



## Warming shortens flowering seasons of tundra plant communities

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*Published in:*

Nature Ecology & Evolution

*DOI:*

[10.1038/s41559-018-0745-6](https://doi.org/10.1038/s41559-018-0745-6)

*Publication date:*

2019

*Document version*

Peer reviewed version

*Citation for published version (APA):*

Prevéy, J. S., Rixen, C., Rüger, N., Høye, T. T., Bjørkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Ashton, I. W., Cannone, N., Chisholm, C. L., Clark, K., Cooper, E. J., Elberling, B., Fosaa, A. M., Henry, G. H. R., Hollister, R. D., Jónsdóttir, I. S., Klanderud, K., Kopp, C. W., ... Wipf, S. (2019). Warming shortens flowering seasons of tundra plant communities. *Nature Ecology & Evolution*, 3(1), 45-52. <https://doi.org/10.1038/s41559-018-0745-6>

1 **Classification:** Biological Sciences, Ecology

2 **Title:** Warming shortens flowering seasons of tundra plant communities

3 **Running head:** Warming shortens flowering seasons

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70

71 **Keywords:** climate change, ITEX, open-top chambers, phenology, tundra

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83 **Abstract**

84 Advancing phenology is one of the most visible effects of climate change on plant  
85 communities, and has been especially pronounced in temperature-limited tundra ecosystems.  
86 However, phenological responses have been shown to differ greatly between species, with  
87 some species shifting phenology more than others. We analyzed a database of 42,689 tundra  
88 plant phenological observations to show that warmer temperatures are leading to a contraction  
89 of community-level flowering seasons in tundra ecosystems due to a greater advancement in  
90 flowering times of late-flowering species than of early-flowering species. Shorter flowering  
91 seasons with a changing climate have the potential to alter trophic interactions in tundra  
92 ecosystems. Interestingly, these findings differ from those of warmer ecosystems, where early  
93 flowering species have been found to be more sensitive to temperature change, suggesting that  
94 community-level phenological responses to warming can vary greatly between biomes.

95

96 **Main**

97 Warmer temperatures associated with climate change have advanced the phenology of  
98 organisms around the world <sup>1-3</sup>, and both temperature increases and phenological changes  
99 have been especially pronounced in temperature-limited tundra ecosystems <sup>4-7</sup>. Tundra  
100 ecosystems encompass cold regions above latitudinal treeline (Arctic tundra) or altitudinal  
101 treeline (alpine tundra). Remote sensing studies indicate broad patterns of changing  
102 seasonality of vegetation productivity at high latitudes over time in relation to climate  
103 warming <sup>8-10</sup>, however, phenological responses to warmer temperatures have been shown to  
104 differ greatly among species and locations, with some species shifting dates of flowering and  
105 flower senescence more than others <sup>11-15</sup>. Studies from temperate ecosystems have found that  
106 early-flowering species often advance phenological events more in response to warmer  
107 temperatures than later-flowering species <sup>16,1,17-19</sup>, however, to date, the relationship between

108 flowering time and phenological sensitivity has not been tested across high-altitude tundra  
109 ecosystems.

110 Evidence suggests that across northern tundra ecosystems, phenology of plants from  
111 colder sites at higher latitudes changes more with warmer temperatures than phenology of  
112 plants from warmer, more southern latitudes<sup>7,15,20</sup>. However, within tundra plant  
113 communities, phenological responses to warming are often species-specific, with no clear  
114 responses of specific functional groups<sup>21–27,3</sup> or phylogenetic relationships<sup>28</sup>. A better  
115 understanding of the drivers of variation in phenological sensitivity will help determine how  
116 species and plant communities will respond to climate change in the future<sup>23,29,3</sup>, as well as  
117 contribute to our understanding of the adaptive nature of species-specific phenological  
118 responses to climate change.

119 The timing of life history events, such as flowering, is of critical importance in harsh  
120 tundra ecosystems, and the fitness consequences of different phenological responses to  
121 climatic drivers can be substantial<sup>30,31</sup>. Plants that track snowmelt dates and not temperature  
122 (or thermal sums) may risk exposure to freezing events that can damage flowers and reduce  
123 seed production during early snowmelt years<sup>32–35</sup>, whereas plants that flower too late risk not  
124 being able to fully develop seeds before the end of the growing season, and may be at a  
125 competitive disadvantage to plants that do respond<sup>22,36</sup>.

