drop in regional sea-ice extent as it represents the shift

273 from ice covered to ice "free" ocean (the minimum sea ice extent in a given year) in the

274 region surrounding the study site, and hence a change in microclimatic conditions that may

275 act as phenological cues to the tundra plants at our study sites. We hypothesised that, if sea-

276 ice influences plant phenology due to changing light and moisture availability, the time point

277 at which the system shifts its state would carry the highest explanatory power for spring plant

278 phenology at the sites. If air temperatures alone act as the proximate cue, any influence of

279 sea-ice on air temperatures would appear as an effect of temperature in our statistical

280 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

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-phenology 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:

$$unif\left[y_{lo,i}, y_{up,i}\right] = \bar{\mu} + \bar{\beta}_{snow} + \bar{\beta}_{temp} + \bar{\beta}_{ice} + \bar{\beta}_{year}$$
$$+\beta_{snow,i} + \beta_{temp,i} + \beta_{ice,i} + \beta_{year,i}$$
$$+ \alpha_{site} + \alpha_{plot} + \alpha_{year} + \alpha_{site:year} + \varepsilon$$

Where $y_{lo,i}$ and $y_{up,i}$ 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; $\bar{\beta}_{snow}$, $\bar{\beta}_{temp}$, $\bar{\beta}_{ice}$ and $\bar{\beta}_{year}$ the mean slope parameters for snowmelt, spring temperature, day of spring drop in sea ice extent and year respectively; $\beta_{snow,i}$, $\beta_{temp,i}$, $\beta_{ice,i}$ and $\beta_{year,i}$ the site-species-phenological event specific slopes for snowmelt, spring temperature, spring drop in sea-ice extent and year respectively; α_{site}, α_{plot}, α_{year} and $\alpha_{site:year}$ the random intercepts for site, plot, year and site-year interaction; 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.

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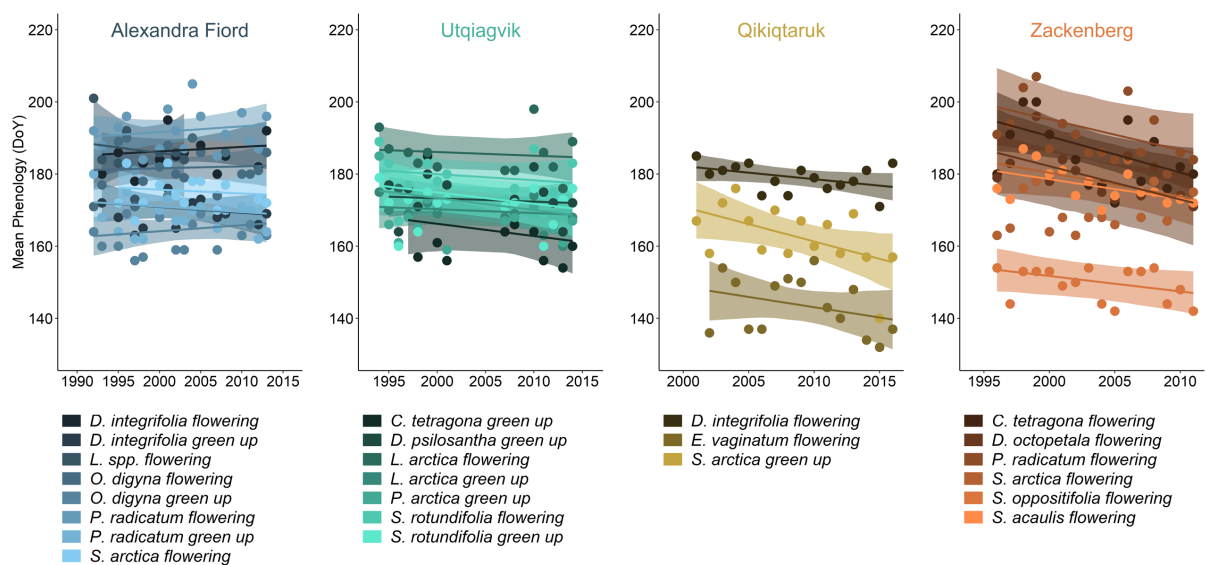
435   **Figure 2** Advancing phenology trends were observed for some but not all species and sites.

