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### Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes

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1 **I. Title:** Greater temperature sensitivity of plant phenology at colder sites: implications for  
2 convergence across northern latitudes

3

4 **Running head:** Higher phenological sensitivity at colder sites

5

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49 ITEX, tundra
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51 **Abstract**

52           Warmer temperatures are accelerating the phenology of organisms around the world.  
53 Temperature sensitivity of phenology might be greater in colder, higher-latitude sites than in  
54 warmer regions, in part because small changes in temperature constitute greater relative  
55 changes in thermal balance at colder sites. To test this hypothesis, we examined up to 20  
56 years of phenology data for 47 tundra plant species at 18 high-latitude sites along a climatic  
57 gradient. Across all species, the timing of leaf emergence and flowering were more sensitive  
58 to a given increase in summer temperature at colder than warmer high-latitude locations. A  
59 similar pattern was seen over time for the flowering phenology of a widespread species,  
60 *Cassiope tetragona*. These are among the first results highlighting differential phenological  
61 responses of plants across a climatic gradient, and suggest the possibility of convergence in  
62 flowering times and therefore an increase in gene flow across latitudes as the climate warms.

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## 76 **Introduction**

77           Changes in plant phenology are among the most notable and widespread examples of  
78 climate change impacts across all biomes (Walther et al., 2002; Parmesan & Yohe, 2003;  
79 Badeck et al., 2004; Post, 2013; IPCC, 2014; Thackeray et al., 2016). High-latitude regions  
80 are excellent places to study phenological responses to climate change, as northern regions  
81 are experiencing more rapid warming than lower latitudes (IPCC, 2014; Anderegg &  
82 Diffenbaugh, 2015), and phenological changes may be more pronounced than those  
83 elsewhere on Earth (Høye et al., 2007a; Parmesan, 2007; Oberbauer et al., 2013). Northern  
84 ecosystems are characterized by shorter growing seasons than temperate or tropical  
85 ecosystems, and plants in such environments are under selective pressure to initiate growth  
86 when temperatures become favorable during spring (Shaver & Kummerow, 1992), and thus,  
87 can be particularly sensitive to small changes in temperatures during the growing season  
88 (Bliss, 1962; Billings & Mooney, 1968; Welker et al., 1997).

89           Ecologically important traits, including the timing of phenological events, can vary  
90 within species across environmental and temperature gradients (Weber & Schmid, 1998;  
91 Riihimäki & Savolainen, 2004; Kenta et al., 2011). In the Arctic, small absolute changes in  
92 temperature may represent relatively larger increases in the thermal budgets of plants at cold  
93 sites (Bliss, 1962; Billings, 1992, Oberbauer et al., 2013); hence, one might expect plants at  
94 colder, higher-latitude sites to respond more strongly to the same degree of warming than  
95 those from warmer, lower-latitude sites. Plants growing in high Arctic locations with very  
96 short growing seasons could be under strong selective pressure to initiate growth and  
97 flowering as soon as temperatures are favorable. Differential sensitivity to temperature at  
98 sites with different climatic conditions could, in turn, result in a convergence of flowering  
99 times across sites as the climate warms. Many tundra plant species extend over large  
100 geographical and elevational ranges, with populations of the same species adapted to local

101 environmental conditions (Chapin & Chapin, 1981, McGraw & Antonovics, 1983; Welker et  
102 al., 1997; Bennington et al., 2012). Populations of a species occurring in colder sites have  
103 been found to flower later than those of the same species in warmer sites (Lévesque et al.,  
104 1997; Riihimäki & Savolainen, 2004; Kenta et al., 2011). Consequently, if warmer  
105 temperatures lead to a greater advancement of flowering at colder sites than at warmer sites,  
106 overlap in flowering times across sites will likely increase. This, in turn, could lead to  
107 increased gene flow among populations, with potentially important consequences for  
108 adaptive evolution and the ability of plant species to persist under climate change (Fox, 2003;  
109 Phillimore et al., 2010; Sexton et al., 2011). However, few studies have compared  
110 phenological sensitivities between sites, so we have been unable to predict whether  
111 reproductive phenology will converge, diverge, or show no change as the climate warms in  
112 high latitude regions.

113         Climate change influences the phenology not only of flowering, but also of leaf  
114 emergence and senescence, and therefore ecosystem processes such as carbon dynamics  
115 (Oberbauer et al., 1998; Welker et al., 2004; Oberbauer et al., 2007; Cahoon et al., 2012;  
116 Peñuelas & Filella, 2009). Current process-based vegetation models – which are linked to  
117 global carbon models – assume similar temperature sensitivities of plant species responses  
118 across the Arctic (e.g. Miller & Smith, 2012). However, if growth initiation of plants from  
119 colder regions responds more quickly to warmer temperatures than plants from warmer  
120 regions, then the net balance of carbon exchange from Arctic ecosystems might change  
121 considerably (Oechel et al., 2000; Welker et al., 2004; Sharp et al., 2012; Myers-Smith et al.,  
122 2015; Cahoon et al., 2012). Studies examining differences in the phenological sensitivity of  
123 growth to temperature across species' ranges can thus help improve predictions of the  
124 cumulative responses of high-latitude ecosystems, and associated ecosystem services, to  
125 climate change.

126 In this study, we investigate the variation in phenological responses to warmer  
127 temperatures among sites along a climatic gradient in high northern latitudes. This is one of  
128 the first studies to examine whether the temperature sensitivity of phenology differs among  
129 sites with different climatic conditions within the tundra biome. We use the largest collection  
130 of plot-based high-latitude plant phenological data to date, consisting of more than 23,000  
131 phenological observations, to test the hypothesis that plants from colder northern sites will  
132 have greater temperature sensitivity of leaf and flowering phenology than plants from warmer  
133 northern sites. To specifically investigate if warmer temperatures could lead to converging  
134 flowering times within the distributional range of a given species, we also examined how the  
135 flowering dates of the single most common species in the dataset, *Cassiope tetragona*, have  
136 responded to temperature, and have changed over time, in colder versus warmer sites.  
137 Finally, we examined whether sites with colder mean temperatures and at higher latitudes  
138 have experienced greater changes in spring and summer temperatures over the last 50 years  
139 than warmer or lower-latitude sites. The combination of greater temperature sensitivity of  
140 phenology and greater temperature increases could act synergistically to magnify  
141 phenological convergence across latitudes as the climate warms.