126 There are a diversity of life history strategies among species in tundra plant  
127 communities, even within the short growing seasons experienced at high latitudes and  
128 altitudes<sup>21,22,37</sup>. These various strategies could influence the species-specific responses of  
129 plants to warmer temperatures<sup>37,38,12</sup>. The relative flowering time of a species compared to  
130 other species in the plant community (hereafter its “phenological niche”) could help explain  
131 the variation in phenological responses among species in tundra ecosystems. The existence of  
132 different phenological niches could promote species coexistence in many ecosystems<sup>39–41</sup>, as  
133 phenological niches can strongly influence competitive and trophic interactions<sup>42</sup>. Differential

134 shifts in the phenological niche could lead to trophic mismatches in tundra ecosystems,  
135 altering food webs and influencing the abundance of pollinators or herbivores<sup>43–45,12</sup>.  
136 Classifying organisms using phenological niches could thus be a useful way to predict how  
137 species will respond to changes in environmental conditions in the future<sup>38</sup>.

138         Measuring the relative importance of different environmental cues for Arctic and  
139 alpine species, such as temperature and snowmelt date, will help determine how species will  
140 respond as the climate warms<sup>23,29</sup>. Although temperature influences the date of snowmelt,  
141 snowmelt can be decoupled from temperature because snowmelt is also influenced by the  
142 amount and quality of precipitation over winter and spring<sup>13</sup>. The phenology of early-  
143 flowering plant species may be influenced more by photoperiod or the timing of snowmelt,  
144 whereas the phenology of late-flowering species is probably more dependent on thermal heat  
145 sums accumulated over the growing season<sup>22,46</sup>. If early-flowering tundra species are less  
146 responsive to changes in summer temperature than late-flowering ones, then increases in  
147 summer temperature will likely accelerate the flowering phenology of late-flowering species  
148 more than early-flowering ones. Additionally, if temperatures towards the end of the growing  
149 season are rising more rapidly than temperatures at the beginning of the year, then flowering  
150 phenology of late-flowering species will advance more than that of early-flowering species  
151<sup>14,15</sup>. In both cases, a more rapid advance of late- than early-flowering species would result in  
152 a contraction of the community-level flowering season (Fig. 1,<sup>12</sup> which could substantially  
153 change competitive and trophic interactions<sup>47,44,12,31</sup>. In particular, shorter flowering seasons  
154 could also strongly limit resource availability for pollinators, especially if the phenology of  
155 pollinator species are responding to different drivers than plant communities<sup>12,48</sup>.

156         In this data synthesis, we test how the temperature sensitivity of flowering relates to  
157 the phenological niches of tundra species using flowering observations of a total of 253  
158 species, 23 sites, and up to 20 years from Arctic and alpine ecosystems around the world, both  
159 from long-term monitoring plots and warming experiments (Fig. 2). With this global dataset,

160 we tested three main hypotheses: **1)** flowering phenology of late-flowering tundra species is  
161 more sensitive to warmer summer temperatures than flowering phenology of early-flowering  
162 species. We tested this hypothesis with both observational and experimental data, and  
163 hypothesized that: **1a)** results would be similar for both observational and experimental data;  
164 that is, late-flowering species would be more sensitive to natural *and* experimental warming.  
165 **2)** If late-flowering species are flowering earlier, but early-flowering species are not, then the  
166 community-level flowering seasons will be shorter in warmer years, and thus, **3)** as average  
167 summer temperatures at tundra sites have warmed in the recent past, the duration of  
168 community-level flowering seasons have decreased over this time period. We examined how  
169 the phenological niche of a species influenced the sensitivity of first flowering dates (FFDs)  
170 and flower senescence dates (LFDs) to summer temperature indices, snowmelt date, and  
171 experimental warming. To test for a contraction of community-level flowering seasons with  
172 warmer summers and over time, we compared the community flowering season length to  
173 mean June-July temperatures and year for six sites with observations of four or more species  
174 over 10 or more years.