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
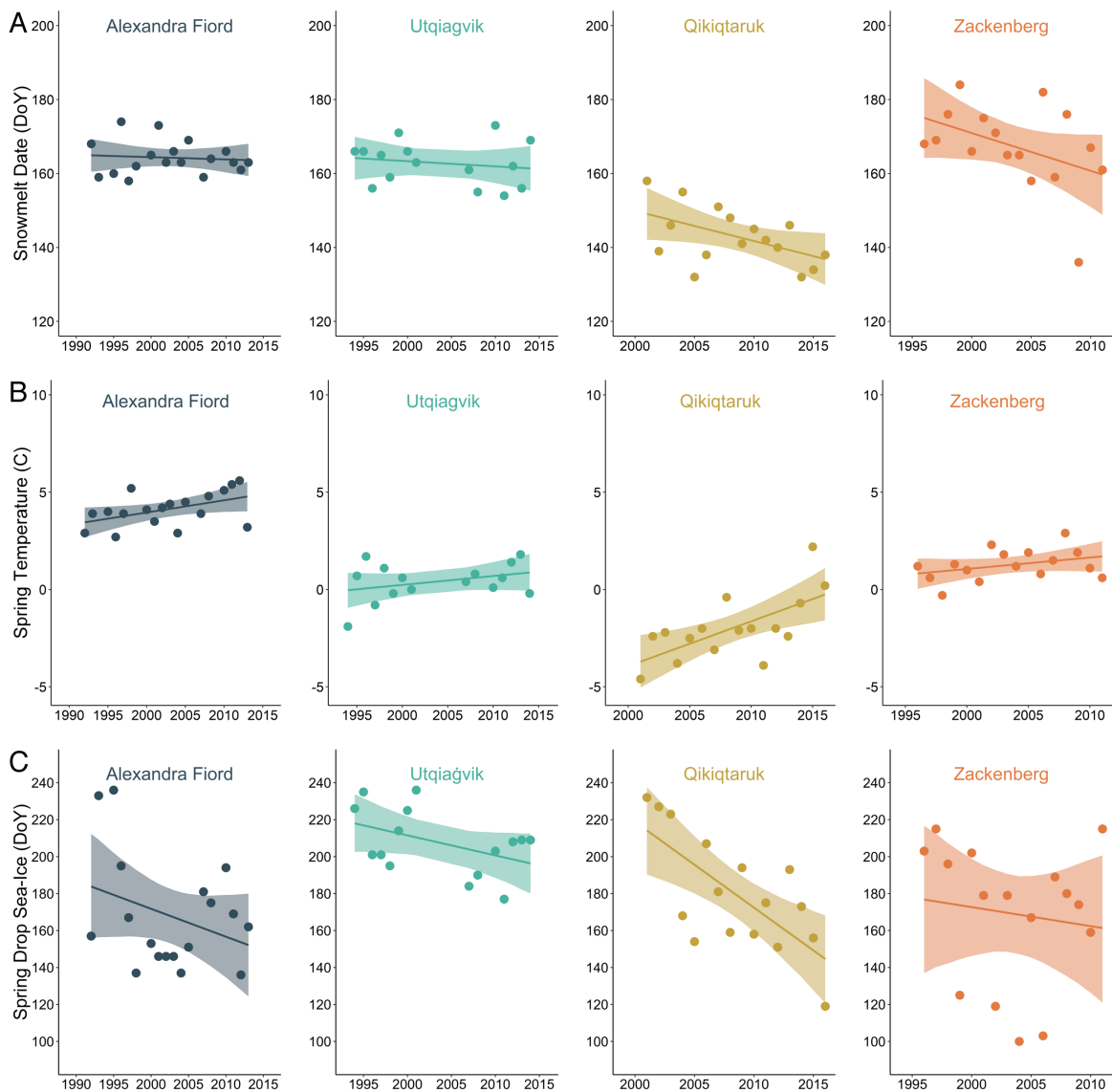
Figure 3 While spring drop in regional sea-ice extent advanced and temperatures increased across sites and study periods, snowmelt only advanced at some sites. Trends in site averages for snowmelt date (A), 'spring' temperature (B) and onset of regional sea-ice melt (C) for Alexandra Fiord, Utqiaġvik, 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
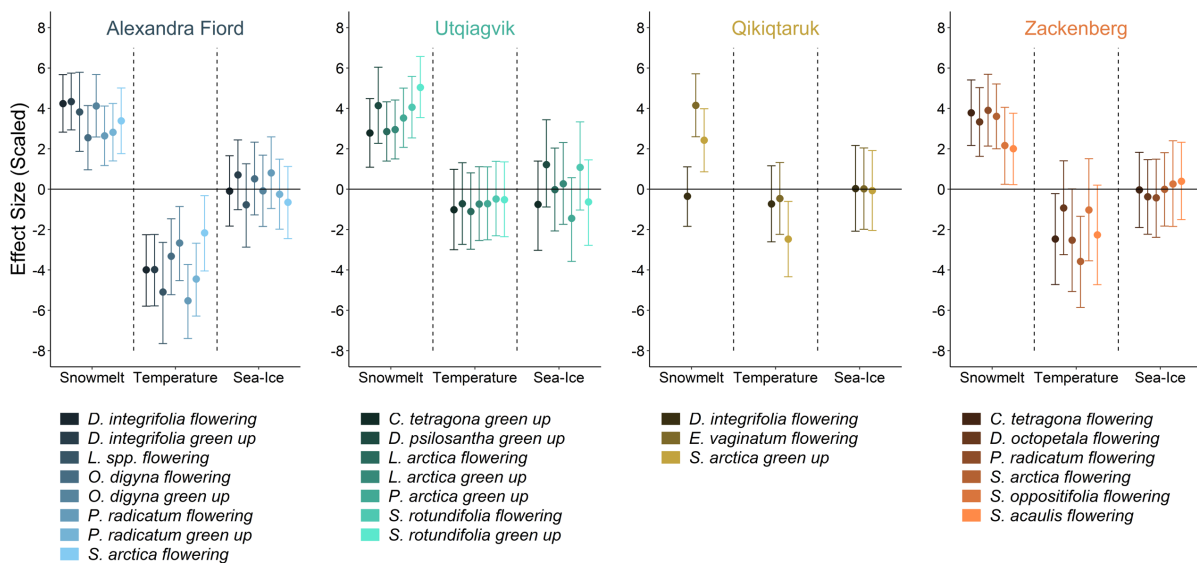
502

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

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.

764

782

805

806 **References**

807   AMAP. (2017). *Snow, Water, Ice and Permafrost. Summary for Policy-makers.* (p. 20). Oslo,

808   Norway: Arctic Monitoring and Assessment Programme (AMAP). Retrieved from

809   https://www.amap.no/documents/doc/Snow-Water-Ice-and-Permafrost.-Summary-

810   for-Policy-makers/1532

811   Andresen, C. G., Tweedie, C. E., & Lougheed, V. L. (2018). Climate and nutrient effects on

812   Arctic wetland plant phenology observed from phenocams. *Remote Sensing of*

813   *Environment*, *205*, 46–55. https://doi.org/10.1016/j.rse.2017.11.013

814   Armstrong, J. B., Takimoto, G., Schindler, D. E., Hayes, M. M., & Kauffman, M. J. (2016).

815   Resource waves: phenological diversity enhances foraging opportunities for mobile

816   consumers. *Ecology*, *97*(5), 1099–1112. https://doi.org/10.1890/15-0554.1

