

Warming shortens flowering seasons of tundra plant communities

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

Warmer temperatures associated with climate change have advanced the phenology of organisms around the world^{1–3}, and both temperature increases and phenological changes have been especially pronounced in temperature-limited tundra ecosystems^{4–7}. Tundra ecosystems encompass cold regions above the latitudinal tree line (Arctic tundra) or altitudinal tree line (alpine tundra). Remote sensing studies indicate broad patterns of changing seasonality of vegetation productivity

at high latitudes over time in relation to climate warming^{8–10}; however, phenological responses to warmer temperatures have been shown to differ greatly among species and locations, with some species shifting dates of flowering and flower senescence more than others^{11–15}. Studies from temperate ecosystems have found that early-flowering species often advance phenological events more in response to warmer temperatures than later-flowering species^{1,16–19}; however, to date, the relationship between flower-

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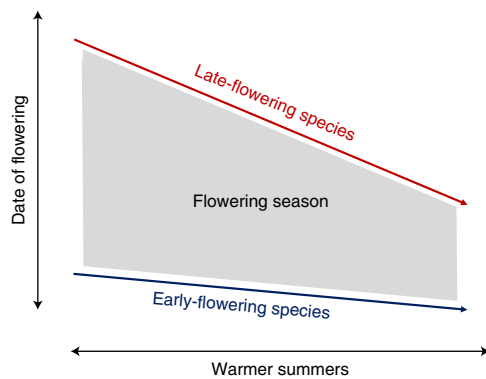


Fig. 1 | Conceptual diagram showing how warmer summer temperatures may shorten the length of the flowering season in tundra ecosystems. If the phenology of early-flowering plant species is influenced primarily by photoperiod or the timing of snowmelt, and does not respond appreciably to warmer summer 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, there may be a contraction of the overall flowering season during warmer years.

ing time and phenological sensitivity has not been tested across tundra ecosystems.

Evidence suggests that across northern tundra ecosystems, the phenology of plants from colder sites at higher latitudes changes more with warmer temperatures than the 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^{3,21–27} 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^{3,23,29}, 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 compared with plants that do respond^{22,36}.

There are diverse 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^{12,37,38}. The relative flowering time of a species compared with 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^{12,43–45}. 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.

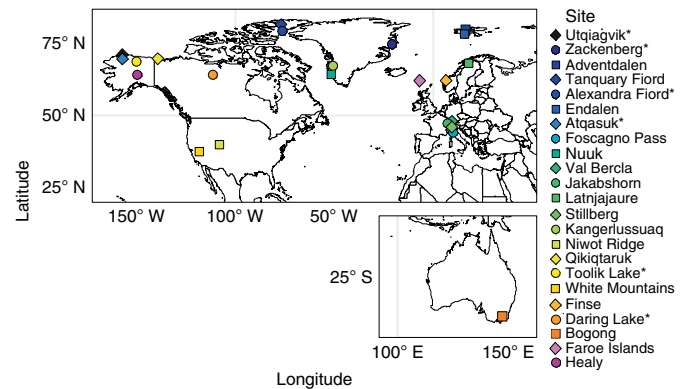


Fig. 2 | Map of long-term observational and experimental warming studies. Site names are listed in order from the site with the coldest (2.8 °C) to the site with the warmest (11.9 °C) summer temperatures (June–August for Northern Hemisphere sites, and December to February for the Southern Hemisphere site; Supplementary Fig. 1). Site symbols shown on the map correspond to the symbols and colours in Figs. 3 and 4. Asterisks indicate sites used in community flowering season analyses.

