Warming shortens flowering seasons of tundra plant communities

Prevéy, Janet S.; Rixen, Christian; Rüger, Nadja; Høye, Toke T.; Bjørkman, Anne D.; Myers-Smith, Isla H.; Elmendorf, Sarah C.; Ashton, Isabel W.; Cannone, Nicoletta; Chisholm, Chelsea Lee; Clark, Karin; Cooper, Elisabeth J.; Elberling, Bo; Fosaa, Anna Maria; Henry, Greg H. R.; Hollister, Robert D.; Jónsdóttir, Ingibjörg Svala; Klanderud, Kari; Kopp, Christopher W.; Lévesque, Esther; Mauritz, Marguerite; Molau, Ulf; Natali, Susan M.; Oberbauer, Steven F.; Panchen, Zoe A.; Post, Eric; Rumpf, Sabine B.; Schmidt, Niels Martin; Schuur, Edward; Semenchuk, Philipp R.; Smith, Jane G.; Suding, Katharine N.; Totland, Ørjan; Troxler, Tiffany; Venn, Susanna; Wahren, Carl-Henrik; Welker, Jeffrey M.; Wipf, Sonja

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

4 **Authors:** Janet S. Prevy^{*1,2}, Christian Rixen², Nadja Rger^{3,4}, Toke T. Hye⁵, Anne D.
 5 Bjorkman^{6,7}, Isla H. Myers-Smith⁸, Sarah C. Elmendorf^{9,10}, Isabel W. Ashton¹¹, Nicoletta
 6 Cannone¹², Chelsea Chisholm^{13,2}, Elisabeth J. Cooper¹⁴, Bo Elberling¹⁵, Anna Maria Fosaa¹⁶,
 7 Greg H.R. Henry¹⁷, Robert D. Hollister¹⁸, Ingibjrg Svala Jnsdttir¹⁹, Kari Klanderud²⁰,
 8 Christopher W. Kopp²¹, Esther Lvesque²², Marguerite Mauritz²³, Ulf Molau²⁴, Susan
 9 Natali²⁵, Steve Oberbauer²⁶, Zoe A. Panchen²⁷, Eric Post²⁸, Sabine B. Rumpf²⁹, Niels Martin
 10 Schmidt⁵, Edward Schuur³⁰, Philipp R. Semenchuk^{29,14}, Jane G. Smith³¹, Katharine N.
 11 Suding^{10,31}, rjan Totland³², Tiffany Troxler²⁶, Susanna Venn³³, Carl-Henrik Wahren³⁴,
 12 Jeffrey M. Welker^{35,36}, Sonja Wipf²

13
 14 **Author affiliations:**

- 15 1. Pacific Northwest Research Station, USDA-Forest Service, 3625 93rd Avenue SW,
- 16 Olympia, Washington 98512
- 17 2. WSL Institute for Snow and Avalanche Research SLF, 7260 Davos, Switzerland
- 18 3. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher
- 19 Platz 5e, 04103 Leipzig, Germany
- 20 4. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancn, Panama
- 21 5. Department of Bioscience and Arctic Research Centre, Aarhus University, Denmark
- 22 6. Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Denmark
- 23 7. Senckenberg Gesellschaft fr Naturforschung, Biodiversity and Climate Research Centre
- 24 (BiK-F), Frankfurt am Main, Germany
- 25 8. University of Edinburgh, Scotland
- 26 9. National Ecological Observatory Network, 1685 38th Street, Suite 100, Boulder,
- 27 Colorado 80301, USA.
- 28 10. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder,
- 29 Colorado 80309, USA.
- 30 11. Northern Great Plains Inventory and Monitoring Network, National Park Service, Rapid
- 31 City, SD, USA
- 32 12. Department of Science and High Technology, Universit degli Studi dell'Insubria, Como,
- 33 Italy
- 34 13. Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
- 35 Universitetsparken 15, DK-2100 Copenhagen
- 36 14. Institute for Arctic and Marine Biology, The Arctic University of Norway, N-9037
- 37 Troms, Norway
- 38 15. Center for Permafrost (CENPERM), Department of Geosciences and Natural
- 39 Resource Management, University of Copenhagen, Copenhagen, Denmark
- 40 16. Faroese Museum of Natural History, Faroe Islands
- 41 17. Department of Geography, University of British Columbia, Vancouver, BC, Canada
- 42 18. Biology Department, Grand Valley State University, 1 Campus Drive, Allendale, MI
- 43 49401, USA
- 44 19. School of Engineering and Natural Sciences, University of Iceland, Iceland
- 45 20. Department of Ecology and Natural Resources, Norwegian University of Life Sciences,
- 46 Norway
- 47 21. Department of Botany, University of British Columbia, Vancouver, BC, Canada