817   Barboza, P. S., Van Someren, L. L., Gustine, D. D., & Bret-Harte, M. S. (2018). The nitrogen

818   window for arctic herbivores: plant phenology and protein gain of migratory caribou

819   (Rangifer tarandus). *Ecosphere*, *9*(1), e02073. https://doi.org/10.1002/ecs2.2073

820   Barrett, R. T. S., Hollister, R. D., Oberbauer, S. F., & Tweedie, C. E. (2015). Arctic plant

821   responses to changing abiotic factors in northern Alaska. *American Journal of Botany*,

822   *102*(12), 2020–2031. https://doi.org/10.3732/ajb.1400535

823   Bennington, C. C., Fetcher, N., Vavrek, M. C., Shaver, G. R., Cummings, K. J., & McGraw,

824   J. B. (2012). Home site advantage in two long-lived arctic plant species: results from

825   two 30-year reciprocal transplant studies. *Journal of Ecology*, *100*(4), 841–851.

826   https://doi.org/10.1111/j.1365-2745.2012.01984.x

827   Bhatt, U. S., Walker, D. A., Raynolds, M. K., Comiso, J. C., Epstein, H. E., Jia, G., …

828   Webber, P. J. (2010). Circumpolar Arctic Tundra Vegetation Change Is Linked to Sea

829   Ice Decline. *Earth Interactions*, *14*(8), 1–20. https://doi.org/10.1175/2010EI315.1

830   Billings, W. D., & Bliss, L. C. (1959). An Alpine Snowbank Environment and Its Effects on

831   Vegetation, Plant Development, and Productivity. *Ecology*, *40*(3), 388–397.

832   https://doi.org/10.2307/1929755

833   Billings, W. D., & Mooney, H. A. (1968). The ecology of Arctic and alpine plants. *Biological*

834   *Reviews*, *43*(4), 481–529. https://doi.org/10.1111/j.1469-185X.1968.tb00968.x

835   Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud,

836   A. (2012). A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or

837   Surfing the Green Wave? *The American Naturalist*, *180*(4), 407–424.

838   https://doi.org/10.1086/667590

839   Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M., & Henry, G. H. R. (2015).

840   Contrasting effects of warming and increased snowfall on Arctic tundra plant

841   phenology over the past two decades. *Global Change Biology*, *21*, 4651–4661.

842   https://doi.org/10.1111/gcb.13051

843   Bjorkman, A. D., Vellend, M., Frei, E. R., & Henry, G. H. R. (2017). Climate adaptation is

844   not enough: warming does not facilitate success of southern tundra plant populations

845   in the high Arctic. *Global Change Biology*, *23*(4), 1540–1551.

846   https://doi.org/10.1111/gcb.13417

847   Bokhorst, S., Bjerke, J. W., Street, L. E., Callaghan, T. V., & Phoenix, G. K. (2011). Impacts

848   of multiple extreme winter warming events on sub-Arctic heathland: phenology,

849   reproduction, growth, and CO_2 flux responses. *Global Change Biology*, *17*(9), 2817–

850   2830. https://doi.org/10.1111/j.1365-2486.2011.02424.x

851   Burgess, M. D., Smith, K. W., Evans, K. L., Leech, D., Pearce-Higgins, J. W., Branston, C.

852   J., … Phillimore, A. B. (2018). Tritrophic phenological match–mismatch in space and

853   time. *Nature Ecology & Evolution*, *2*(6), 970–975. https://doi.org/10.1038/s41559-

854   018-0543-1

855   Canadian Ice Service. (2009). *Canadian Ice Service Arctic Regional Sea Ice Charts in*

856   *SIGRID-3 Format, Version 1*. Boulder, Colorado USA: NSIDC: National Snow and

857   Ice Data Center. Retrieved from https://doi.org/10.7265/N51V5BW9

858   CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape

859   a subalpine plant community. *Proceedings of the National Academy of Sciences*,

860   *111*(13), 4916–4921. https://doi.org/10.1073/pnas.1323073111

861   CaraDonna, P. J., & Inouye, D. W. (2015). Phenological responses to climate change do not

862   exhibit phylogenetic signal in a subalpine plant community. *Ecology*, *96*(2), 355–361.

863   https://doi.org/10.1890/14-1536.1

864   Cavalieri, D. J., Parkinson, C. L., Gloersen, P., Comiso, J. C., & Zwally, H. J. (1999).

865   Deriving long-term time series of sea ice cover from satellite passive-microwave

866   multisensor data sets. *Journal of Geophysical Research: Oceans*, *104*(C7), 15803–

867   15814. https://doi.org/10.1029/1999JC900081

868   Chmielewski, F.-M., & Rötzer, T. (2001). Response of tree phenology to climate change

869   across Europe. *Agricultural and Forest Meteorology*, *108*(2), 101–112.

870   https://doi.org/10.1016/S0168-1923(01)00233-7

871   Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting

872   plant phenology in response to global change. *Trends in Ecology & Evolution*, *22*(7),

873   357–365. https://doi.org/10.1016/j.tree.2007.04.003

874   Comiso, J. C., & Nishio, F. (2008). Trends in the sea ice cover using enhanced and

875   compatible AMSR-E, SSM/I, and SMMR data. *Journal of Geophysical Research:*

876   *Oceans*, *113*(C2), C02S07. https://doi.org/10.1029/2007JC004257

877   Cooley, D., Eckert, C. D., & Gordon, R. R. (2012). *Herschel Island - Qikiqtaruk Inventory,*

878   *Monitoring and Research Program*. Whitehorse, YT, Canada: Yukon Parks.

879   Cooper, E. J., Dullinger, S., & Semenchuk, P. R. (2011). Late snowmelt delays plant

880   development and results in lower reproductive success in the High Arctic. *Plant*

881   *Science*, *180*(1), 157–167. https://doi.org/10.1016/j.plantsci.2010.09.005

882   Cortés, A. J., Waeber, S., Lexer, C., Sedlacek, J., Wheeler, J. A., van Kleunen, M., …

883   Karrenberg, S. (2014). Small-scale patterns in snowmelt timing affect gene flow and

884   the distribution of genetic diversity in the alpine dwarf shrub Salix herbacea.