175

## 176 **Results**

177 First flowering dates (FFDs) of late-flowering species were more temperature sensitive  
178 than early-flowering species (i.e., FFDs of late-flowering species advanced more per °C  
179 increase in summer temperature, and in response to experimental warming, than early-  
180 flowering species, Figs. 3A and 4A, Supplementary Fig. 1, Supplementary Table 4). Results  
181 of analyses using June temperature for all species, or the average daily temperature from  
182 snowmelt through the average flowering date, also indicated a significant influence of  
183 phenological niche on temperature sensitivity of flowering (Figs. 3B and 3C, Supplementary  
184 Table 4). However, the phenological niche of a species did not influence the sensitivity of  
185 FFDs to snowmelt timing (Fig. 3D, Supplementary Table 4). Overall, species from sites with

186 colder summer temperatures had greater temperature sensitivity of FFDs (Supplementary  
187 Table 4). Analyses from warming experiments yielded similar results, with greater differences  
188 in FFDs between experimentally warmed and control plots for late-flowering species than for  
189 early-flowering species (Fig. 4A). There was no influence of phenological niche on the  
190 temperature sensitivity of flower senescence dates (LFDs) in either long-term monitoring  
191 plots or warming experiments (Supplementary Table 5 and Fig. 4B).

192 The community-level flowering seasons across the six sites with 10 or more years of  
193 data were 3.96 days shorter per 1 °C warmer June-July temperature (95% CI = -7.31, -0.79,  
194 Fig. 5A, Supplementary Table 5). The length of the flowering season was estimated as the  
195 duration between the average FFD of the earliest and average LFD of the latest flowering  
196 species per site in each year. Community-level flowering seasons became shorter over time in  
197 all six sites, but the change was significant only at Alexandra Fiord, Daring, and Zackenberg.  
198 Across all sites, flowering season length shortened by 0.43 days per year, but the credible  
199 interval on this parameter overlapped zero (95% CIs = -0.87, 0.06, Fig. 5B). Annual June-July  
200 temperatures

201

## 202 **Discussion**

203 Our results reveal an overall shortening of community-level flowering seasons with  
204 summer warming across the tundra biome. We additionally found evidence of a contraction of  
205 the community-level flowering season over time at a subset of sites. In both cases, the  
206 shortening of the flowering season was due to greater temperature sensitivity of flowering of  
207 late-flowering than early-flowering species. On average, the temperature sensitivity of first  
208 flowering dates was greater for tundra species that flowered later in the growing season  
209 compared to those that flowered earlier. This pattern was evident both in long-term  
210 monitoring plots over time and in warming experiments. Additionally, observations from  
211 long-term monitoring plots indicated that, on average, plants at colder sites were more



212 phenologically sensitive, consistent with results from Prevéy et al. (2018) using a largely  
213 overlapping dataset, and that late-flowering plant species at the coldest tundra sites exhibited  
214 the highest phenological sensitivities in the dataset. Our analyses of long-term monitoring and  
215 experimental warming data indicate that late-flowering tundra species may alter their  
216 flowering phenology more than early-flowering ones in a warmer world, resulting in a  
217 shortening of community-level flowering seasons at sites across the tundra biome.

218         The finding of greater temperature sensitivity of late-flowering species differs from  
219 results of many studies conducted at lower latitudes and altitudes<sup>6,49,18,19</sup>. Studies from warmer  
220 biomes found that early-flowering species often advance phenological events more in  
221 response to warmer temperatures than late-flowering species<sup>16,1,17–19,50,51</sup>. Mid- and late-  
222 season moisture limitation probably plays a greater role in structuring the phenology of plants  
223 in warmer ecosystems<sup>52</sup>. However, in cold tundra ecosystems with relatively short summers,  
224 moisture limitation may not be as important a phenological driver as in warmer, drier  
225 ecosystems<sup>53</sup>. Additionally, selection might be stronger at the start of the growing season  
226 under the harsher climate conditions experienced by early flowering plants in tundra sites  
227 relative to more temperate biomes<sup>46</sup>.

228         Our finding of a contraction of the flowering season with warmer temperatures also  
229 differs from studies in other ecosystems. Some studies have found a divergence of flowering  
230 dates of early- versus late-flowering species with warming in temperate grasslands<sup>49</sup>,  
231 montane and subalpine meadows<sup>54,55</sup>, and deserts<sup>53</sup>, with less overlap in the flowering times  
232 of species<sup>49</sup>, and a mid-season depression in flower abundance<sup>54,55</sup>. Individual studies  
233 conducted in temperate ecosystems and global meta-analyses of phenology experiments and  
234 long-term monitoring projects have concluded that early-flowering species are more  
235 responsive to climate warming<sup>18,6,51</sup>. However, our results show that Arctic and alpine plants  
236 exhibit the opposite pattern, suggesting that community-level phenological responses to  
237 warming can vary greatly among biomes<sup>19,56</sup>.