- 48 22. Université du Québec à Trois-Rivières, Québec, Canada
49 23. Center for Ecosystem Science and Society Center, Northern Arizona University, Flagstaff,
50 AZ, USA
51 24. Department of Biology and Environmental Sciences, University of Gothenburg, Sweden
52 25. Woods Hole Research Center, Falmouth, MA, USA
53 26. Department of Biological Sciences, Florida International University, FL, USA
54 27. Department of Biology, Dalhousie University, Canada
55 28. Department of Wildlife, Fish, & Conservation Biology, University of California, Davis
56 29. Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14,
57 1030 Vienna, Austria
58 30. Center for Ecosystem Science and Society Center, Northern Arizona University, Flagstaff,
59 AZ, USA
60 31. Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO, USA
61 32. Department of Biology, University of Bergen, Bergen, Norway
62 33. Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin
63 University, Victoria, Australia 3125
64 34. Research Centre for Applied Alpine Ecology, La Trobe University, Bundoora 3086,
65 Australia
66 35. UArctic and University of Oulu, Finland
67 36. Department of Biological Sciences, University of Alaska Anchorage, AK, USA
68

69 ***Corresponding author details:** Janet Prevy, +1 360-701-6466, jprevey@fs.fed.us

70

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

72

73

74

75

76

77

78

79

80

81

82

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 ¹⁻³, and both temperature increases and phenological changes
99 have been especially pronounced in temperature-limited tundra ecosystems ⁴⁻⁷. 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 warming ⁸⁻¹⁰, 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 others ¹¹⁻¹⁵. 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

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

Evidence suggests that across northern tundra ecosystems, phenology of plants from colder sites at higher latitudes changes more with warmer temperatures than phenology of plants from warmer, more southern latitudes^{7,15,20}. However, within tundra plant communities, phenological responses to warming are often species-specific, with no clear responses of specific functional groups^{21–27,3} or phylogenetic relationships²⁸. A better understanding of the drivers of variation in phenological sensitivity will help determine how species and plant communities will respond to climate change in the future^{23,29,3}, as well as contribute to our understanding of the adaptive nature of species-specific phenological responses to climate change.

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

There are a diversity of life history strategies among species in tundra plant communities, even within the short growing seasons experienced at high latitudes and altitudes^{21,22,37}. These various strategies could influence the species-specific responses of plants to warmer temperatures^{37,38,12}. The relative flowering time of a species compared to other species in the plant community (hereafter its “phenological niche”) could help explain the variation in phenological responses among species in tundra ecosystems. The existence of different phenological niches could promote species coexistence in many ecosystems^{39–41}, as phenological niches can strongly influence competitive and trophic interactions⁴². Differential

shifts in the phenological niche could lead to trophic mismatches in tundra ecosystems, altering food webs and influencing the abundance of pollinators or herbivores^{43–45,12}. Classifying organisms using phenological niches could thus be a useful way to predict how species will respond to changes in environmental conditions in the future³⁸.