142

## 143 **Material and methods**

### 144 *Site and phenological data description*

145 We examined phenological data for flowering and leaf emergence/senescence from 18  
146 sites along a climatic gradient including sub-Arctic, sub-Arctic alpine, and Arctic tundra  
147 ecosystems (Table 1, Fig. 1). Eleven of the 18 sites in this analysis were established as part of  
148 the International Tundra Experiment (ITEX) network (Webber & Walker, 1991; Henry &  
149 Molau, 1997), and observers at all 18 sites collected data following a standardized phenology  
150 protocol developed for ITEX (Molau & Molgaard, 1996). The phenological status of plant

151 species within plots was recorded one to three times per week over the snow free season, and  
152 this allowed for the estimation of the average day of year when each phenological event  
153 occurred per species per site. Four phenological events were recorded: first flowering, flower  
154 senescence, greening, and leaf senescence (Arft et al., 1999). Phenological events were  
155 defined differently depending on plant species (Molau & Molgaard, 1996), but were recorded  
156 consistently over time for each species in each plot. Depending on the species, ‘flowering’  
157 was defined as the date when either the first flower was open, the first pollen was visible, or  
158 the first anthers were exposed; ‘flower senescence’ was when anthers withered, or petals  
159 dropped; ‘greening’ was the date of leaf emergence, when the first new leaf was visible or  
160 open; and ‘leaf senescence’ was when the first color change of a leaf was observed.

161 We used the database compiled by an earlier ITEX synthesis (Oberbauer et al., 2013),  
162 with the addition of recent years of phenology observations for five of the eight sites in that  
163 database, and observations from 10 new sites. For our analyses, we included only plant  
164 species that occurred at two or more sites, and that had three or more years of phenological  
165 observations. Overall, five sites in the analyses had over 15 years of phenological  
166 observations, six sites had over ten years of observations, one site had 5 years, and six sites  
167 had 4 years of observations (Table 1). This screening resulted in a compilation of  
168 phenological observations for a total of 45 species at 18 sites for flowering, 15 species at 11  
169 sites for flower senescence, 19 species at nine sites for greening, and 18 species at ten sites  
170 for leaf senescence (Table S1).

171

### 172 *Temperature sensitivity of phenology*

173 Temperature sensitivities of phenological events for each species at each site were  
174 calculated as the slope of the relationship between the day of year of a phenological event  
175 (flowering, flower senescence, greening, or leaf senescence) and average temperature in that



176 year over a summer time-window (model structure described below). The summer time-  
177 window was defined as either average May-June, June, June-July, or June-August mean  
178 monthly temperatures per year. We specified the summer time-window separately for each  
179 species and phenological event on the basis of the average time of that phenological event  
180 over the period observed across all sites (Table S1). Species at different sites initiated  
181 phenological events at different times, however, we use a common summer temperature  
182 window for each species and event across all sites to ensure that the units of the sensitivity  
183 estimates **were** identical for each species across sites. All monthly temperature data used to  
184 calculate sensitivities were obtained from local site climate records (**Data S2**). We used  
185 average monthly temperatures because they were the only climate variable available from  
186 local weather stations for all sites included in our analyses. While we recognize that  
187 cumulative daily temperatures and the timing of snowmelt have a strong influence on tundra  
188 plant phenology (Høye et al., 2007b; Semenchuk et al., 2013; Bjorkman et al., 2015), those  
189 data were not available for many of the sites. To address potential biases resulting from  
190 species reaching phenological stages at different times at different sites, we also analyzed  
191 data using separate summer time-windows based on the average time of a phenological event  
192 for each species at each site. We additionally analyzed data using only June temperature for  
193 all species, phenological events, and sites, because June temperature was the strongest  
194 predictor of the timing of all phenological events across the dataset (Table S6).

195 Chilling temperatures over winter (Cook et al., 2012; Clark et al., 2014), extreme  
196 events (Phoenix & Bjerke, 2016), and lag effects from temperatures experienced the previous  
197 year (Mulder et al., 2016) can also influence the timing of phenology of plants. However, in  
198 this dataset, we found no relationships between winter temperatures or monthly temperatures  
199 of the previous year and the timing of phenological events (data not shown).

200 To statistically test if species at colder sites shifted phenological dates more strongly  
201 in response to the same degree of warming than those from warmer sites, we then modeled  
202 the response of temperature sensitivities (described above) to the mean summer (June-  
203 August) temperature of sites from 1981 to 2010 using a Bayesian hierarchical modeling  
204 approach (described below). We used a two-level model in which species-level phenological  
205 sensitivities to temperature and the associated uncertainties were used to estimate site-level  
206 phenological responses and their relationship with mean summer temperature across sites.  
207 We chose mean summer temperature over the last 30 years as the main predictor variable at  
208 the site level because summer temperatures are strongly associated with growth and  
209 phenology of many tundra species (Thórhallsdóttir, 1998; Elmendorf et al., 2012a;  
210 Oberbauer, et al. 2013; Myers-Smith et al., 2015). Average June-August temperatures at sites  
211 ranged from 2.8° C to 11.9° C (Fig. 1). Mean summer temperatures for sites were obtained  
212 from local weather stations when available (Table 1; Data S2). For several sites, temperature  
213 data were not available for months or years when the phenological events were not recorded.  
214 If no long-term (1981 – 2010) weather data were available near sites, mean summer  
215 temperatures were estimated using 0.5° gridded temperature data from the Climate Research  
216 Unit (CRU) TS3.21 (Harris et al., 2014; Table 1). June-August CRU data were strongly  
217 correlated with local temperature data for those cases where both were available ( $R^2$  from  
218 0.71 to 0.99).