238 For the six Arctic sites with over ten years of observations, we documented a  
239 contraction of the flowering season with warmer temperatures, and a trend toward shorter  
240 flowering seasons over time, although this pattern was not significant at all sites. A  
241 contraction of the flowering season is in agreement with previous single-site studies in arctic  
242 ecosystems<sup>5,12,48</sup>. Shorter flowering seasons could lead to possible phenological mismatches  
243 if late-season pollinators or herbivores are not following the same cues as late-season plant  
244 species<sup>48,57</sup>. Additionally, less dispersion among the flowering times of species in a  
245 community may increase competition for pollinators<sup>58</sup> or, alternatively, increase exposure to  
246 more pollinators because plant species are all flowering at similar times<sup>59</sup>. However, it is  
247 important to note that we did not directly measure how the abundance of plant species, or the  
248 abundance of open flowers, changed with temperature or over time. The timing of peak  
249 flowering may shift less than the timing of first flowering dates<sup>55</sup>, thus changes in coverage  
250 and abundance of flowers over the season may exhibit different patterns than changes in the  
251 overall length of the flowering season<sup>60</sup>.

252 Increased temperature sensitivity of flowering may be advantageous if it allows plants  
253 to track ideal temperature conditions for growth and reproduction<sup>61,30</sup>. Our results suggest  
254 that late-flowering species that track temperature more than snowmelt date or photoperiod  
255 may be more able to optimize the timing of flowering and could have an advantage as  
256 temperature increases or becomes more variable<sup>62</sup>. Phenological plasticity may also be  
257 indicative of plasticity of other plant traits, so plant species that can shift phenology to  
258 changing conditions may be better able to adjust to climate change over time. To date, there  
259 have been few studies comparing phenological traits to other plant traits and changes in plant  
260 abundance (but see 30, 61). However, as the amount of phenological data available for tundra  
261 plant species accumulates, the next logical step will be linking phenological measurements to  
262 performance measurements to aid predictions of vegetation change in tundra ecosystems in  
263 the future<sup>64</sup>.

264 Phenological responses are one of the most easily observable effects of climate change  
265 on plant communities<sup>2</sup>, but identifying the underlying mechanisms driving phenological  
266 responses to warming is crucial to accurately estimating food-web dynamics and plant-  
267 pollinator interactions. Our data synthesis demonstrates an agreement between long-term and  
268 experimental data to identify how plants respond to warmer temperatures<sup>65,66</sup>. In temperature-  
269 limited tundra ecosystems, late-flowering species advance flowering more in warmer years,  
270 and this can lead to a contraction of the flowering season of the entire plant community.  
271 Additionally, these changes are most pronounced at the coldest tundra sites where temperature  
272 increases have been greatest<sup>20</sup>. Thus, our study demonstrates that the phenological niches of  
273 plant species can be useful predictors of how the flowering of tundra species will respond to  
274 warmer temperatures, and can aid predictions of plant and ecosystem responses to climate  
275 change in the future.

276

## 277 **Methods**

### 278 *Compilation of the flowering phenology database*

279 We compiled a database of flowering phenology observations from a total of 253  
280 species at 23 sites in Arctic and alpine ecosystems from both long-term monitoring plots and  
281 warming experiments (Supplementary Table 1, Fig. 2). Portions of the dataset were analyzed  
282 and reported in Oberbauer et al. (2013) and Prevéy et al. (2017), however, two additional  
283 monitoring sites and 10 additional warming experiments are included in this analysis  
284 (Supplementary Table 1). Each site collected phenological observations following a  
285 standardized protocol that was originally developed for the International Tundra Experiment  
286 (ITEX) network<sup>67,68</sup>. Following the ITEX protocol, observers recorded the phenological  
287 status of plants one to three times per week over the snow-free season, and specifically  
288 recorded the first flowering date (FFD) and last flowering date (LFD) of each species per  
289 individual or plot. The FFD was defined as the date when the first flower was open, the first

290 pollen was visible, or the first anthers were exposed. The LFD was defined as the date when  
291 the withering of anthers, first petal drop, or last petal drop was observed. However, both FFD  
292 and LFD were recorded consistently at each site over time. We include data only from long-  
293 term monitoring plots that had three or more years of flowering phenology observations per  
294 species per plot.