Measuring the relative importance of different environmental cues for Arctic and alpine species, such as temperature and snowmelt date, will help determine how species will respond as the climate warms^{23,29}. Although temperature influences the date of snowmelt, snowmelt can be decoupled from temperature because snowmelt is also influenced by the amount and quality of precipitation over winter and spring¹³. The phenology of early-flowering plant species may be influenced more by photoperiod or the timing of snowmelt, whereas the phenology of late-flowering species is probably more dependent on thermal heat sums accumulated over the growing season^{22,46}. If early-flowering tundra species are less responsive to changes in summer temperature than late-flowering ones, then increases in summer temperature will likely accelerate the flowering phenology of late-flowering species more than early-flowering ones. Additionally, if temperatures towards the end of the growing season are rising more rapidly than temperatures at the beginning of the year, then flowering phenology of late-flowering species will advance more than that of early-flowering species^{14,15}. In both cases, a more rapid advance of late- than early-flowering species would result in a contraction of the community-level flowering season (Fig. 1,¹² which could substantially change competitive and trophic interactions^{47,44,12,31}. In particular, shorter flowering seasons could also strongly limit resource availability for pollinators, especially if the phenology of pollinator species are responding to different drivers than plant communities^{12,48}.

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

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

Results

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

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

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

Discussion

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

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

The finding of greater temperature sensitivity of late-flowering species differs from results of many studies conducted at lower latitudes and altitudes^{6,49,18,19}. Studies from warmer biomes found that early-flowering species often advance phenological events more in response to warmer temperatures than late-flowering species^{16,1,17–19,50,51}. Mid- and late-season moisture limitation probably plays a greater role in structuring the phenology of plants in warmer ecosystems⁵². However, in cold tundra ecosystems with relatively short summers, moisture limitation may not be as important a phenological driver as in warmer, drier ecosystems⁵³. Additionally, selection might be stronger at the start of the growing season under the harsher climate conditions experienced by early flowering plants in tundra sites relative to more temperate biomes⁴⁶.

Our finding of a contraction of the flowering season with warmer temperatures also differs from studies in other ecosystems. Some studies have found a divergence of flowering dates of early- versus late-flowering species with warming in temperate grasslands⁴⁹, montane and subalpine meadows^{54,55}, and deserts⁵³, with less overlap in the flowering times of species⁴⁹, and a mid-season depression in flower abundance^{54,55}. Individual studies conducted in temperate ecosystems and global meta-analyses of phenology experiments and long-term monitoring projects have concluded that early-flowering species are more responsive to climate warming^{18,6,51}. However, our results show that Arctic and alpine plants exhibit the opposite pattern, suggesting that community-level phenological responses to warming can vary greatly among biomes^{19,56}.

For the six Arctic sites with over ten years of observations, we documented a contraction of the flowering season with warmer temperatures, and a trend toward shorter flowering seasons over time, although this pattern was not significant at all sites. A contraction of the flowering season is in agreement with previous single-site studies in arctic ecosystems^{5,12,48}. Shorter flowering seasons could lead to possible phenological mismatches if late-season pollinators or herbivores are not following the same cues as late-season plant species^{48,57}. Additionally, less dispersion among the flowering times of species in a community may increase competition for pollinators⁵⁸ or, alternatively, increase exposure to more pollinators because plant species are all flowering at similar times⁵⁹. However, it is important to note that we did not directly measure how the abundance of plant species, or the abundance of open flowers, changed with temperature or over time. The timing of peak flowering may shift less than the timing of first flowering dates⁵⁵, thus changes in coverage and abundance of flowers over the season may exhibit different patterns than changes in the overall length of the flowering season⁶⁰.

Increased temperature sensitivity of flowering may be advantageous if it allows plants to track ideal temperature conditions for growth and reproduction^{61,30}. Our results suggest that late-flowering species that track temperature more than snowmelt date or photoperiod may be more able to optimize the timing of flowering and could have an advantage as temperature increases or becomes more variable⁶². Phenological plasticity may also be indicative of plasticity of other plant traits, so plant species that can shift phenology to changing conditions may be better able to adjust to climate change over time. To date, there have been few studies comparing phenological traits to other plant traits and changes in plant abundance (but see 30, 61). However, as the amount of phenological data available for tundra plant species accumulates, the next logical step will be linking phenological measurements to performance measurements to aid predictions of vegetation change in tundra ecosystems in the future⁶⁴.