219

#### 220 *Phenology model description*

221 We assumed that the phenology of a species could vary among different plots within a  
222 site due to effects of local topography on microclimate (plot-by-species-combinations are  
223 indexed by the letter *i*), but that the phenological response of a species to temperature would  
224 not differ among plots within a site (site-by-species-combinations are indexed by the letter *j*).

225 We modeled the date of the phenological event ( $DOY$ ) as a function of temperature over the  
 226 summer time-window per site ( $s$ ) in a given year ( $y$ ) ( $temp_{y,s}$ ), with  $a_i$  being the plot-by-  
 227 species-level intercept,  $b_j$  the site-by-species-level slope, and  $\sigma_j$  the variation of observed  
 228 dates ( $DOY_{i,y}$ ) around the prediction at the site-by-species level

$$229 \quad DOY_{i,y} \sim Normal(a_i + b_j \cdot temp_{y,s}, \sigma_j).$$

230 Site-by-species level slopes ( $b_j$ ), or the temperature sensitivities of phenology per species,  
 231 were assumed to be normally distributed around the average community response of  
 232 phenology to temperature at that site ( $\beta_s$ )

$$233 \quad b_j \sim Normal(\beta_s, \sigma_s),$$

234 which was fitted as a function of average summer temperature ( $avsummertemp_s$ ):

$$235 \quad \beta_s \sim Normal(\gamma_0 + \gamma_1 \cdot avsummertemp_s, \sigma_\beta).$$

236 If there was only one species at a site, the site-level slope was estimated directly:

$$237 \quad DOY_{i,y} \sim Normal(a_i + \beta_s \cdot temp_{y,s}, \sigma_j).$$

238 Slopes of the same species at different sites were assumed to be independent of each other.

239 We tested the normality of the data by running a model where species-by-site slopes were fit  
 240 independently from each other and by visually assessing the distribution for each site. Our  
 241 results demonstrated that the assumption of a normal distribution was not violated at any site  
 242 and that a normal distribution is a good description of site-level variation of species'  
 243 temperature sensitivity. Because we do not investigate how phenology varies directly with  
 244 summer temperature between sites; but rather, we investigate how the temperature sensitivity  
 245 of phenology (i.e. the change in phenology per °C) varies among sites with different mean  
 246 summer temperatures, we have not within-subject mean-centered the site-level temperature  
 247 data as recommended in other similar hierarchical modelling approaches where site is  
 248 included as a random effect (Phillimore et al., 2013; van de Pol and Wright, 2009).

249 For this model, we did not include both plot and year random effects (to account for  
250 the non-independence of plots measured repeatedly over time as well as the non-  
251 independence of observations conducted in the same year at a given site) because some sites  
252 had very few yearly observations, and including both plot and year random effects resulted in  
253 a model that did not converge. We thus included only the plot effect in the model presented  
254 here, and ran a separate version of the analysis including a year random effect (but no plot  
255 random effect), which demonstrated the same overall relationship (Data S3.1). Finally, we  
256 also analyzed data using simple linear regressions and a mixed-model framework using the R  
257 package lme4 (Bates et al. 2015), which gave similar results (Data S3.2). To investigate if  
258 the variation in the number of years that sites were sampled influenced our results, we also  
259 performed two separate analyses for the flowering data, one limited to sites with ten or more  
260 years of data, and the other limited to sites with less than ten years of data. Both analyses  
261 gave similar results to the analysis that included all sites (Table S3.3).

262 Bayesian hierarchical modeling allowed us to incorporate the uncertainties of species-  
263 and site-level phenological responses in the final correlation of site climate and site-level  
264 phenological responses (Data S4, Latimer, 2007). We fit Bayesian models using the program  
265 Stan, accessed using the package Rstan (Stan Development team, 2015). We used flat priors  
266 for all parameter estimates. Each model was run with two chains of 20,000 iterations, using  
267 Hamiltonian Monte Carlo (HMC) sampling. We checked for convergence of chains for all  
268 parameters both visually with trace plots and with the Gelman-Rubin convergence statistic  
269 (Gelman & Rubin, 1992). Trace plots showed that chains mixed well and converged to  
270 stationary distributions for all parameters estimates. Gelman-Rubin convergence statistics for  
271 parameter estimates of all models were  $< 1.02$ .

272

273

274 *Flowering of Cassiope tetragona*

275           We additionally tested whether the flowering times of the single most common  
276 species in the dataset, the evergreen dwarf shrub *Cassiope tetragona*, showed greater  
277 temperature sensitivity in colder versus warmer locations. We had flowering observations of  
278 *C. tetragona* at eight sites, with four or more years of observations per site, so we were able  
279 to perform a robust intraspecific analysis using this species. The relatively long times-series  
280 of *C. tetragona* observations at sites (4-19 years) also allowed us to test whether the  
281 flowering dates of *C. tetragona* have advanced more at colder sites than at warmer sites over  
282 time. For these analyses, we calculated the temperature sensitivities of flowering of *C.*  
283 *tetragona* to yearly June temperatures, and the change in the day of year of flowering of *C.*  
284 *tetragona* per year at each site. We then compared these temperature sensitivities and  
285 temporal changes to the mean summer (June-August) temperature of sites from 1981 to 2010  
286 using the Bayesian modelling framework described above. Stan model specifications for the  
287 phenological models used for all species and *C. tetragona* are presented in Data S4.

