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Warming shortens flowering seasons of tundra plant communities

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70

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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 world¹⁻³, and both temperature increases and phenological changes
99 have been especially pronounced in temperature-limited tundra ecosystems⁴⁻⁷. 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 warming⁸⁻¹⁰, 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 others¹¹⁻¹⁵. 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^{16,1,17-19}, 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^{7,15,20}. However, within tundra plant
113 communities, phenological responses to warming are often species-specific, with no clear
114 responses of specific functional groups^{21–27,3} or phylogenetic relationships²⁸. 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^{23,29,3}, 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^{30,31}. 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^{32–35}, 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^{22,36}.

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^{21,22,37}. These various strategies could influence the species-specific responses of
129 plants to warmer temperatures^{37,38,12}. 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^{39–41}, as
133 phenological niches can strongly influence competitive and trophic interactions⁴². 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^{43–45,12}.
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 future³⁸.

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^{23,29}. 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 spring¹³. 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^{22,46}. 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^{14,15}. 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. 1,¹² which could substantially
153 change competitive and trophic interactions^{47,44,12,31}. 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^{12,48}.

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^{6,49,18,19}. 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^{16,1,17–19,50,51}. Mid- and late-
222 season moisture limitation probably plays a greater role in structuring the phenology of plants
223 in warmer ecosystems⁵². 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 ecosystems⁵³. 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 biomes⁴⁶.

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 grasslands⁴⁹,
231 montane and subalpine meadows^{54,55}, and deserts⁵³, with less overlap in the flowering times
232 of species⁴⁹, and a mid-season depression in flower abundance^{54,55}. 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^{18,6,51}. 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^{19,56}.

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^{5,12,48}. 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^{48,57}. Additionally, less dispersion among the flowering times of species in a
245 community may increase competition for pollinators⁵⁸ or, alternatively, increase exposure to
246 more pollinators because plant species are all flowering at similar times⁵⁹. 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 dates⁵⁵, 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 season⁶⁰.

252 Increased temperature sensitivity of flowering may be advantageous if it allows plants
253 to track ideal temperature conditions for growth and reproduction^{61,30}. 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 variable⁶². 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 future⁶⁴.

264 Phenological responses are one of the most easily observable effects of climate change
265 on plant communities², 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^{65,66}. 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 greatest²⁰. 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^{67,68}. 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 measurements⁵⁰ (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 30th, then mean June temperature was used as the summer temperature variable for that
310 species. However, if the phenological niche was July 15th, 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 sites²⁰. 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)⁶⁹
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 m² fiberglass or polycarbonate OTCs, in either cone or hexagonal shapes, that
356 increased air temperature by 0.5-3 °C^{67,70-72}, 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 ⁷³.

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 ⁷⁴, which was accessed using the
391 package Rstan ⁷⁵ in the statistical program R 3.2.2 ⁷⁶. 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 ⁷⁷. 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 ^{78,55}, 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 ⁷.

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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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
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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.,
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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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