Phenological responses are one of the most easily observable effects of climate change on plant communities², but identifying the underlying mechanisms driving phenological responses to warming is crucial to accurately estimating food-web dynamics and plant-pollinator interactions. Our data synthesis demonstrates an agreement between long-term and experimental data to identify how plants respond to warmer temperatures^{65,66}. In temperature-limited tundra ecosystems, late-flowering species advance flowering more in warmer years, and this can lead to a contraction of the flowering season of the entire plant community. Additionally, these changes are most pronounced at the coldest tundra sites where temperature increases have been greatest²⁰. Thus, our study demonstrates that the phenological niches of plant species can be useful predictors of how the flowering of tundra species will respond to warmer temperatures, and can aid predictions of plant and ecosystem responses to climate change in the future.

Methods

Compilation of the flowering phenology database

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

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

Effects of species phenological niches on the sensitivity of flowering

We calculated the phenological niche of a species at each site as the average first flowering date of the species at each site across all years of measurements⁵⁰ (Supplementary Table 2). We examined the relationship between phenological niche and temperature (expressed in several ways) and snowmelt dates at long-term monitoring plots. Temperature was expressed as the mean monthly temperature until flowering, mean June temperature, or the mean daily temperature between snowmelt and flowering. Flowering dates for the Southern hemisphere alpine site were adjusted by 210 days to match that of the Northern hemisphere growing season, and to assist with model convergence in analyses. We specified mean monthly temperature until flowering separately for each species and site as the average monthly air-temperature from June through the average month of flowering, except for 29 site by species combinations where species flowered in May, for which we used average May temperature (Supplementary Table 2). For example, if the phenological niche of a species was June 30th, then mean June temperature was used as the summer temperature variable for that species. However, if the phenological niche was July 15th, then average June-July temperature was used (Supplementary Table 2). To test the influence of the temperature windows on the results we obtained, we also performed the analyses with June temperature as the predictor variable for all sites and species, because preliminary analysis showed that June temperature was the strongest predictor of flowering across all species and sites (Supplementary Table 2). We used average monthly temperatures because they were available for all sites in the

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

Models also included the effect of mean site-level summer temperatures (June-Aug) from 1981-2000 as an additional predictor variable of species phenological responses, since a previous synthesis found that flowering dates of species from colder tundra sites were more sensitive to changes in temperature than those from warmer sites²⁰. Mean monthly temperatures for sites were obtained from local weather stations when available. If no long-term (1981–2010) weather data were available near sites, then mean monthly temperatures were estimated using 0.5° gridded temperature data from the Climate Research Unit (CRU)⁶⁹ (Supplementary Table 1). Temperatures and phenological niches were mean-centered by site for all species for long-term monitoring plot data. Plot within site, and year within site, were included as random variables. We also tested for the interaction between phenological niche and temperature.

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

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

Effects of phenological niches on the temperature sensitivity of flowering in warming experiments

We examined observations from warming experiments that utilized open-top chambers (OTCs) to investigate how experimental warming influenced the flowering dates of species with different phenological niches. In the warming experiments, plots were warmed with ca. 1 m² fiberglass or polycarbonate OTCs, in either cone or hexagonal shapes, that increased air temperature by 0.5-3 °C^{67,70-72}, Supplementary Table 3). The OTCs were placed on plots either only over the summer, or left on plots year-round, depending on the site (Supplementary Table S3).

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

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

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

Statistical analyses of effects of phenological niches on sensitivity of flowering

To statistically analyze phenological observations over the different numbers of sites, years of observations, and species, we used Bayesian hierarchical modeling. This approach allowed for estimation of the uncertainties of phenological responses among sites, plots, years, and species, and the incorporation of these uncertainties in the final correlation of phenological niche and phenological responses per species per site⁷³.

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

We fit Bayesian models using the program Stan⁷⁴, which was accessed using the package Rstan⁷⁵ in the statistical program R 3.2.2⁷⁶. Each model was run with 2 chains of 20,000 iterations, using Hamiltonian Monte Carlo (HMC) sampling. We used flat priors for all parameter estimates. Full model details and code are included in S7. We checked for convergence of chains for all parameters both visually with trace plots and with the Gelman–

Rubin convergence statistic⁷⁷. Trace plots showed that chains mixed well and converged to stationary distributions for all parameter estimates. Gelman–Rubin convergence statistics for parameter estimates of all models were < 1.02 .