295

### 296 *Effects of species phenological niches on the sensitivity of flowering*

297 We calculated the phenological niche of a species at each site as the average first  
298 flowering date of the species at each site across all years of measurements<sup>50</sup> (Supplementary  
299 Table 2). We examined the relationship between phenological niche and temperature  
300 (expressed in several ways) and snowmelt dates at long-term monitoring plots. Temperature  
301 was expressed as the mean monthly temperature until flowering, mean June temperature, or  
302 the mean daily temperature between snowmelt and flowering. Flowering dates for the  
303 Southern hemisphere alpine site were adjusted by 210 days to match that of the Northern  
304 hemisphere growing season, and to assist with model convergence in analyses. We specified  
305 mean monthly temperature until flowering separately for each species and site as the average  
306 monthly air-temperature from June through the average month of flowering, except for 29 site  
307 by species combinations where species flowered in May, for which we used average May  
308 temperature (Supplementary Table 2). For example, if the phenological niche of a species was  
309 June 30<sup>th</sup>, then mean June temperature was used as the summer temperature variable for that  
310 species. However, if the phenological niche was July 15<sup>th</sup>, then average June-July temperature  
311 was used (Supplementary Table 2). To test the influence of the temperature windows on the  
312 results we obtained, we also performed the analyses with June temperature as the predictor  
313 variable for all sites and species, because preliminary analysis showed that June temperature  
314 was the strongest predictor of flowering across all species and sites (Supplementary Table 2).  
315 We used average monthly temperatures because they were available for all sites in the

316 analyses; thus allowing us to incorporate the largest set of phenological data available. We  
317 recognize that using monthly mean temperatures may bias results, as sensitivity of flowering  
318 time for species flowering in the early parts of months are obviously not affected by  
319 temperatures experienced after they flower. Thus, for the subset of 12 sites with both daily  
320 temperature data and snowmelt dates available we calculated the mean daily temperature  
321 between snowmelt and flowering as the average daily air temperature from the date of  
322 snowmelt through the average date of flowering for each species and year. Finally, we  
323 examined the association between the timing of snowmelt and flowering in long-term  
324 monitoring plots by comparing the phenological niches of species to snowmelt timing for the  
325 subset of 13 sites that had recorded snowmelt dates over time.

326         Models also included the effect of mean site-level summer temperatures (June-Aug)  
327 from 1981-2000 as an additional predictor variable of species phenological responses, since a  
328 previous synthesis found that flowering dates of species from colder tundra sites were more  
329 sensitive to changes in temperature than those from warmer sites<sup>20</sup>. Mean monthly  
330 temperatures for sites were obtained from local weather stations when available. If no long-  
331 term (1981–2010) weather data were available near sites, then mean monthly temperatures  
332 were estimated using 0.5° gridded temperature data from the Climate Research Unit (CRU)<sup>69</sup>  
333 (Supplementary Table 1). Temperatures and phenological niches were mean-centered by site  
334 for all species for long-term monitoring plot data. Plot within site, and year within site, were  
335 included as random variables. We also tested for the interaction between phenological niche  
336 and temperature.

337         In total, the analyses of FFDs with summer temperature windows or mean June  
338 temperatures as predictor variables included 14,324 observations from 318 unique site by  
339 species combinations at 19 sites. The analyses of FFDs with snowmelt date included 9,918  
340 observations from 141 unique site by species combinations at 13 sites, and the analyses of  
341 FFDs using average daily temperatures included 9,713 observations from 143 unique site by

342 species combinations at 11 sites. The analyses of LFDs with summer temperature windows or  
343 mean June temperatures as predictor variables included 9,226 observations from 88 unique  
344 site by species combinations at 11 sites. The analyses of LFDs with snowmelt date included  
345 7,661 observations from 80 unique site by species combinations at 11 sites, and the analyses  
346 of LFDs using average daily temperatures included 7,341 observations from 74 unique site by  
347 species combinations at 9 sites.