885   *Heredity*, *113*(3), 233–239. https://doi.org/10.1038/hdy.2014.19

886   D'Odorico, P., Yoo, J. C., & Jaeger, S. (2002). Changing Seasons: An Effect of the North

887   Atlantic Oscillation? *Journal of Climate*, *15*(4), 435–445.

888   https://doi.org/10.1175/1520-0442(2002)015<0435:CSAEOT>2.0.CO;2

889   Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the

890   growth of young in an Arctic herbivore. *Global Change Biology*, *21*(12), 4364–4376.

891   https://doi.org/10.1111/gcb.13057

892   Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D.,

893   Callaghan, T. V., … Wookey, P. A. (2012). Global assessment of experimental

894   climate warming on tundra vegetation: heterogeneity over space and time. *Ecology*

895   *Letters*, *15*(2), 164–175. https://doi.org/10.1111/j.1461-0248.2011.01716.x

896   Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N.,

897   Cooper, E. J., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and

898   links to recent summer warming. *Nature Climate Change*, *2*(6), 453–457.

899   https://doi.org/10.1038/nclimate1465

900   Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Fosaa, A. M., Gould, W. A., Hermanutz,

901   L., … Walker, M. (2015). Experiment, monitoring, and gradient methods used to infer

902   climate change effects on plant communities yield consistent patterns. *Proceedings of*

903   *the National Academy of Sciences*, *112*(2), 448–452.

904   https://doi.org/10.1073/pnas.1410088112

905   Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J.,

906   Steltzer, H., & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine

907   ecosystems to altered seasonality under climate change. *Global Change Biology*,

908   *20*(10), 3256–3269. https://doi.org/10.1111/gcb.12568

909   Forchhammer, M. C. (2017). Sea-ice induced growth decline in Arctic shrubs. *Biology*

910   *Letters*, *13*(8), 20170122. https://doi.org/10.1098/rsbl.2017.0122

911   Forchhammer, M. C., Post, E., & Stenseth, N. C. (1998). Breeding phenology and climate¨.

912   *Nature*, *391*(6662), 29–30. https://doi.org/10.1038/34070

913   Forkel, M., Carvalhais, N., Rodenbeck, C., Keeling, R., Heimann, M., Thonicke, K., …

914   Reichstein, M. (2016). Enhanced seasonal CO_2 exchange caused by amplified plant

915   productivity in northern ecosystems. *Science*. https://doi.org/10.1126/science.aac4971

916   Freedman, B., Svoboda, J., & Henry, G. H. R. (1994). Alexandra Fiord – An ecological oasis

917   in the polar desert. In J. Svoboda & B. Freedman (Eds.), *Ecology of a polar oasis:*

918   *Alexandra Fiord, Ellesmere Island, Canada* (pp. 1–9). Toronto: Captus University

919   Publications.

920   Gelman, A., & Rubin, D. B. (1992). Inference from Iterative Simulation Using Multiple

921   Sequences. *Statistical Science*, *7*(4), 457–472.

922   Gustine, D., Barboza, P., Adams, L., Griffith, B., Cameron, R., & Whitten, K. (2017).

923   Advancing the match-mismatch framework for large herbivores in the Arctic:

924   Evaluating the evidence for a trophic mismatch in caribou. *PLOS ONE*, *12*(2),

925   e0171807. https://doi.org/10.1371/journal.pone.0171807

926   Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed

927   Models: The **MCMCglmm** *R* Package. *Journal of Statistical Software*, *33*(2).

928   https://doi.org/10.18637/jss.v033.i02

929   Hadfield, J. D. (2017). MCMCglmm Course Notes. Retrieved 12 March 2018, from

930   https://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf

931   Hadfield, J. D., Heap, E. A., Bayer, F., Mittell, E. A., & Crouch, N. M. A. (2013). Intraclutch

932   Differences in Egg Characteristics Mitigate the Consequences of Age-Related

933   Hierarchies in a Wild Passerine. *Evolution*, *67*(9), 2688–2700.

934   https://doi.org/10.1111/evo.12143

935   Haugen, R. K., & Brown, J. (1980). Coastal-Inland Distributions of Summer Air Temperature

936   and Precipitation in Northern Alaska. *Arctic and Alpine Research*, *12*(4), 403–412.

937   https://doi.org/10.2307/1550491

938   Heide, O. M. (1989). Environmental Control of Flowering and Viviparous Proliferation in

939   Seminiferous and Viviparous Arctic Populations of Two Poa Species. *Arctic and*

940   *Alpine Research*, *21*(3), 305. https://doi.org/10.2307/1551570

941   Heide, O. M. (1992). Experimental Control of Flowering in Carex bigelowii. *Oikos*, *65*(3),

942   371. https://doi.org/10.2307/3545552

943   Henry, G. H. R., & Molau, U. (1997). Tundra plants and climate change: the International

944   Tundra Experiment (ITEX). *Global Change Biology*, *3*(S1), 1–9.

945   https://doi.org/10.1111/j.1365-2486.1997.gcb132.x

946   Hinkler, J., Hansen, B. U., Tamstorf, M. P., Sigsgaard, C., & Petersen, D. (2008). Snow and

947   Snow-Cover in Central Northeast Greenland. In *Advances in Ecological Research*

948   (Vol. 40, pp. 175–195). Academic Press. https://doi.org/10.1016/S0065-

949   2504(07)00008-6

Hobbie, J. E., Shaver, G. R., Rastetter, E. B., Cherry, J. E., Goetz, S. J., Guay, K. C., …
Kling, G. W. (2017). Ecosystem responses to climate change at a Low Arctic and a
High Arctic long-term research site. *Ambio*, *46*(1), 160–173.
https://doi.org/10.1007/s13280-016-0870-x