Duration of flowering season

To test for a contraction of community-level flowering seasons in association with warmer summers, we conducted analyses that only included sites with FFDs and LFDs for four or more species over 10 or more years. This limited analyses to the six Arctic sites with long-term monitoring data: Alexandra Fiord, Atkasuk, Utqiagvik, Daring Lake, Toolik Lake, and Zackenberg. Flower count or peak flowering data were not available for all sites, so we used a proxy for the community flowering season calculated as the number of days between the average FFD of the earliest flowering species at a site per year and the average LFD of the latest flowering species at a site per year. We used the earliest and latest flowering species in each year to avoid any bias caused by uneven shifts in flowering times among species. Although changes in first and last flowering dates are not always representative of changes over the entire flowering season^{78,55}, we believe our proxy can provide an estimate of how the length of the flowering season may change with future warming. Additionally, a previous synthesis found that reproductive phenological events within the same species are highly correlated⁷.

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

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

Data Availability Statement

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

References

1. Fitter, A. H. & Fitter, R. S. R. Rapid changes in flowering time in british plants. *Science* **296**, 1689–1691 (2002).
2. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
3. Thackeray, S. J. *et al.* Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245 (2016).
4. Arft, A. M. *et al.* Responses of tundra plants to experimental warming:meta-analysis of the international tundra experiment. *Ecological Monographs* **69**, 491–511 (1999).
5. Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M. & Forchhammer, M. C. Rapid advancement of spring in the High Arctic. *Current Biology* **17**, R449–R451 (2007).
6. Parmesan, C. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* **13**, 1860–1872 (2007).

- 447 7. Oberbauer, S. F. *et al.* Phenological response of tundra plants to background climate
448 variation tested using the International Tundra Experiment. *Philosophical Transactions of*
449 *the Royal Society B: Biological Sciences* **368**, 20120481 (2013).
- 450 8. Xu, L. *et al.* Temperature and vegetation seasonality diminishment over northern lands.
451 *Nature Climate Change* **3**, 581 (2013).
- 452 9. Park, T. *et al.* Changes in growing season duration and productivity of northern vegetation
453 inferred from long-term remote sensing data. *Environ. Res. Lett.* **11**, 084001 (2016).
- 454 10. Xu, C., Liu, H., Williams, A. P., Yin, Y. & Wu, X. Trends toward an earlier peak of the
455 growing season in Northern Hemisphere mid-latitudes. *Global Change Biology* **22**, 2852–
456 2860 (2016).
- 457 11. Bradley, N. L., Leopold, A. C., Ross, J. & Huffaker, W. Phenological changes reflect
458 climate change in Wisconsin. *PNAS* **96**, 9701–9704 (1999).
- 459 12. Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K. & Forchhammer, M. C. Shorter
460 flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature*
461 *Clim. Change* **3**, 759–763 (2013).
- 462 13. Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M. & Henry, G. H. R.
463 Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology
464 over the past two decades. *Glob Change Biol* **21**, 4651–4661 (2015).
- 465 14. Panchen, Z. A. & Gorelick, R. Flowering and fruiting responses to climate change of two
466 Arctic plant species, purple saxifrage (*Saxifraga oppositifolia*) and mountain avens (*Dryas*
467 *integrifolia*). *Arctic Science* **1**, 45–58 (2015).
- 468 15. Panchen, Z. A. & Gorelick, R. Prediction of Arctic plant phenological sensitivity to
469 climate change from historical records. *Ecol Evol* **7**, 1325–1338 (2017).
- 470 16. Price, M. V. & Waser, N. M. Effects of experimental warming on plant reproductive
471 phenology in a subalpine meadow. *Ecology* **79**, 1261–1271 (1998).