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 it 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 species, increases in summer temperature will probably accelerate the flowering phenology of late-flowering species more than early-flowering species. Additionally, if temperatures towards the end of the growing season are rising more rapidly than temperatures at the beginning of the year, the 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^{12,31,44,47}. In particular, shorter flowering seasons could also strongly limit resource availability for pollinators, especially if the phenologies of pollinator species are responding to different drivers than those of 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) The flowering phenology of late-flowering tundra species is more sensitive to warmer summer temperatures than the flowering phenology of early-flowering species. We tested this hypothesis with both observational and experimental data, and hypothesized that the 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, the community-level flowering seasons will be shorter in warmer years. (3) As average summer temperatures at tundra sites have warmed in the recent past, the duration of community-level flowering seasons has

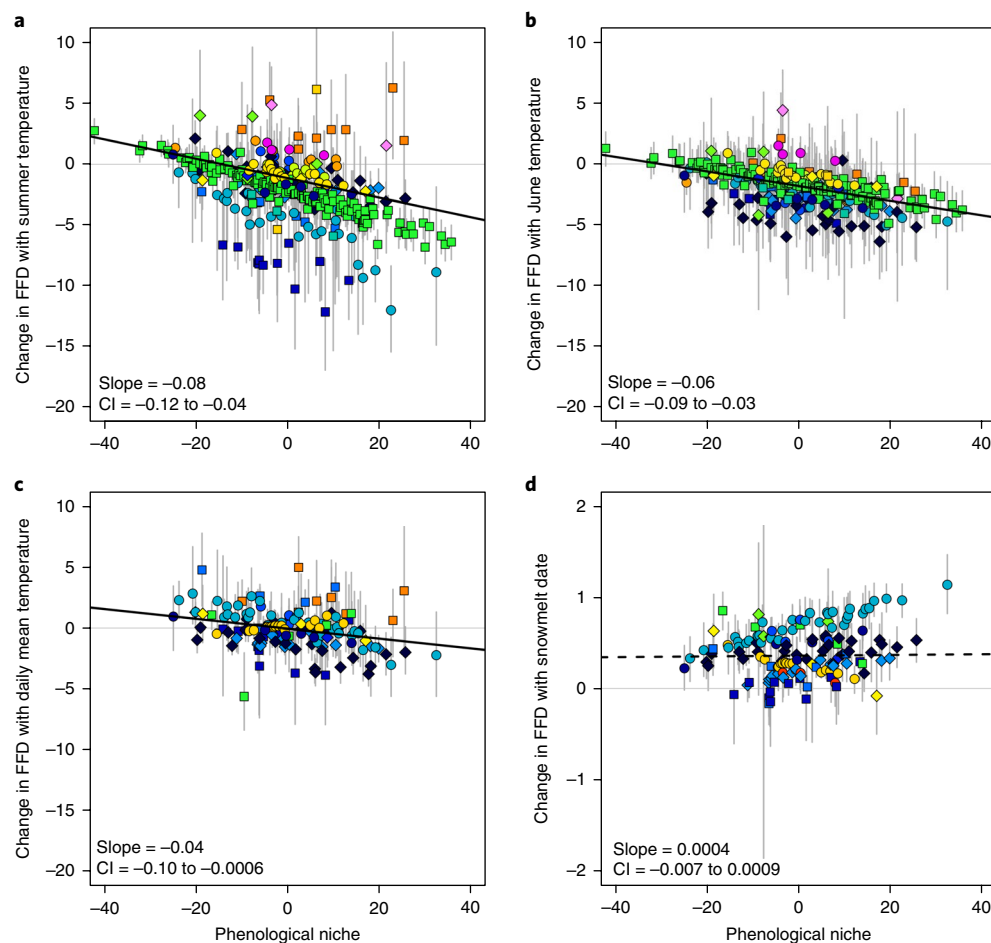


Fig. 3 | Temperature sensitivity of FFDs was greater for late- versus early-flowering species. a–d, Relationships between the phenological niches of species and sensitivities of FFDs to mean monthly temperature until flowering (**a**), mean June temperature (**b**), mean daily temperature between snowmelt and flowering (**c**) and the date of snowmelt (**d**). Points represent the estimated temperature sensitivities for each species at each site, and vertical grey lines span the 95% credible intervals (CIs) for each species-by-site-level estimate. Colours and symbols correspond to site names in Fig. 2. The ‘phenological niche’ is the average flowering date of a species compared with 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% CIs are listed in the bottom left of each graph. The phenological niches significantly predict phenological responses (at the 5% level) if the 95% CIs do not overlap zero.