288

289 *Temperature change over time*

290           To test whether sites with colder or higher-latitude sites have experienced greater  
291 changes in spring and summer temperatures over the last 50 years than warmer or lower-  
292 latitude sites, we analyzed the temperature data for the 18 sites included in these analyses. To  
293 identify longer-term trends in temperature change, we used CRU 0.5° gridded temperature  
294 data (Harris et al., 2014) to examine temperature change over a longer period (1960–2013)  
295 than the period we used to estimate mean summer temperature at each site (1981–2010). To  
296 determine how spring and summer temperature have changed at northern sites over time, we  
297 regressed CRU temperature data for each site against year to calculate the change in May,  
298 June, July, and August temperatures from 1960–2013. Then, to examine if colder sites at

299 higher latitudes had experienced more warming over time than lower, warmer sites, we  
300 compared the temperature changes to both the mean summer temperature of sites from 1981–  
301 2010, and also to site latitude using simple linear regressions. All statistical analyses were  
302 conducted in the statistical program R 3.2.2 (R Core Team, 2015).

303

## 304 **Results**

### 305 *Temperature sensitivity of phenology*

306 Overall, the temperature sensitivity of the timing of flowering was greater (i.e., the  
307 slopes of the relationship between flowering date and temperature were more strongly  
308 negative) at colder sites than at warmer sites (Fig. 2a, Fig. S5). The temperature sensitivity of  
309 greening was also greater at colder sites (Fig. 2c). However, there were no differences  
310 between colder and warmer Arctic sites in the temperature sensitivity of either flower or leaf  
311 senescence dates (Figs. 2b, 2d). Alternative analyses that calculated slopes for phenological  
312 sensitivities using either different summer temperature time-windows for each species and  
313 site or using June temperature for all species and sites gave similar results to those presented  
314 in the main text (Table S6).

### 315 *Flowering of *Cassiope tetragona**

316 Similar to results for all species, the temperature sensitivity of flowering of *C.*  
317 *tetragona* was greater at colder sites than at warmer sites, however, the 95% credible interval  
318 for the common slope across sites overlapped with zero (Fig. 3a). Additionally, flowering  
319 dates of *C. tetragona* have shifted earlier per year at colder than at warmer sites over time  
320 (Fig. 3b).

321

322

323

324 *Temperature change over time*

325 Over the period 1960–2013, May and June temperatures increased slightly more at  
326 colder sites than warmer sites (May:  $F_{1,16} = 2.98$ ,  $P = 0.10$ ; June:  $F_{1,16} = 5.07$ ,  $P = 0.04$ , Fig.  
327 4a,b) and at higher latitudes than at lower latitudes (May:  $F_{1,16} = 8.62$ ,  $P = 0.01$ ; June:  $F_{1,16} =$   
328  $10.59$ ,  $P = 0.005$  Fig. S7a,b). Changes in July and August temperatures over the last 40 years  
329 showed no significant trends with mean summer temperature or latitude of sites (all  $F_{1,16} <$   
330  $0.45$ ,  $P > 0.51$ , Figs. 4c,d and S7c,d).

331

332 **Discussion**

333 We found evidence across species for greater temperature sensitivity of greening and  
334 flowering phenology of tundra plants in colder, higher-latitude sites than at warmer, lower-  
335 latitude sites. We also observed that a single widespread species, *Cassiope tetragona*, has  
336 shifted dates of flowering earlier at colder locations than at warmer locations over time.  
337 Thus, our study demonstrates that tundra plant species respond differently to environmental  
338 variation across large-scale climatic gradients. Additionally, we found that the magnitude of  
339 spring and early summer temperature increase over the past 50 years has been greater in  
340 colder, higher-latitude sites than in warmer, lower-latitude sites, which is in agreement with  
341 previous findings and predictions of climate change in the Arctic (Overpeck et al., 1997;  
342 Hinzman et al., 2005; Hill & Henry, 2011; IPCC, 2014). The combination of greater  
343 temperature sensitivity of flowering phenology in colder versus warmer sites, and more rapid  
344 warming in the north, strongly suggest the likelihood of flowering times converging across  
345 climatic gradients as the climate continues to warm.

346 The greater temperature sensitivity of flowering phenology we observed at colder,  
347 more northern sites contrasts with other individual- and population-level responses of tundra  
348 plants to warming (Elmendorf et al., 2012a, 2012b; Myers-Smith et al., 2015). Specifically,

349 previous studies have found greater plant abundance changes with warming (Walker et al.,  
350 2006; Elmendorf et al., 2012a, 2012b) and greater climate sensitivity of shrub growth rings  
351 (Myers-Smith et al., 2015) in warmer, low- and mid-Arctic rather than high-Arctic  
352 ecosystems. Temperature sensitivity of flowering phenology may be greater in higher latitude  
353 ecosystems because reproductive strategies involving flowering and seed development may  
354 be more important where there is often more bare ground for seeds to successfully colonize  
355 (Wookey et al., 1993; Welker et al., 1997; Klady et al., 2011). Conversely, temperature  
356 sensitivity of vegetative growth may be greater at lower Arctic sites because reproductive  
357 strategies involved in vegetative growth may be under stronger selection in sub- and low-  
358 Arctic ecosystems with dense, closed canopies (Wookey et al., 1993; Parsons et al., 1994).  
359 The differences between our results and those of previous syntheses indicate that not all plant  
360 traits will respond in the same way to environmental change (Shaver & Kummerow, 1992;  
361 Arft et al., 1999; Kremers et al., 2015; Barrett et al., 2015).