Hollister, R. D., Webber, P. J., & Tweedie, C. E. (2005). The response of Alaskan arctic
tundra to experimental warming: differences between short- and long-term responses.
Global Change Biology, *11*(4), 525–536. https://doi.org/10.1111/j.1365-
2486.2005.00926.x

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid
advancement of spring in the High Arctic. *Current Biology*, *17*(12), R449–R451.
https://doi.org/10.1016/j.cub.2007.04.047

Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K., & Forchhammer, M. C. (2013).
Shorter flowering seasons and declining abundance of flower visitors in a warmer
Arctic. *Nature Climate Change*, *3*(8), 759–763. https://doi.org/10.1038/nclimate1909

Huelber, K., Gottfried, M., Pauli, H., Reiter, K., Winkler, M., & Grabherr, G. (2006).
Phenological Responses of Snowbed Species to Snow Removal Dates in the Central
Alps: Implications for Climate Warming. *Arctic, Antarctic, and Alpine Research*,
38(1), 99–103. https://doi.org/10.1657/1523-0430(2006)038[0099:PROSST]2.0.CO;2

Iler, A. M., Inouye, D. W., Schmidt, N. M., & Høye, T. T. (2017). Detrending phenological
time series improves climate–phenology analyses and reveals evidence of plasticity.
Ecology, *98*(3), 647–655.

IPCC. (2014). *Climate change 2014: Synthesis Report. Contribution of Working Groups I, II
and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate
Change*. (R. K. Pachauri & L. Mayer, Eds.). Geneva, Switzerland: IPCC.

974   Jonas, T., Rixen, C., Sturm, M., & Stoeckli, V. (2008). How alpine plant growth is linked to

975   snow cover and climate variability. *Journal of Geophysical Research*, *113*(G3).

976   https://doi.org/10.1029/2007JG000680

977   Jones, H. G. (2013). *Plants and Microclimate: A Quantitative Approach to Environmental*

978   *Plant Physiology* (3rd ed.). Cambridge University Press.

979   https://doi.org/10.1017/CBO9780511845727

980   Kankaanpää, T., Skov, K., Abrego, N., Lund, M., Schmidt, N. M., & Roslin, T. (2018).

981   Spatiotemporal snowmelt patterns within a high Arctic landscape, with implications

982   for flora and fauna. *Arctic, Antarctic, and Alpine Research*, *50*(1), e1415624.

983   https://doi.org/10.1080/15230430.2017.1415624

984   Keller, F., & Körner, C. (2003). The Role of Photoperiodism in Alpine Plant Development.

985   *Arctic, Antarctic, and Alpine Research*, *35*(3), 361–368. https://doi.org/10.1657/1523-

986   0430(2003)035[0361:TROPIA]2.0.CO;2

987   Keogan, K., Daunt, F., Wanless, S., Phillips, R. A., Walling, C. A., Agnew, P., … Lewis, S.

988   (2018). Global phenological insensitivity to shifting ocean temperatures among

989   seabirds. *Nature Climate Change*, *8*(4), 313–318. https://doi.org/10.1038/s41558-018-

990   0115-z

991   Kerby, J. T., & Post, E. (2013a). Advancing plant phenology and reduced herbivore

992   production in a terrestrial system associated with sea ice decline. *Nature*

993   *Communications*, *4*. https://doi.org/10.1038/ncomms3514

994   Kerby, J. T., & Post, E. (2013b). Capital and income breeding traits differentiate trophic

995   match–mismatch dynamics in large herbivores. *Philosophical Transactions of the*

996   *Royal Society of London B: Biological Sciences*, *368*(1624), 20120484.

997   https://doi.org/10.1098/rstb.2012.0484

998   Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., &

999   Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species

1000   interactions over recent decades. *Proceedings of the National Academy of Sciences*,

1001   201714511. https://doi.org/10.1073/pnas.1714511115

1002   Klosterman, S. T., Melaas, E., Wang, J., Martinez, A., Frederick, S., O'Keefe, J., …

1003   Richardson, A. D. (2018). Fine-scale perspectives on landscape phenology from

1004   unmanned aerial vehicle (UAV) photography. *Agricultural and Forest Meteorology*,

1005   *248*, 397–407. https://doi.org/10.1016/j.agrformet.2017.10.015

1006   Kuoo, G., & Suzuki, S. (1999). Flowering phenology of alpine plant Communities along a

1007   gradient of snowmelt timing. *Polar Bioscience*, *12*, 100–113.

1008   Larsen, K. S., Ibrom, A., Jonasson, S., Michelsen, A., & Beier, C. (2007). Significance of

1009   cold-season respiration and photosynthesis in a subarctic heath ecosystem in Northern

1010   Sweden. *Global Change Biology*, *13*(7), 1498–1508. https://doi.org/10.1111/j.1365-

1011   2486.2007.01370.x

1012   Linkosalmi, M., Aurela, M., Tuovinen, J.-P., Peltoniemi, M., Tanis, C. M., Arslan, A. N., …

1013   Laurila, T. (2016). Digital photography for assessing the link between vegetation

1014   phenology and CO_2 exchange in two contrasting northern ecosystems. *Geoscientific*

1015   *Instrumentation, Methods and Data Systems*, *5*(2), 417–426.

1016   https://doi.org/10.5194/gi-5-417-2016

1017   Liston, G. E., Mcfadden, J. P., Sturm, M., & Pielke, R. A. (2008). Modelled changes in arctic

1018   tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change*

1019   *Biology*, *8*(1), 17–32. https://doi.org/10.1046/j.1354-1013.2001.00416.x

1020   Lundell, R., Saarinen, T., & Hänninen, H. (2010). Effects of snowmelt on the springtime

1021   photosynthesis of the evergreen dwarf shrub Vaccinium vitis-idaea. *Plant Ecology &*

1022   *Diversity*, *3*(2), 121–130. https://doi.org/10.1080/17550874.2010.497195

1023   MacDonald, M. K., Pomeroy, J. W., & Pietroniro, A. (2010). On the importance of

1024   sublimation to an alpine snow mass balance in the Canadian Rocky Mountains.