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 (that is, last flowering 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 investigated the relationship between community flowering season length and both mean June–July temperatures and year for six sites with observations of four or more species over ten or more years.

Results

FFDs of late-flowering species were more temperature sensitive than those of early-flowering species (that is, FFDs of late-flowering species advanced more per °C increase in summer temperature, and in response to experimental warming, than those of early-flowering species; Figs. 3a and 4a, Supplementary Fig. 1 and Supplementary Table 4). The 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 (Fig. 3b,c and Supplementary Table 4). However, the phenological niche of a species did not influence the sensitivity of FFDs to snowmelt timing

(Fig. 3d and 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 LFDs in either long-term monitoring plots or warming experiments (Supplementary Table 5 and Fig. 4b).

The community-level flowering seasons across the 6 sites with 10 or more years of data were 3.96 d shorter per 1 °C warmer June–July temperature (95% CI = −7.31 to −0.79; Fig. 5a and Supplementary Table 5). The length of the flowering season was estimated as the duration between the average FFD of the earliest-flowering species and the average LFD of the latest-flowering species per site in each year. Community-level flowering seasons became shorter over time at all six sites, but the change was significant only at Alexandra Fiord, Daring Lake and Zackenberg. Across all sites, the flowering season length shortened by 0.43 d yr^{−1}, but the credible interval (CI) on this parameter overlapped 0 (95% CI = −0.87 to 0.06; Fig. 5b). Annual June–July temperatures increased by 0.07 °C yr^{−1} (95% CI = 0.02 to 0.12; Fig. 5c).

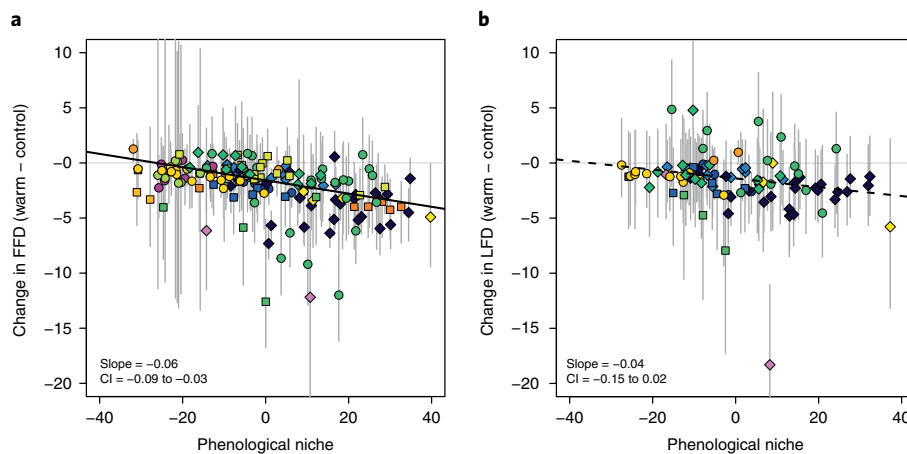


Fig. 4 | The change in FFDs in response to experimental warming was greater for late- versus early-flowering species. a,b, Relationships are shown between phenological niches of species and the timing of FFDs (**a**) and LFDs (**b**) in experimentally warmed plots compared with control plots. Points represent the estimated temperature sensitivities for each species at each site, and vertical grey lines span the 95% CIs for each species-by-site-level estimate. Colours and symbols correspond to site names in Fig. 2. The ‘phenological niche’ is the average flowering date of a species compared with 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% CIs are listed in the bottom left of each graph. The phenological niches significantly predict phenological responses (at the 5% level) if the 95% CIs do not overlap zero.