362         Phenological responses to climate change have been well studied, either on their own  
363 (e.g. Fitter et al., 1995; Miller-Rushing & Primack, 2008), or in the context of phenological  
364 synchrony between interacting species and potential feedbacks to fitness (Both et al. 2009;  
365 Kharouba et al., 2015; Kharouba & Vellend, 2015). Here, we focus on phenological  
366 synchrony both among different species, and of one species situated at different sites along a  
367 temperature gradient. Our results point to an important, yet often overlooked, consequence of  
368 phenological synchrony: variation in the temperature sensitivity of phenology among  
369 populations – as demonstrated here with *C. tetragona*– could alter the potential for pollen  
370 transfer and therefore gene flow, which could either promote adaptive evolution and  
371 persistence via increased genetic variation and reduced inbreeding depression (Alleaume-  
372 Benharira et al., 2006), or counteract adaptive evolution via the introduction of locally  
373 maladapted alleles (Lenormand, 2002; Sexton et al., 2011). Although many of the sites in this



374 study are too distant for pollen transport by pollinators, the variation observed in the  
375 temperature sensitivities of flowering from these sites can inform the manner in which  
376 flowering times in regions with strong elevational or continental climatic gradients may  
377 converge with warmer summer temperatures. Specifically, our results suggest that increased  
378 summer temperatures will shift the flowering times of plants from colder, higher latitude sites  
379 earlier to overlap more with those of populations from warmer sites, thus potentially  
380 increasing gene flow between populations across latitudes.

381         We also found a trend for greater sensitivity of greening to temperature change at  
382 colder versus warmer sites. If the timing of initiating physiological activity differs among  
383 populations in response to warming, this could have a major influence on carbon uptake  
384 across the tundra biome as a whole (Buitenwerf et al., 2015). Remote-sensing studies of  
385 northern areas have found high variability in greenness indices early in the growing season  
386 (Tucker et al., 2001; Macias Fauria et al., 2012), and warmer temperatures may reduce the  
387 variability observed between warmer and colder sites if the phenology of greening converges  
388 with warming. Additionally, if plant phenology is more temperature sensitive at colder sites,  
389 this could also increase chances of trophic mismatch for herbivores (Herfindal et al., 2006;  
390 Post & Forchhammer, 2008; Post et al., 2008; Kerby et al., 2013), especially if the greater  
391 sensitivity of plant phenology is coupled with greater early-season warming at colder sites.  
392 Our results indicate that the timing of food availability in early season may shift more in  
393 higher and colder sites, and this could alter foodwebs to a greater extent in high Arctic  
394 locations.

395         There was no relationship between the phenological sensitivity of flower or leaf  
396 senescence and summer temperature across sites, similar to results of an earlier synthesis of  
397 tundra plant phenology (Oberbauer et al. 2013). Non-temperature related cues, such as  
398 successful pollination, may exert a greater influence on the timing of flower senescence than

399 temperature (Stead, 1992). Multiple factors, such as photoperiod, soil moisture, and frost and  
400 insect damage may be more important cues than temperature for leaf senescence (Körner,  
401 2003; Panchen et al., 2015). Growing seasons are predicted to expand in polar ecosystems as  
402 temperatures increase, snow melt occurs earlier, and snow fall occurs later (Oberbauer et al.,  
403 1998). Our findings suggest that growing season duration may extend due to earlier greening  
404 or flowering in warmer years, but not as a result of a longer period of photosynthetic activity  
405 in the fall in the above-ground parts of plants (Macias-Fauria et al., 2012; Rumpf et al., 2014;  
406 Khorsand et al., 2015). However, below-ground phenology might differ, as longer growing  
407 seasons could occur with later freeze-up due to an extended period of root growth (Blume-  
408 Werry et al. 2016; Radville et al. 2016; Sloan et al. 2016).

409         Although these results indicate potential for a convergence of flowering and greening  
410 phenology as summer temperatures become warmer in the future, they should be interpreted  
411 with caution. Other factors, such as snow accumulation and the timing of snowmelt, may be  
412 decoupled from temperature changes in northern latitudes (Kohler et al., 2006; Bjorkman et  
413 al., 2015) and alter the phenology of tundra plant communities in different ways than warmer  
414 temperatures alone (Cooper et al., 2011; Semenchuk et al., 2013; Bjorkman et al., 2015;  
415 Phoenix & Bjerke, 2016). Additionally, our use of average monthly temperatures here may  
416 not reflect the exact temperatures experienced by each species at each site before completion  
417 of phenological stages. It will be important to continue to gather detailed phenological and  
418 temperature measurements on common species across the Arctic to elucidate how  
419 environmental factors shape phenological responses, and how these responses are changing  
420 through time. Bridging the gap between research that links the effects of climate change on  
421 phenology, and research that addresses the effects of phenology on plant adaptation and  
422 evolutionary processes is the next step in understanding how plants will continue to respond  
423 to global change over longer timescales.

424           The results of our study substantially advance our understanding of tundra plant  
425 phenology by illustrating how the temperature sensitivity of phenological events can vary  
426 across large-scale climatic gradients. This increased sensitivity of flowering and greening  
427 phenology, coupled with increased spring and summer warming in the far north, may amplify  
428 the phenological convergence across latitudes as the climate warms. Given that phenology is  
429 among the most important traits influencing the fitness, evolution, and distribution of plant  
430 species (Chuine & Beaubien, 2001; Fox, 2003; Chuine, 2010), incorporating spatial  
431 differences in the temperature sensitivity of phenology into bioclimatic envelope models and  
432 dynamic vegetation models could improve our ability to accurately predict how plant  
433 communities will respond to climate change (Morin & Thuiller, 2009; Valladares et al.,  
434 2014). Integrating spatial variation in temperature sensitivity of phenology with fine-grained  
435 climate scenarios will allow us to predict where and when plant phenology will change most  
436 rapidly in the future.

437

#### 438 **Data accessibility**

439 The data used in this synthesis are archived at the Polar Data catalogue  
440 ([www.polardata.ca/pdcsearch/?doi\\_id=12722](http://www.polardata.ca/pdcsearch/?doi_id=12722)).