348

349

350 *Effects of phenological niches on the temperature sensitivity of flowering in warming*

351 *experiments*

352 We examined observations from warming experiments that utilized open-top  
353 chambers (OTCs) to investigate how experimental warming influenced the flowering dates of  
354 species with different phenological niches. In the warming experiments, plots were warmed  
355 with ca. 1 m<sup>2</sup> fiberglass or polycarbonate OTCs, in either cone or hexagonal shapes, that  
356 increased air temperature by 0.5-3 °C<sup>67,70-72</sup>, Supplementary Table 3). The OTCs were placed  
357 on plots either only over the summer, or left on plots year-round, depending on the site  
358 (Supplementary Table S3).

359 To examine how the phenological niche of a species influenced its phenological  
360 sensitivity to experimental warming, we first calculated the average difference in the timing of  
361 phenological events (either FFD or LFD) between control and experimentally warmed plots at  
362 each site and year for every species that occurred in both treatments. Then the phenological  
363 niches of each species were compared to the difference in the number of days between the  
364 FFD or the LFD in experimentally warmed and control plots for each species, site, and year  
365 combination. Mean site-level summer temperature was not included as a predictor variable in  
366 the warming experiment analyses because the amount of experimental warming differed  
367 between experiments at different sites (Supplementary Table 3). We also examined how  
368 differences in the amount of warming in different warming experiments may have altered

369 results by calculating the difference in the number of days between the FFDs or the LFDs in  
370 experimentally warmed and control plots divided the mean number of degrees of warming  
371 reported for chambers at each site or subsite within site (Supplementary Table 3) to get an  
372 estimate of the change in flowering date per °C of warming.

373 In total, the analyses of FFDs in warming experiments included 1219 flowering  
374 observations from 164 unique site by species combinations at 16 sites. Analyses of LFDs in  
375 warming experiments included 743 observations from 96 unique site by species combinations  
376 at 11 sites.

377

### 378 *Statistical analyses of effects of phenological niches on sensitivity of flowering*

379 To statistically analyze phenological observations over the different numbers of sites,  
380 years of observations, and species, we used Bayesian hierarchical modeling. This approach  
381 allowed for estimation of the uncertainties of phenological responses among sites, plots,  
382 years, and species, and the incorporation of these uncertainties in the final correlation of  
383 phenological niche and phenological responses per species per site<sup>73</sup>.

384 For data from long-term monitoring plots, we used two-level regression models. At the  
385 lower level, we estimated phenological sensitivities by relating the date of phenological events  
386 (FFD or LFD) to temperature or snowmelt date. At the higher (species-) level, we related  
387 species' phenological sensitivities to their phenological niches. For data from warming  
388 experiments, the difference (in days) of FFD or LFD between warmed and control plots was  
389 directly included as a response variable in the species-level regression.

390 We fit Bayesian models using the program Stan<sup>74</sup>, which was accessed using the  
391 package Rstan<sup>75</sup> in the statistical program R 3.2.2<sup>76</sup>. Each model was run with 2 chains of  
392 20,000 iterations, using Hamiltonian Monte Carlo (HMC) sampling. We used flat priors for  
393 all parameter estimates. Full model details and code are included in S7. We checked for  
394 convergence of chains for all parameters both visually with trace plots and with the Gelman–

395 Rubin convergence statistic <sup>77</sup>. Trace plots showed that chains mixed well and converged to  
396 stationary distributions for all parameter estimates. Gelman–Rubin convergence statistics for  
397 parameter estimates of all models were < 1.02.

398

### 399 *Duration of flowering season*

400 To test for a contraction of community-level flowering seasons in association with  
401 warmer summers, we conducted analyses that only included sites with FFDs and LFDs for  
402 four or more species over 10 or more years. This limited analyses to the six Arctic sites with  
403 long-term monitoring data: Alexandra Fiord, Atqasuk, Utqiagvik, Daring Lake, Toolik Lake,  
404 and Zackenberg. Flower count or peak flowering data were not available for all sites, so we  
405 used a proxy for the community flowering season calculated as the number of days between  
406 the average FFD of the earliest flowering species at a site per year and the average LFD of the  
407 latest flowering species at a site per year. We used the earliest and latest flowering species in  
408 each year to avoid any bias caused by uneven shifts in flowering times among species.  
409 Although changes in first and last flowering dates are not always representative of changes  
410 over the entire flowering season <sup>78,55</sup>, we believe our proxy can provide an estimate of how the  
411 length of the flowering season may change with future warming. Additionally, a previous  
412 synthesis found that reproductive phenological events within the same species are highly  
413 correlated <sup>7</sup>.