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 FFDs was greater for tundra species that flowered later in the growing season compared with 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 ref. ²⁰ 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 species 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 the results of many studies conducted at lower latitudes and altitudes^{6,18,19,49}. Studies from warmer biomes found that early-flowering species often advance phenological events more in response to warmer temperatures than late-flowering species^{1,16–19,50,51}. 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

of 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^{6,18,51}. 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 towards 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 FFDs³⁵; thus, changes in the 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^{30,61}. 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 this could be an advantage as the temperature increases or becomes more variable^{29,62}. 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 of the relationship of phenological traits versus other plant traits and changes in plant abundance (but see refs ^{30,61}). However, as phenological data for tundra plant species accumulate, the next logical step will be to

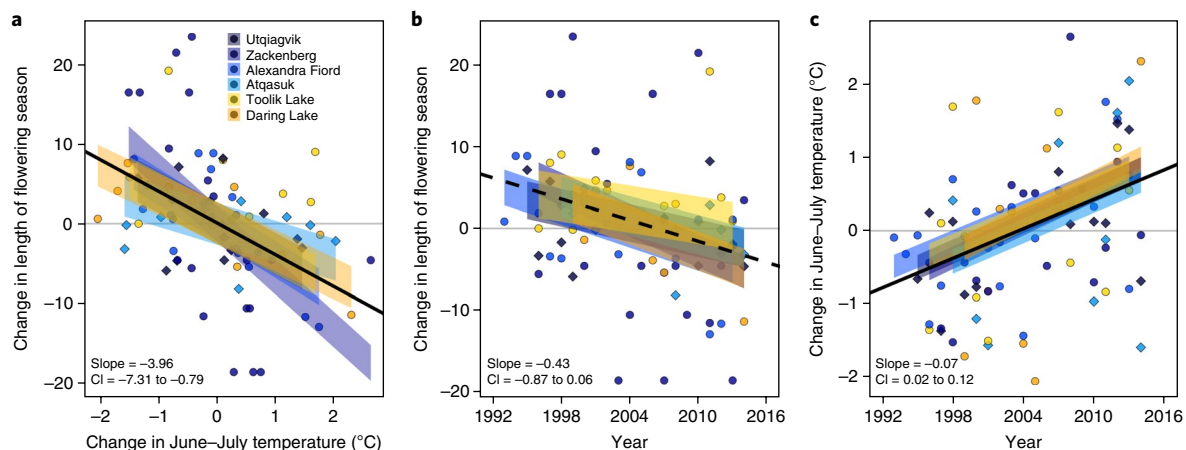


Fig. 5 | Warming was related to the change in the duration of the flowering season over time at sites across the tundra biome. **a**, Difference in the duration of the community-level flowering season compared with the difference in mean June–July temperatures from site averages. **b**, Change in the 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-centred for each site so that 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. Coloured bands show the 95% CIs for site-level slopes. Hierarchical model slopes and 95% CIs are listed in the bottom left of each graph.

link phenological measurements to performance measurements to aid predictions of vegetation change in tundra ecosystems in the future⁶³.

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 in 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^{54,65}. 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 and Fig. 2). Portions of the dataset were analysed and reported in Oberbauer et al.⁷ and Prev  y et al.²⁰; however, two additional monitoring sites and ten additional warming experiments are included in this analysis (Supplementary Table 1). Phenological observations were made at each site following a standardized protocol that was originally developed for the International Tundra Experiment network^{66,67}. Following the International Tundra Experiment protocol, observers recorded the phenological status of plants one to three times per week over the snow-free season, and specifically recorded the FFD and 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 FFD of the species at each site across all years of measurements (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, the mean June temperature or the mean daily temperature between snowmelt and flowering. Flowering dates for the Southern Hemisphere alpine site were adjusted by 210 d to match those 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 the average May temperature (Supplementary Table 2). For example, if the phenological niche of a species was 30 June, the mean June temperature was used as the summer temperature variable for that species. However, if the phenological niche was 15 July, the average June–July temperature was used (Supplementary Table 2). To test the influence of the temperature windows on the results, 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 the results, as the sensitivity of flowering time for species flowering in the early parts of months is 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 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 assessing the phenological niches of species in relation 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–August) 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, mean monthly temperatures were estimated using 0.5° gridded temperature data from the Climate Research Unit⁶⁸ (Supplementary Table 1). Temperatures and phenological niches were mean-centred 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 around 1 m² fibreglass or polycarbonate OTCs, in either cone or hexagonal shapes, that increased the air temperature by 0.5–3.0 °C^{66,69–71} (Supplementary Table 3). The OTCs were either placed on plots only over the summer or left on plots throughout the year, depending on the site (Supplementary Table 3).