441

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461

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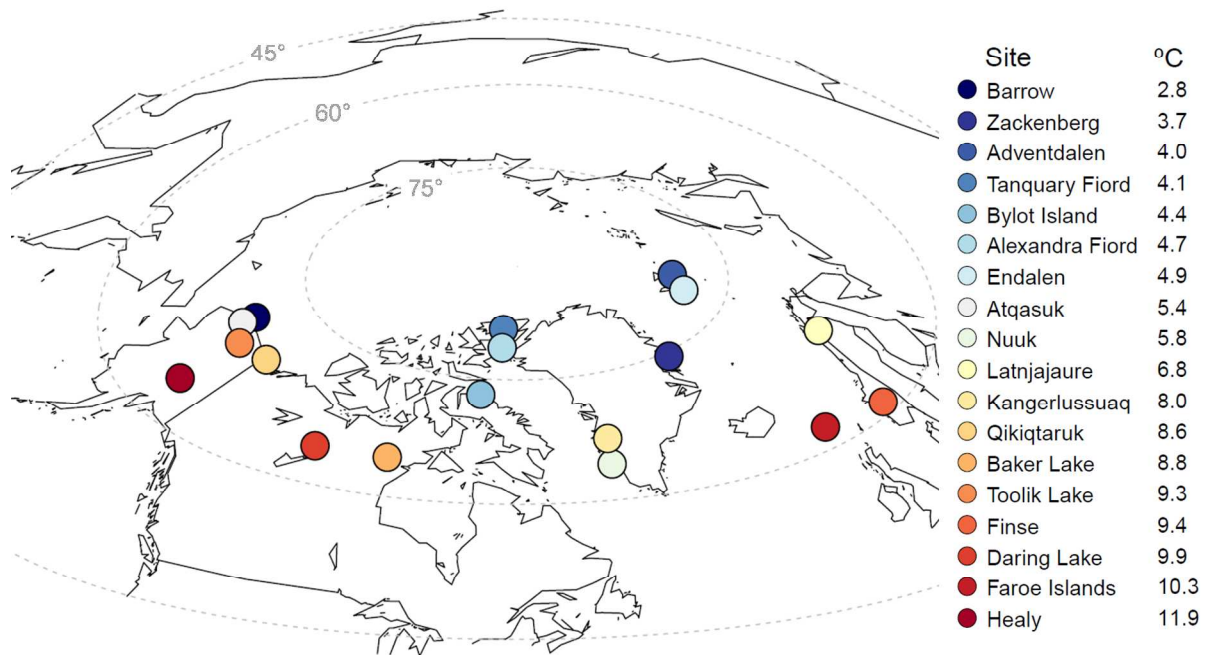
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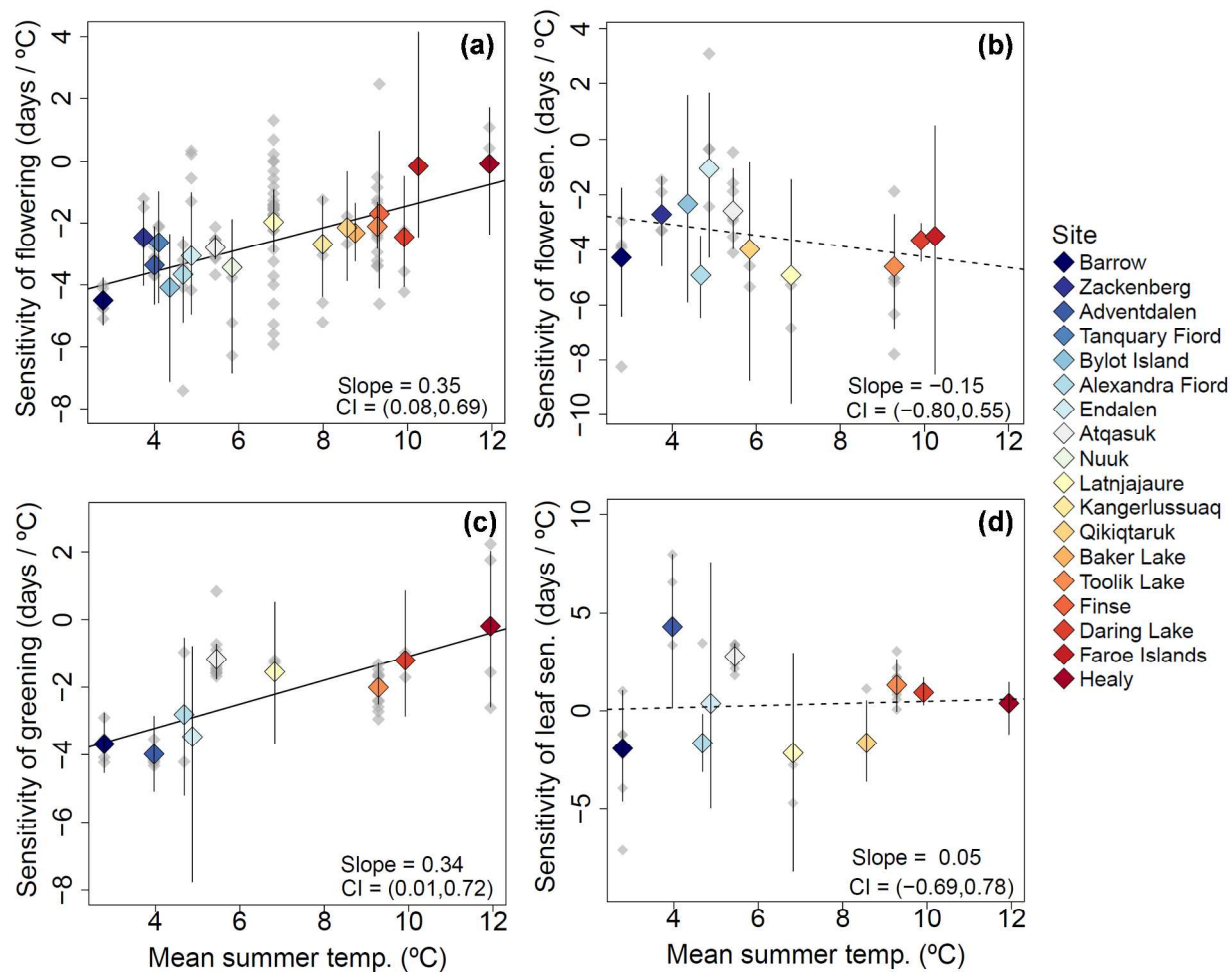