1025   *Hydrology and Earth System Sciences*, *14*(7), 1401–1415.

1026   https://doi.org/10.5194/hess-14-1401-2010

1027   Macias-Fauria, M., Karlsen, S. R., & Forbes, B. C. (2017). Disentangling the coupling

1028   between sea ice and tundra productivity in Svalbard. *Scientific Reports*, *7*(1), 8586.

1029   https://doi.org/10.1038/s41598-017-06218-8

1030   Macias-Fauria, M., & Post, E. (2018). Effects of sea ice on Arctic biota: an emerging crisis

1031   discipline. *Biology Letters*, *14*(3), 20170702. https://doi.org/10.1098/rsbl.2017.0702

1032   Meier, W. N., Fetterer, F., Savoie, M., Mallory, S., Duerr, R., & Stroeve, J. (2017).

1033   *NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration,*

1034   *Version 3. NOAA/NSIDC daily sea Ice CDR.* Boulder, Colorado USA: NSIDC:

1035   National Snow and Ice Data Center. Retrieved from

1036   https://doi.org/10.7265/N59P2ZTG

1037   Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., … Zust, A. (2006).

1038   European phenological response to climate change matches the warming pattern.

1039   *Global Change Biology*, *12*(10), 1969–1976. https://doi.org/10.1111/j.1365-

1040   2486.2006.01193.x

1041   Molau, U., & Mølgaard, P. (1996). International Tundra Experiment Manual. Retrieved from

1042   https://www.gvsu.edu/itex/library-8.htm

1043   Molau, U., Urban Nordenhäll, & Bente Eriksen. (2005). Onset of Flowering and Climate

1044   Variability in an Alpine Landscape: A 10-Year Study from Swedish Lapland.

1045   *American Journal of Botany*, *92*(3), 422–431.

1046 Mølgaard P., & Christensen K. (2003). Response to experimental warming in a population of

1047   Papaver radicatum in Greenland. *Global Change Biology*, *3*(S1), 116–124.

1048   https://doi.org/10.1111/j.1365-2486.1997.gcb140.x

1049 Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., Sæther, B., &

1050   Fryxell, J. (2013). Understanding scales of movement: animals ride waves and ripples

1051   of environmental change. *Journal of Animal Ecology*, *82*(4), 770–780.

1052   https://doi.org/10.1111/1365-2656.12045

1053 Myers-Smith, I. H., Grabowski, M. M., Thomas, H. J. D., Angers-Blondin, S., Daskalova, G.

1054   N., Bjorkman, A. D., … Eckert, C. D. (2019). Eighteen years of ecological

1055   monitoring reveals multiple lines of evidence for tundra vegetation change.

1056   *Ecological Monographs*, e01351. https://doi.org/10.1002/ecm.1351

1057 Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014).

1058   Where is positional uncertainty a problem for species distribution modelling.

1059   *Ecography*, *37*, 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

1060 NSIDC. (2018). Polar Stereographic Projection and Grid | National Snow and Ice Data

1061   Center. Retrieved 7 March 2018, from https://nsidc.org/data/polar-

1062   stereo/ps_grids.html

1063 Oberbauer, S. F., Elmendorf, S. C., Troxler, T. G., Hollister, R. D., Rocha, A. V., Bret-Harte,

1064   M. S., … Welker, J. M. (2013). Phenological response of tundra plants to background

1065   climate variation tested using the International Tundra Experiment. *Philosophical*

1066   *Transactions of the Royal Society of London B: Biological Sciences*, *368*(1624),

1067   20120481. https://doi.org/10.1098/rstb.2012.0481

1068 Panchen, Z. A., & Gorelick, R. (2017). Prediction of Arctic plant phenological sensitivity to

1069   climate change from historical records. *Ecology and Evolution*, *7*(5), 1325–1338.

1070   https://doi.org/10.1002/ece3.2702

1071   Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E. S., Høgda, K.-A., Karlsen, S. R., …

1072   Myneni, R. B. (2016). Changes in growing season duration and productivity of

1073   northern vegetation inferred from long-term remote sensing data. *Environmental*

1074   *Research Letters*, *11*(8), 084001. https://doi.org/10.1088/1748-9326/11/8/084001

1075   Parker, T. C., Tang, J., Clark, M. B., Moody, M. M., & Fetcher, N. (2017). Ecotypic

1076   differences in the phenology of the tundra species Eriophorum vaginatum reflect sites

1077   of origin. *Ecology and Evolution*, *7*(22), 9975–9786.

1078   https://doi.org/10.1002/ece3.3445

1079   Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts

1080   across natural systems. *Nature*, *421*(6918), 37–42.

1081   https://doi.org/10.1038/nature01286

1082   Pedersen, S. H., Liston, G. E., Tamstorf, M. P., Westergaard-Nielsen, A., & Schmidt, N. M.

1083   (2015). Quantifying Episodic Snowmelt Events in Arctic Ecosystems. *Ecosystems*,

1084   *18*(5), 839–856. https://doi.org/10.1007/s10021-015-9867-8

1085   Peng, G., Meier, W. N., Scott, D. J., & Savoie, M. H. (2013). A long-term and reproducible

1086   passive microwave sea ice concentration data record for climate studies and

1087   monitoring. *Earth System Science Data*, *5*(2), 311–318. https://doi.org/10.5194/essd-

1088   5-311-2013

1089   Phoenix, G. K., & Bjerke, J. W. (2016). Arctic browning: extreme events and trends

1090   reversing arctic greening. *Global Change Biology*, *22*(9), 2960–2962.