414 We compared this proxy for the duration of the community-level flowering season to  
415 the average June-July temperature at a site per year using a Bayesian hierarchical modeling  
416 approach. We mean-centered both flowering season length and average June-July  
417 temperatures for each site so we could compare the change in community-level flowering  
418 seasons with the change in June-July temperatures across sites. Because all sites chosen for  
419 these analyses had relatively long records of phenological measurements (>10 years), we also  
420 examined if flowering season length or June-July temperatures have changed significantly



421 over time. We analyzed associations between community flowering season length and  
422 summer temperature and time with a Bayesian hierarchical model using mean-centered June-  
423 July temperature as the predictor variable for the temperature sensitivity models and year as  
424 the predictor variable for the temporal change models and an intercept and slope that varied  
425 by site. We also examined whether mean June-July temperatures changed over time using the  
426 same models with year as the predictor variable. Full model details and code are included in  
427 S7.

#### 428 **Data Availability Statement**

429  
430 The data that support the findings of this study have been archived at the Polar Data Catalogue (data  
431 has been submitted to the Polar data catalogue - CCIN reference number 12961 -DOI will be updated  
432 when data is approved).

433

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624 **Acknowledgements**

625 We are grateful to the many individuals who established experiments and collected detailed  
626 phenological observations, there are too many to name them all, however, we want to especially thank  
627 Michele Dalle Fratte, Dorothy Cooley, Orin Durey, Cameron Eckert, Jill F. Johnstone, Catherine  
628 Kennedy, Vincent Lamarre, Guylaine Levasseur, Carmen Spiech, Josef Svoboda, Renee Wising, the  
629 Herschel Island – Qikiqtaruk Territorial Park staff including Edward McLeod, Samuel McLeod, Ricky  
630 Joe, Paden Lennie, Deon Arey, LeeJohn Meyook, Jordan McLeod, Pierre Foisy, Colin Gordon, Jeremy  
631 Hansen, Albert Rufus, and Richard Gordon, Quttinirpaaq National Park staff, the Greenland  
632 Ecosystem Monitoring team, WARM coordinators Nathan Sanders, Aimee Classen, and Maja  
633 Sundqvist, and others. These observations were made possible with the support of many funding  
634 agencies and grants including: ArcticNet, the Natural Sciences and Engineering Council of Canada,  
635 Canadian International Polar Year Program, Polar Continental Shelf Program of Natural Resources  
636 Canada, the Danish Environmental Protection Agency, the Swiss Federal Institute for Forest, Snow,  
637 and Landscape Research WSL, The National Geographic Society, US National Science Foundation  
638 grant numbers: PLR 1525636, PLR 1504141, PLR 1433063, PLR 1107381, PLR 0119279, PLR  
639 0902125, PLR 0856728, PLR 1312402, PLR 1019324, LTER-1026415, 1433063, 0856728, 0612534,  
640 0119279, 9421755, OPP 1525636, OPP-9907185, 0856710, 9714103, 0632263, 0856516, 1432277,  
641 1432982, 1504381, and 1504224, DEB -1637686, Danish National Research Foundation grant:  
642 CENPERM DNRF100, Danish Council for Independent Research - Natural Sciences grant: DFF 4181-  
643 00565, Deutsche Forschungsgemeinschaft grant: RU 1536/3-1, Natural Environment Research  
644 Council grant: NE/M016323/1, Department of Energy grant: SC006982, a Semper Ardens grant from  
645 the Carlsberg Foundation to N. J. Sanders, and an INTERACT Transnational Access grant.

646 **Author contributions**

647  
648 J.P. and C.R. designed and led the manuscript; J.P. and C.R. led the collection of the phenology  
649 database; J.P., N.R., A.B., I.M.S. and S.E performed statistical analyses; J.P., C.R., N.R., T.H., A.B.,  
650 I.M.S. and S.E drafted the paper; J.P., C.R., A.B., I.M.S., I.A., N.C, C.C., E.C., B.E., A.M.F, G.H.,  
651 R.H., I.S.J., K.K., C.K., E.L., M.M., U.M., S.N., S.O., Z.P., E.P., S.R., N.M.S., E.S., P.S, J.S, K.K,  
652 Ø.T., T.T., S.V., C. W., J.W., and S.W. contributed data; and all authors were involved in writing  
653 and editing the manuscript.