**Table 1.** Information on Arctic sites used in this study. ‘Mean summer temp.’ is the average June–August temperature for each site from 1981–2010. ‘Temp. data source’ lists the name of the weather station data that mean summer temperature data were obtained from, or indicates if mean summer temperature was estimated from 0.5 gridded CRU data. Superscripts listed after summer temperatures data sources correspond to citations and websites listed in Appendix B.

Site	Latitude	Longitude	Elevation (m)	Mean summer temp. (°C)	Years of phenological data	Mean summer temp. data source
Adventdalen, Svalbard	78° 9' N	16° 6' E	50	4.0	2007–2010	CRU data <sup>1</sup>
Alexandra Fiord, Canada	78° 53' N	75° 55' W	30	4.7	1992–2005, 2007–2008, 2010–2013	CRU data <sup>1</sup>
Atqasuk, USA	70° 27' N	157° 24' W	22	5.4	1998–2001, 2007–2008, 2010–2014	CRU data <sup>1</sup>
Baker Lake, Canada	64° 22' N	95° 52' W	68	8.8	1992–2001, 2003–2005	Baker Lake A <sup>2</sup>
Barrow, USA	71° 18' N	156° 40' W	5	2.8	1994–2001, 2007–2008, 2010–2014	Barrow ESRL Baseline Observatory <sup>3</sup>
Bylot, Canada	73° 08' N	80° 00' W	64	4.4	2002–2005	CRU data <sup>1</sup>
Daring Lake, Canada	64° 52' N	111° 35' W	420	9.9	1996–2014	CRU data <sup>1</sup>
Endalen, Svalbard	78° 13' N	15° 39' E	100	4.9	2002–2004	Longyearbyen Svalbard airport <sup>4</sup>
Faroe Islands	62° 04' N	6° 57' W	600	10.3	2002, 2007–2009	Tórshavn weather station <sup>5</sup>
Finse, Norway	60° 36' N	7° 31' E	1475	9.4	1994–1996, 2009	Vestlandet climate station <sup>4</sup>
Healy, USA	63° 53' N	149° 13' W	670	11.9	2010–2014	Healy 2 NW weather station <sup>6</sup>
Kangerlussuaq, Greenland	67° 6' N	50° 19' W	288	8.0	2002–2013	Greenland station 4231 <sup>5</sup>
Latnjajaure, Sweden	68° 20' N	18° 30' E	1000	6.8	1992–2001	CRU data <sup>1</sup>
Nuuk, Greenland	64° 7' N	51° 21' W	5	5.8	2008–2011	Greenland station 04250 <sup>5</sup>
Qikiqtaruk, Canada	69° 34' N	139° 4' W	42	8.6	2001–2014	CRU data <sup>1</sup>
Tanquary Fiord, Canada	81° 24' N	76° 52' W	4	4.1	1995–2014	Eureka weather station <sup>2</sup>
Toolik Lake, USA	68° 38' N	149° 38' W	720	9.3	1996–2001, 2007–2013	CRU data <sup>1</sup>
Zackenbergl, Greenland	74° 30' N	20° 34' W	40	3.7	1996–2014	Greenland station 04330 <sup>2</sup>

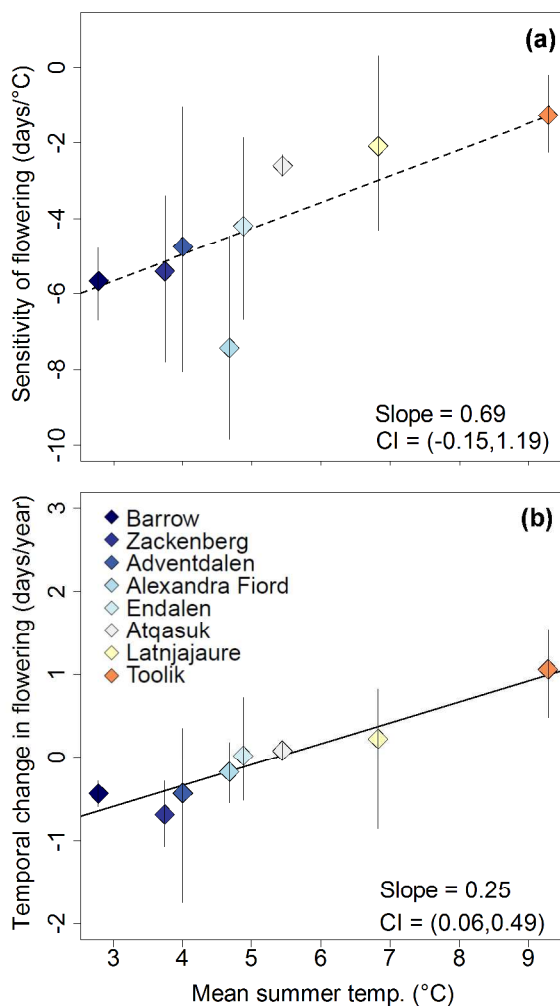


**Figure 1.** Locations of the 18 sites used in this analysis. Colors denote the mean summer (June–August) temperature (°C) for each site from 1981–2010.