1091   https://doi.org/10.1111/gcb.13261

1092   Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., … Vesala, T.

1093   (2008). Net carbon dioxide losses of northern ecosystems in response to autumn

1094   warming. *Nature*, *451*(7174), 49–52. https://doi.org/10.1038/nature06444

1095   Pomeroy, J. W., Marsh, P., & Gray, D. M. (1997). Application of a distributed blowing snow

1096   model to the Arctic. *Hydrological Processes*, *11*(11), 1451–1464.

1097   https://doi.org/10.1002/(SICI)1099-1085(199709)11:11<1451::AID-

1098   HYP449>3.0.CO;2-Q

1099   Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., … Walker,

1100   D. A. (2013). Ecological Consequences of Sea-Ice Decline. *Science*, *341*(6145), 519–

1101   524. https://doi.org/10.1126/science.1235225

1102   Post, E., & Høye, T. T. (2013). Advancing the long view of ecological change in tundra

1103   systems. *Philosophical Transactions of the Royal Society of London B: Biological*

1104   *Sciences*, *368*(1624), 20120477. https://doi.org/10.1098/rstb.2012.0477

1105   Post, E., Kerby, J. T., Pedersen, C., & Steltzer, H. (2016). Highly individualistic rates of plant

1106   phenological advance associated with arctic sea ice dynamics. *Biology Letters*,

1107   *12*(12), 20160332. https://doi.org/10.1098/rsbl.2016.0332

1108   Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R.,

1109   Elberling, B., … Aastrup, P. (2009). Ecological Dynamics Across the Arctic

1110   Associated with Recent Climate Change. Science, 325(5946), 1355–1358.

1111   https://doi.org/10.1126/science.1173113

1112   Post, E., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Warming, plant

1113   phenology and the spatial dimension of trophic mismatch for large herbivores.

1114   *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1646), 2005–

1115   2013. https://doi.org/10.1098/rspb.2008.0463

1116   Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and

1117   warming with latitude over the past century. *Scientific Reports*, *8*(1), 3927.

1118   https://doi.org/10.1038/s41598-018-22258-0

1119   Prevéy, J. S., Rixen, C., Rüger, N., Høye, T. T., Bjorkman, A. D., Myers-Smith, I. H., …

1120   Wipf, S. (2019). Warming shortens flowering seasons of tundra plant communities.

1121   *Nature Ecology & Evolution*, *3*(1), 45. https://doi.org/10.1038/s41559-018-0745-6

1122   Prevéy, J. S., Vellend, M., Rüger, N., Hollister, R. D., Bjorkman, A. D., Myers-Smith, I. H.,

1123   … Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder

1124   sites: implications for convergence across northern latitudes. *Global Change Biology*,

1125   *23*(7), 2660–2671. https://doi.org/10.1111/gcb.13619

1126   R Core Team. (2018). *R: A Language and Environment for Statistical Computing*. Vienna,

1127   Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-

1128   project.org

1129   Rango, A., & Martinec, J. (1995). Revisiting the Degree-Day Method for Snowmelt

1130   Computations. *Journal of the American Water Resources Association*, *31*(4), 657–

1131   669. https://doi.org/10.1111/j.1752-1688.1995.tb03392.x

1132   Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., …

1133   Frolking, S. (2018). Tracking vegetation phenology across diverse North American

1134   biomes using PhenoCam imagery. *Scientific Data*, *5*, 180028.

1135   https://doi.org/10.1038/sdata.2018.28

1136   Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M.

1137   (2013). Climate change, phenology, and phenological control of vegetation feedbacks

1138   to the climate system. *Agricultural and Forest Meteorology*, *169*, 156–173.

1139   https://doi.org/10.1016/j.agrformet.2012.09.012

1140   Sawyer, H., & Kauffman, M. J. (2011). Stopover ecology of a migratory ungulate. *Journal of*

1141   *Animal Ecology*, *80*(5), 1078–1087. https://doi.org/10.1111/j.1365-

1142   2656.2011.01845.x

1143   Scheifinger, H., Menzel, A., Koch, E., Peter, C., & Ahas, R. (2002). Atmospheric

1144   mechanisms governing the spatial and temporal variability of phenological phases in

1145   central Europe. *International Journal of Climatology*, *22*(14), 1739–1755.

1146   https://doi.org/10.1002/joc.817

1147   Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.

1148   *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-

1149   210X.2010.00012.x

1150   Schmidt, N. M., Christensen, T. R., & Roslin, T. (2017). A high arctic experience of uniting

1151   research and monitoring. *Earth's Future*, *5*(7), 650–654.

1152   https://doi.org/10.1002/2017EF000553

1153   Schmidt, N. M., Hansen, L. H., Hansen, J., Berg, T. B., & Meltofte, H. (2016). BioBasis

1154   Manual - 19th Edition. Aarhus University Department of Bioscience. Retrieved from

1155   http://zackenberg.dk/fileadmin/Resources/DMU/GEM/Zackenberg/Nye_Zac_files/Bi

1156   oBasis_manual_2016.pdf

1157   Schmidt, N. M., Mosbacher, J. B., Nielsen, P. S., Rasmussen, C., Høye, T. T., & Roslin, T.

1158   (2016). An ecological function in crisis? The temporal overlap between plant

1159   flowering and pollinator function shrinks as the Arctic warms. *Ecography*, *39*(12),

1160   1250–1252. https://doi.org/10.1111/ecog.02261

1161   Schwartz, M. D. (Ed.). (2013). *Phenology: An Integrative Environmental Science*. Dordrecht:

1162   Springer Netherlands. Retrieved from http://link.springer.com/10.1007/978-94-007-

1163   6925-0

1164   Screen, J. A., & Simmonds, I. (2010). The central role of diminishing sea ice in recent Arctic

1165   temperature amplification. *Nature*, *464*(7293), 1334–1337.