- 472 17. Dunne, J. A., Harte, J. & Taylor, K. J. Subalpine meadow flowering phenology responses
473 to climate change: integrating experimental and gradient methods. *Ecological*
474 *Monographs* **73**, 69–86 (2003).
- 475 18. Menzel, A. *et al.* European phenological response to climate change matches the warming
476 pattern. *Global Change Biology* **12**, 1969–1976 (2006).
- 477 19. Miller-Rushing, A. J. & Inouye, D. W. Variation in the impact of climate change on
478 flowering phenology and abundance: an examination of two pairs of closely related
479 wildflower species. *Am. J. Bot.* **96**, 1821–1829 (2009).
- 480 20. Prevéy, J. *et al.* Greater temperature sensitivity of plant phenology at colder sites:
481 implications for convergence across northern latitudes. *Glob Change Biol* **23**, 2660–2671
482 (2017).
- 483 21. Shaver & Kummerow, J. *Arctic Ecosystems in a Changing Climate: An Ecophysiological*
484 *Perspective*. (Academic Press, 1992).
- 485 22. Molau, U. Relationships between flowering phenology and life history strategies in tundra
486 plants. *Arctic and Alpine Research* **25**, 391–402 (1993).
- 487 23. Keller, F. & Körner, C. The role of photoperiodism in alpine plant development. *Arctic,*
488 *Antarctic, and Alpine Research* **35**, 361–368 (2003).
- 489 24. Hollister, R. D., Webber, P. J. & Tweedie, C. E. The response of Alaskan arctic tundra to
490 experimental warming: differences between short- and long-term responses. *Global*
491 *Change Biology* **11**, 525–536 (2005).
- 492 25. Semenchuk, P. R., Elberling, B. & Cooper, E. J. Snow cover and extreme winter warming
493 events control flower abundance of some, but not all species in high arctic Svalbard. *Ecol*
494 *Evol* **3**, 2586–2599 (2013).
- 495 26. Iler, A. M. *et al.* Maintenance of temporal synchrony between syrphid flies and floral
496 resources despite differential phenological responses to climate. *Glob Change Biol* **19**,
497 2348–2359 (2013).

- 498 27. Post, E., Kerby, J., Pedersen, C. & Steltzer, H. Highly individualistic rates of plant
499 phenological advance associated with arctic sea ice dynamics. *Biology Letters* **12**,
500 20160332 (2016).
- 501 28. CaraDonna, P. J. & Inouye, D. W. Phenological responses to climate change do not
502 exhibit phylogenetic signal in a subalpine plant community. *Ecology* **96**, 355–361 (2015).
- 503 29. Körner, C. & Basler, D. Phenology under global warming. *Science* **327**, 1461–1462
504 (2010).
- 505 30. Cleland, E. E. *et al.* Phenological tracking enables positive species responses to climate
506 change. *Ecology* **93**, 1765–1771 (2012).
- 507 31. Wheeler, H. C., Høye, T. T., Schmidt, N. M., Svenning, J.-C. & Forchhammer, M. C.
508 Phenological mismatch with abiotic conditions—implications for flowering in Arctic
509 plants. *Ecology* **96**, 775–787 (2015).
- 510 32. Inouye, D. W. Effects of climate change on phenology, frost damage, and floral
511 abundance of montane wildflowers. *Ecology* **89**, 353–362 (2008).
- 512 33. Wipf, S., Stoeckli, V. & Bebi, P. Winter climate change in alpine tundra: plant responses
513 to changes in snow depth and snowmelt timing. *Climatic Change* **94**, 105–121 (2009).
- 514 34. Wheeler, J. A. *et al.* Increased spring freezing vulnerability for alpine shrubs under early
515 snowmelt. *Oecologia* **175**, 219–229 (2014).
- 516 35. Wheeler, J. A. *et al.* The snow and the willows: earlier spring snowmelt reduces
517 performance in the low-lying alpine shrub *Salix herbacea*. *J Ecol* **104**, 1041–1050 (2016).
- 518 36. Cooper, E. J., Dullinger, S. & Semenchuk, P. Late snowmelt delays plant development
519 and results in lower reproductive success in the High Arctic. *Plant Science* **180**, 157–167
520 (2011).
- 521 37. Parsons, A. N. *et al.* Growth responses of four sub-arctic dwarf shrubs to simulated
522 environmental change. *Journal of Ecology* **82**, 307–318 (1994).