654 **Competing Interests**

655

656 The authors declare no competing interests.

657 **Figure Legends**

658

659 **Fig. 1.** Conceptual diagram showing how warmer summer temperatures may shorten the length of the  
660 flowering season in tundra ecosystems. If the phenology of early-flowering plant species is influenced  
661 primarily by photoperiod or the timing of snowmelt and does not respond appreciably to warmer  
662 summer temperatures, but the phenology of late-flowering species is mostly dependent on  
663 accumulated heat sums over the growing season, and does shift earlier with warmer summers, then  
664 there may be a contraction of the overall flowering season during warmer years.

665  
666 **Fig. 2.** Map of long-term observational and experimental warming studies. Site names are listed in  
667 order from the site with the coldest (2.8 °C) to the site with the warmest (11.9 °C) summer  
668 temperatures (June-Aug. for northern hemisphere sites, Dec-Feb. for the southern hemisphere site,  
669 Supplementary Fig. 1). Site symbols shown on the map correspond to symbols and colors in Figs. 3-4.  
670 Asterisks indicate sites used in community flowering season analyses.

671  
672 **Fig. 3.** Temperature sensitivity of first flowering dates (FFDs) was greater for late- versus early-  
673 flowering species. Relationships are shown between phenological niches of species and sensitivities of  
674 FFDs to (a) mean monthly temperature until flowering (b) mean June temperature (c) mean daily  
675 temperature between the snowmelt and flowering, and (d) the date of snowmelt. Points represent the  
676 estimated temperature sensitivities for each species at each site, and vertical gray lines span the 95%  
677 credible intervals for each species-by-site level estimate. Colors and symbols correspond to site  
678 names in Fig. 2. The ‘phenological niche’ is the average flowering date of a species compared to the  
679 site-level mean-flowering date of all species at a site. Solid black lines denote significant hierarchical  
680 model slopes, dashed black lines indicate non-significant model slopes, and the horizontal grey line  
681 denotes the zero line. Hierarchical model slopes and 95% credible intervals (CIs) are listed in the  
682 bottom left of each graph. The phenological niches significantly predict phenological responses (at the  
683 5% level) if the 95% credible intervals do not overlap zero.

684  
685 **Fig. 4.** The change in first flowering dates (FFDs) in response to experimental warming was greater  
686 for late- versus early-flowering species. Relationships are shown between phenological niches of  
687 species and timing of (a) FFDs and (b) Last flowering dates (LFDs) in experimentally warmed plots  
688 compared to control plots. Points represent the estimated temperature sensitivities for each species at  
689 each site, and vertical gray lines span the 95% credible intervals for each species-by-site level  
690 estimate. Colors and symbols correspond to site names in Fig. 2. The ‘phenological niche’ is the  
691 average flowering date of a species compared to the site-level mean-flowering date of all species at a  
692 site. Solid black lines denote significant hierarchical model slopes, dashed black lines indicate non-  
693 significant model slopes, and the horizontal grey line denotes the zero line. Hierarchical model slopes  
694 and 95% credible intervals (CIs) are listed in the bottom left of each graph. The phenological niches  
695 significantly predict phenological responses (at the 5% level) if the 95% credible intervals do not  
696 overlap zero.

697  
698 **Fig. 5.** Warming was related to the change in the duration of the flowering season over time at sites  
699 across the tundra biome. (a) Difference in the duration of the community level flowering season  
700 compared to the difference in mean June-July temperatures from site averages. (b) Change in the  
701 duration of the community level flowering season over time. (c) Yearly June-July temperature over  
702 time. Flowering season length and average June-July temperatures were mean-centered for each site so  
703 they could be compared across sites. Points represent the change in the community-level flowering  
704 season per site and year. Solid black lines denote significant hierarchical model slopes, and dashed  
705 black lines indicate non-significant model slopes. Colored bands show the 95% credible intervals for  
706 site-level slopes. Hierarchical model slopes and 95% credible intervals (CIs) are listed in the bottom  
707 left of each graph.

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