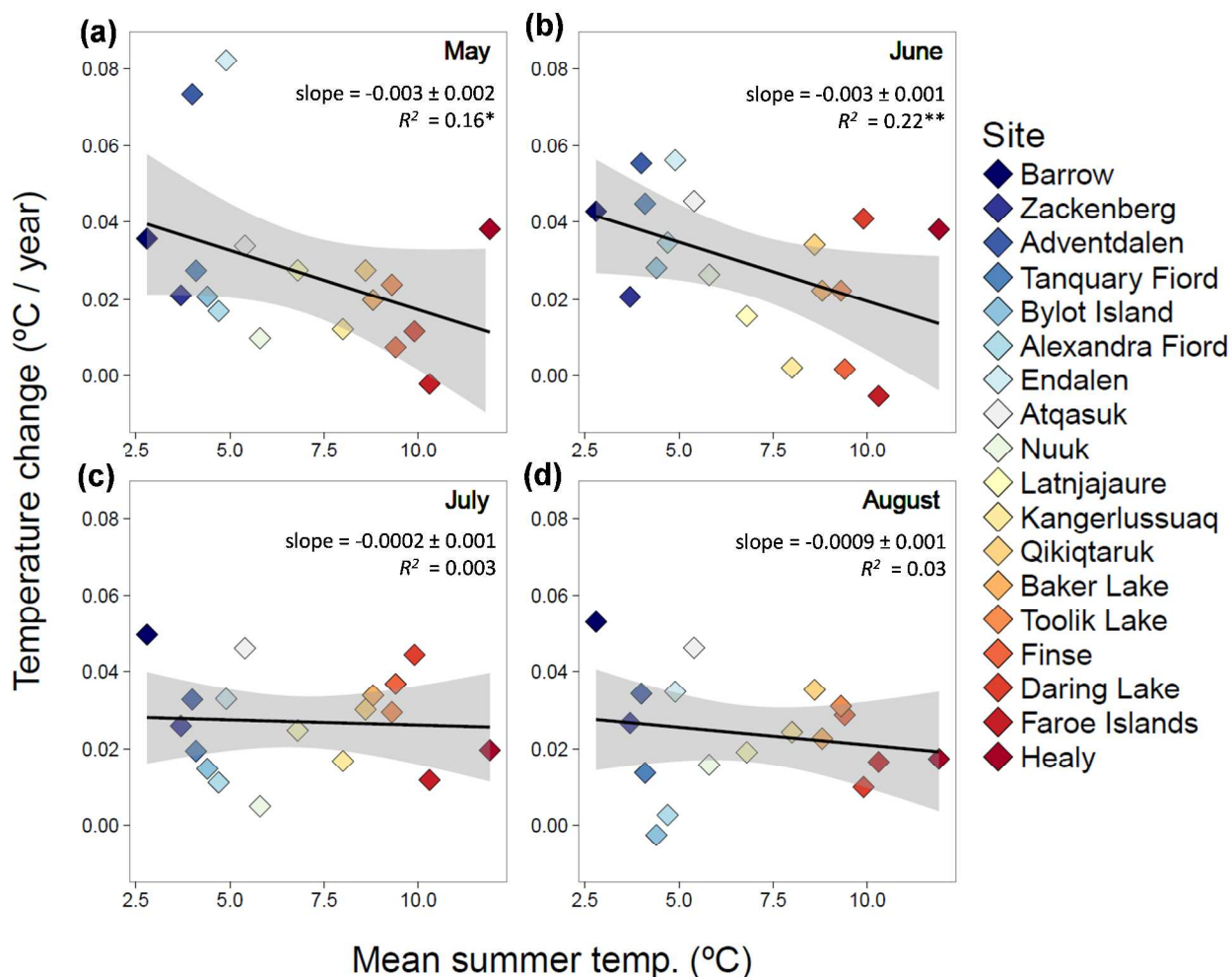
**Figure 2.** Relationships between the mean summer (June–August) temperature and the temperature sensitivity of (a) flowering, (b) flower senescence, (c) greening, and (d) leaf senescence at northern latitude sites. Temperature sensitivity is the slope of the relationship between the timing of a given phenological event and temperature, and is expressed as the number of days the phenological event changed per 1 °C of warming. Colored points represent the estimated temperature sensitivity for each site ( $\beta_s$ ), and vertical black lines span the 95% credible intervals for each site level estimate. Grey points represent the estimated temperature sensitivity for each species at each site ( $b_j$ ). The hierarchical model fits for the common slopes across sites and the 95% credible intervals (CIs) are listed in the bottom right of each graph. Site temperature is related to phenological responses when the 95% credible intervals do not overlap

zero; overall model slopes that differed from zero are shown with a solid line, while a lack of a relationship is shown with a dashed line.



**Figure 3.** Relationships between the mean summer (June–August) temperature and (a) the temperature sensitivity of flowering of *Cassiope tetragona*, and (b) the temporal change (days per year) of flowering of *C. tetragona* across northern latitude sites. Temperature sensitivity is expressed as the number of days that flowering changed per 1 °C of warming. Temporal change is the number of days that flowering changed per year. Colored points represent the estimates for *C. tetragona* at each site ( $\beta_s$ ), and vertical black lines span the 95% credible intervals for each site-level estimate. The hierarchical model fits for the common slopes across sites and the 95% credible intervals (CIs) are listed in the bottom right of each graph.





**Figure 4.** Comparisons between the mean summer (June–August) temperature of sites from 1981–2010 and the average annual change in temperature from 1960–2013 for the months of May (a), June (b), July (c), and August (d). Lines and grey shading represent slopes and 95% confidence intervals of simple linear regressions. Asterisks indicate significant relationships at: \*  $P < 0.1$ , and \*\*  $P < 0.05$ . Mean monthly temperature data for each site from 1960–2013 were obtained from the Climate Research Unit (CRU) TS3.21 0.5° gridded temperature data (Harris et al. 2014).