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

In total, the analyses of FFDs in warming experiments included 1,219 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 analyse phenological observations over the different numbers of sites, years of observations and species, we used Bayesian hierarchical modelling. 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 site⁷².

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 the 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 programme Stan⁷³, which was accessed using the package Rstan⁷⁴ in the statistical programme R 3.2.2 (ref. ⁷⁵). Each model was run with 2 chains of 20,000 iterations, using Hamiltonian Monte Carlo sampling. We used flat priors for all parameter estimates. Full model details and codes are included in Supplementary Information Section 7. We checked for convergence of chains for all parameters both visually with trace plots and with the Gelman–Rubin convergence statistic⁷⁶. 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 ten 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 FFDs and LFDs are not always representative of changes over the entire flowering season^{55,77}, 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 related 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 modelling approach. We mean-centred both flowering season length and average June–July temperatures for each site so we could assess the relationship between the change in community-level flowering seasons and 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 whether flowering season length or June–July temperatures have changed significantly over time. We analysed associations between community flowering season length and summer temperature and time with a Bayesian hierarchical model using mean-centred 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 codes are included in Supplementary Information Section 7.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study have been archived in the Polar Data Catalogue: <https://doi.org/10.21963/12961>.

Received: 3 April 2018; Accepted: 6 November 2018

Published online: 10 December 2018

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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 especially thank: M. Dalle Fratte, D. Cooley, O. Durey, C. Eckert, J. F. Johnstone, C. Kennedy, V. Lamarre, G. Levasseur, C. Spiech, J. Svoboda and R. Wising; the Herschel Island Qikiqtaruk Territorial Park staff, including E. McLeod, S. McLeod, R. Joe, P. Lennie, D. Arey, L. Meyook, J. McLeod, P. Fois, C. Gordon, J. Hansen, A. Rufus and R. Gordon; Quttinirpaaq National Park staff; the Greenland Ecosystem Monitoring team; and Warming and species Removal in Mountains (WaRM) coordinators N. Sanders, A. Classen and M. Sundqvist. These observations were made possible with the support of many funding agencies and grants, including: ArcticNet; the Natural Sciences and Engineering Research Council of Canada; the Canadian International Polar

Year Program; the Polar Continental Shelf Program of Natural Resources Canada; the Danish Environmental Protection Agency; the Swiss Federal Institute for Forest, Snow and Landscape Research; the National Geographic Society; the US National Science Foundation (grant numbers PLR1525636, PLR1504141, PLR1433063, PLR1107381, PLR0119279, PLR0902125, PLR0856728, PLR1312402, PLR1019324, LTER 1026415, OPP1525636, OPP9907185, DEB1637686, 0856710, 9714103, 0632263, 0856516, 1432277, 1432982, 1504381, 1504224, 1433063, 0856728, 0612534, 0119279 and 9421755; the Danish National Research Foundation (grant CENPERM DNRF100); the Danish Council for Independent Research (Natural Sciences grant DFF 4181-00565); the Deutsche Forschungsgemeinschaft (grant: RU 1536/3-1); the Natural Environment Research Council (grant NE/M016323/1); the 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.S.P. and C.R. designed and led the study. J.S.P. and C.R. led the collection of data for the phenology database. J.S.P., N.R., A.D.B., I.H.M.-S. and S.C.E. performed the statistical analyses. J.S.P., C.R., N.R., T.T.H., A.D.B., I.H.M.-S. and S.C.E. drafted the paper. J.S.P.,

C.R., A.D.B., I.H.M.-S., I.W.A., N.C., K.C., C.C., E.J.C., B.E., A.M.F., G.H.R.H., R.D.H., I.S.J., K.K., C.W.K., E.L., M.M., U.M., S.N., S.O., Z.A.P., E.P., S.B.R., N.M.S., E.S., P.R.S., J.G.S., K.N.S., Ø.T., T.T., S.V., C.-H.W., J.M.W. and S.W. contributed data. All authors were involved in writing and editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-018-0745-6>.