- 523 38. Molau, U., Nordenhäll, U. & Eriksen, B. Onset of flowering and climate variability in an
524 alpine landscape: a 10-year study from Swedish Lapland. *Am. J. Bot.* **92**, 422–431 (2005).
- 525 39. Grubb, P. J. The maintenance of species-richness in plant communities: the importance of
526 the regeneration niche. *Biological Reviews* **52**, 107–145 (1977).
- 527 40. Higgins, S. I., Delgado-Cartay, M. D., February, E. C. & Combrink, H. J. Is there a
528 temporal niche separation in the leaf phenology of savanna trees and grasses? *Journal of*
529 *Biogeography* **38**, 2165–2175 (2011).
- 530 41. Sanz-Aguilar, A., Carrete, M., Edelaar, P., Potti, J. & Tella, J. L. The empty temporal
531 niche: breeding phenology differs between coexisting native and invasive birds. *Biol*
532 *Invasions* **17**, 3275–3288 (2015).
- 533 42. Wolkovich, E. M. & Cleland, E. E. The phenology of plant invasions: a community
534 ecology perspective. *Frontiers in Ecology and the Environment* **9**, 287–294 (2011).
- 535 43. Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. How does climate
536 warming affect plant-pollinator interactions? *Ecology Letters* **12**, 184–195 (2009).
- 537 44. McKinnon, L., Picotin, M., Bolduc, E., Juillet, C. & Bêty, J. Timing of breeding, peak
538 food availability, and effects of mismatch on chick growth in birds nesting in the High
539 Arctic. *Can. J. Zool.* **90**, 961–971 (2012).
- 540 45. Kerby, J. T. & Post, E. Advancing plant phenology and reduced herbivore production in a
541 terrestrial system associated with sea ice decline. *Nature Communications* **4**, 2514 (2013).
- 542 46. Wipf, S. Phenology, growth, and fecundity of eight subarctic tundra species in response to
543 snowmelt manipulations. *Plant Ecol* **207**, 53–66 (2010).
- 544 47. Post, E., Pedersen, C., Wilmers, C. C. & Forchhammer, M. C. Warming, plant phenology
545 and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the*
546 *Royal Society of London B: Biological Sciences* **275**, 2005–2013 (2008).

- 547 48. Schmidt, N. M. *et al.* An ecological function in crisis? The temporal overlap between
548 plant flowering and pollinator function shrinks as the Arctic warms. *Ecography* **39**, 1250–
549 1252 (2016).
- 550 49. Sherry, R. A. *et al.* Divergence of reproductive phenology under climate warming. *PNAS*
551 **104**, 198–202 (2007).
- 552 50. Steltzer, H. & Post, E. Seasons and Life Cycles. *Science* **324**, 886–887 (2009).
- 553 51. Wolkovich, E. M. *et al.* Warming experiments underpredict plant phenological responses
554 to climate change. *Nature* **485**, 494–497 (2012).
- 555 52. Prevéy, J. S. & Seastedt, T. R. Seasonality of precipitation interacts with exotic species to
556 alter composition and phenology of a semi-arid grassland. *J Ecol* **102**, 1549–1561 (2014).
- 557 53. Diez, J. M. *et al.* Forecasting phenology: from species variability to community patterns.
558 *Ecology Letters* **15**, 545–553 (2012).
- 559 54. Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A. & Miller-Rushing, A. J.
560 Emergence of a mid-season period of low floral resources in a montane meadow
561 ecosystem associated with climate change. *Journal of Ecology* **99**, 905–913 (2011).
- 562 55. CaraDonna, P. J., Iler, A. M. & Inouye, D. W. Shifts in flowering phenology reshape a
563 subalpine plant community. *PNAS* **111**, 4916–4921 (2014).
- 564 56. Cook, B. I. *et al.* Sensitivity of spring phenology to warming across temporal and spatial
565 climate Gradients in Two Independent Databases. *Ecosystems* **15**, 1283–1294 (2012).
- 566 57. Høye, T. T. *et al.* Phenology of high-arctic butterflies and their floral resources: Species-
567 specific responses to climate change. *Curr Zool* **60**, 243–251 (2014).
- 568 58. Hocking, B. Insect-flower associations in the high arctic with special reference to nectar.
569 *Oikos* **19**, 359–387 (1968).
- 570 59. Janzen, D. H. Synchronization of sexual reproduction of trees within the dry season in
571 central america. *Evolution* **21**, 620–637 (1967).