1166   https://doi.org/10.1038/nature09051

1167 Semenchuk, P. R., Gillespie, M. A. K., Rumpf, S. B., Baggesen, N., Elberling, B., & Cooper,

1168   E. J. (2016). High Arctic plant phenology is determined by snowmelt patterns but

1169   duration of phenological periods is fixed: an example of periodicity. *Environmental*

1170   *Research Letters*, *11*(12), 125006. https://doi.org/10.1088/1748-9326/11/12/125006

1171 Sherwood, J. A., Debinski, D. M., Caragea, P. C., & Germino, M. J. (2017). Effects of

1172   experimentally reduced snowpack and passive warming on montane meadow plant

1173   phenology and floral resources. *Ecosphere*, *8*(3). https://doi.org/10.1002/ecs2.1745

1174 Sørensen, T. (1941). Temperature relations and phenology of northeast Greenland flowering

1175   plants. *Meddelelser Om Grønland*, (125), 1–305.

1176 Starr, G., & Oberbauer, S. F. (2003). Photosynthesis of arctic evergreens under snow:

1177   implications for tundra ecosystem carbon balance. *Ecology*, *84*(6), 1415–1420.

1178   https://doi.org/10.1890/02-3154

1179 Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin, F. S., & Racine, C. H.

1180   (2001). Snow–Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic

1181   Implications. *Journal of Climate*, *14*(3), 336–344. https://doi.org/10.1175/1520-

1182   0442(2001)014<0336:SSIIAT>2.0.CO;2

1183 Thackeray, S. J. (2016). Casting your network wide: a plea to scale-up phenological research.

1184   *Biology Letters*, *12*(6), 20160181. https://doi.org/10.1098/rsbl.2016.0181

1185 Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., …

1186   Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels.

1187   *Nature*, *535*(7611), 241–245. https://doi.org/10.1038/nature18608

1188 Thórhallsdóttir, T. E. (1998). Flowering phenology in the central highland of Iceland and

1189   implications for climatic warming in the Arctic. *Oecologia*, *114*(1), 43–49.

1190   https://doi.org/10.1007/s004420050418

1191 Tjernström, M., Shupe, M. D., Brooks, I. M., Persson, P. O. G., Prytherch, J., Salisbury, D. J.,

1192   … Wolfe, D. (2015). Warm-air advection, air mass transformation and fog causes

1193   rapid ice melt. *Geophysical Research Letters*, *42*(13), 5594–5602.

1194   https://doi.org/10.1002/2015GL064373

1195 Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H., & Silkin, P. P.

1196   (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia.

1197   *Nature*, *400*(6740), 149–151. https://doi.org/10.1038/22087

1198 van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus

1199   between-subject effects using mixed models. *Animal Behaviour*, *77*(3), 753–758.

1200   https://doi.org/10.1016/j.anbehav.2008.11.006

1201 Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need

1202   for a yardstick. *Proceedings of the Royal Society of London B: Biological Sciences*,

1203   *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

1204 Webber, P. J., & Walker, M. D. (1991). The International Tundra Experiment (ITEX):

1205   resolution. *Arctic Antarctic and Alpine Research*, *23*, 124.

1206 Wheeler, H. C., Høye, T. T., Schmidt, N. M., Svenning, J.-C., & Forchhammer, M. C.

1207   (2015). Phenological mismatch with abiotic conditions—implications for flowering in

1208   Arctic plants. *Ecology*, *96*(3), 775–787. https://doi.org/10.1890/14-0338.1

1209 Wheeler, J. A., Cortés, A. J., Sedlacek, J., Karrenberg, S., Kleunen, M., Wipf, S., …

1210   Cornelissen, H. (2016). The snow and the willows: earlier spring snowmelt reduces

1211   performance in the low-lying alpine shrub Salix herbacea. *Journal of Ecology*, *104*(4),

1212   1041–1050. https://doi.org/10.1111/1365-2745.12579

1213 Winton, M. (2006). Amplified Arctic climate change: What does surface albedo feedback

1214   have to do with it? *Geophysical Research Letters*, *33*(3).

1215   https://doi.org/10.1029/2005GL025244

1216   Wipf, S. (2009). Phenology, growth, and fecundity of eight subarctic tundra species in

1217   response to snowmelt manipulations. *Plant Ecology*, *207*(1), 53–66.

1218   https://doi.org/10.1007/s11258-009-9653-9

1219   Wipf, S., & Rixen, C. (2010). A review of snow manipulation experiments in Arctic and

1220   alpine tundra ecosystems. *Polar Research*, *29*(1), 95–109.

1221   https://doi.org/10.1111/j.1751-8369.2010.00153.x

1222   Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: plant

1223   responses to changes in snow depth and snowmelt timing. *Climatic Change*, *94*(1–2),

1224   105–121. https://doi.org/10.1007/s10584-009-9546-x

1225   Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S.

1226   E., … Cleland, E. E. (2012). Warming experiments underpredict plant phenological

1227   responses to climate change. *Nature*, *485*(7399), 494–497.

1228   https://doi.org/10.1038/nature11014

1229   Wolkovich, E. M., Cook, B. I., & Davies, T. J. (2014). Progress towards an interdisciplinary

1230   science of plant phenology: building predictions across space, time and species

1231   diversity. *New Phytologist*, *201*(4), 1156–1162. https://doi.org/10.1111/nph.12599

1232   Worby, A., & Comiso, J. C. (2004). Studies of the Antarctic sea ice edge and ice extent from

1233   satellite and ship observations. *Remote Sensing of Environment*, *92*(1), 98–111.

1234   https://doi.org/10.1016/j.rse.2004.05.007

1235   Xu, L., Myneni, R. B., Iii, F. S. C., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., … Stroeve,

1236   J. C. (2013). Temperature and vegetation seasonality diminishment over northern

1237   lands. *Nature Climate Change*, *3*(6), 581–586. https://doi.org/10.1038/nclimate1836

1238