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No software was used for data collection.

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Study description

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. 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 measurements. For the analyses of long-term monitoring plot data, we examined the relationship between phenological niche and temperature (expressed in several ways) and snowmelt dates at long-term monitoring plots with hierarchical models in a Bayesian framework. Mean site-level summer temperatures from 1981–2000 were included in models as an additional predictor variable of species phenological responses. 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. 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 flowering 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 flowering dates 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. 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 flowering 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 flowering dates between warmed and control plots was directly included as a response variable in the species-level regression. Finally, to test for a contraction of community-level flowering seasons in association with warmer summers, we conducted analyses that included 6 sites with flowering dates for four or more species over 10 or more years. 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.

Research sample

We compiled a database of observations 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 (Table S1, Fig. 2). Portions of the dataset were analyzed and reported in Oberbauer et al. (2013) and Prev  y et al. (2017), however, two additional monitoring sites and 10 additional warming experiments are included in this analysis.

Sampling strategy

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.

Data collection

Site PIs, field technicians, or graduate students recorded the phenological status of plants one to three times per week over the snow-free season.

Timing and spatial scale

Observers recorded the phenological status of plants one to three times per week over the snow-free season. This frequency allowed for estimation of first and last flowering dates without putting undue burden on researchers (i.e., taking phenology observations every single day would be too time consuming and logistically not feasible at some sites). Please see Table S1 for the specific time periods that data were collected at each site.

Data exclusions

All exclusion criteria were established before analyses began. We excluded data from long-term monitoring plots that had two years or less of flowering phenology observations per species per plot because slopes of phenological sensitivity of only 2 years are not very robust, and calculation of phenological sensitivity slopes for only one year of data are not possible. We included all observations for comparisons of control and experimentally warmed plots. For the test of a contraction of community-level flowering seasons in association with warmer summers, we excluded sites with fewer than 10 years of data and fewer than four species in order to examine changes over relatively long time periods, and we only wanted to include sites that had at least four species to give an estimate of flowering changes of the entire plant community.

Reproducibility

This is a data synthesis, so we could not reproduce the experiments per se. We plan to make publicly available all data and code for analyses from this synthesis so that others may use our analytical approach with their own phenological data.

Randomization

The locations of controlled and experimentally warmed plots were randomized within each study area. After appropriately sized plots within each study area were established, site PIs randomly selected which plot would be assigned to a 'control' or 'warmed' treatment.

Blinding Blinding was not relevant to the study as we did not do randomized controlled trials or use other data which could have interpretations of analyses blinded.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions Phenology observations were taken weekly over the summer at the different sites, starting on the date that plots were clear of snow and continuing through leaf senescence (or first persistent snowfall) in autumn.

Location Please see Fig. 2 Table S1 for information for all site locations used in the synthesis.

Access and import/export Phenology observations were taken by site PIs with permission to collect data from various sites. Phenology observations were recorded and sent to the lead author electronically, so no export of samples was necessary.

Disturbance Data collectors only observed phenology of plants in plots, and did not disturb the plants. At many of the tundra sites, wooden walkways were constructed to minimize compaction and trampling when observers were accessing sites. The experimental warming treatments were accomplished with plastic open-topped chambers that were placed around plants in plots, but this did not involve disturbing any plants, unless plants were growing exactly on the edge of plots where the plastic siding of the open topped chambers was placed.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

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Laboratory animals The study did not involve laboratory animals.

Wild animals The study did not involve wild animals.

Field-collected samples The study did not involve samples collected from the field.