- 572 60. Meng, F. D. *et al.* Changes in flowering functional group affect responses of community
573 phenological sequences to temperature change. *Ecology* **98**, 734–740 (2017).
- 574 61. Hulme, P. E. Contrasting impacts of climate-driven flowering phenology on changes in
575 alien and native plant species distributions. *New Phytologist* **189**, 272–281 (2011).
- 576 62. Körner, C. & Basler, D. Plant science. Phenology under global warming. *Science* **327**,
577 1461–1462 (2010).
- 578 63. Craine, J. M., Wolkovich, E. M., Gene Towne, E. & Kembel, S. W. Flowering phenology
579 as a functional trait in a tallgrass prairie. *New Phytologist* **193**, 673–682 (2012).
- 580 64. Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. & Post, E. The effects of phenological
581 mismatches on demography. *Philosophical Transactions of the Royal Society B:*
582 *Biological Sciences* **365**, 3177–3186 (2010).
- 583 65. Elmendorf, S. C. *et al.* Experiment, monitoring, and gradient methods used to infer
584 climate change effects on plant communities yield consistent patterns. *PNAS* **112**, 448–
585 452 (2015).
- 586 66. Hollister, R. D. *et al.* Warming experiments elucidate the drivers of observed directional
587 changes in tundra vegetation. *Ecol Evol* **5**, 1881–1895 (2015).
- 588 67. Molau, U. & Mølgaard, P. International tundra experiment (ITEX) manual. *Danish Polar*
589 *Center, Copenhagen, Denmark* (1996).
- 590 68. Henry, G. h. r. & Molau, U. Tundra plants and climate change: the International Tundra
591 Experiment (ITEX). *Global Change Biology* **3**, 1–9 (1997).
- 592 69. Harris, I., Jones, P. d., Osborn, T. j. & Lister, D. h. Updated high-resolution grids of
593 monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* **34**, 623–642
594 (2014).
- 595 70. Marion, G. m. *et al.* Open-top designs for manipulating field temperature in high-latitude
596 ecosystems. *Global Change Biology* **3**, 20–32 (1997).

71. Hollister, R. D., Webber, P. J., Nelson, F. E. & Tweedie, C. E. Soil Thaw and
Temperature Response to Air Warming Varies by Plant Community: Results from an
Open-top Chamber Experiment in Northern Alaska. *Arctic, Antarctic, and Alpine
Research* **38**, 206–215 (2006).
72. Walker, M. D. *et al.* Plant community responses to experimental warming across the
tundra biome. *PNAS* **103**, 1342–1346 (2006).
73. Latimer, A. M. Geography and Resource Limitation Complicate Metabolism-Based
Predictions of Species Richness. *Ecology* **88**, 1895–1898 (2007).
74. Stan Development Team. Stan Modeling Language Users Guide and Reference Manual,
Version 2.17.0. (2017).
75. Stan Development Team. RStan: the R interface to Stan. R package version 2.17.3.
(2018).
76. R Core Team. R: A language and environment for statistical computing. (2017).
77. Gelman, A. & Rubin, D. B. Inference from Iterative Simulation Using Multiple
Sequences. *Statistical Science* **7**, 457–472 (1992).
78. Miller-Rushing, A. J., Inouye, D. W. & Primack, R. B. How well do first flowering dates
measure plant responses to climate change? The effects of population size and sampling
frequency. *Journal of Ecology* **96**, 1289–1296 (2008).

Acknowledgements

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

Author contributions

J.P. and C.R. designed and led the manuscript; J.P. and C.R. led the collection of the phenology 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., 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., 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, Ø.T., T.T., S.V., C. W., J.W., and S.W. contributed data; and all authors were involved in writing and editing the manuscript.

654 **Competing Interests**

655

656 The authors declare no competing interests.

Figure Legends

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

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

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

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

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