

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

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Abstract

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

Keywords: Arctic, *Cassiope tetragona*, climate change, climatic gradient, flowering, International Tundra Experiment, latitude, tundra

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Introduction

Changes in plant phenology are among the most notable and widespread examples of climate change

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

Ecologically important traits, including the timing of phenological events, can vary within species across environmental and temperature gradients (Weber & Schmid, 1998; Riihimäki & Savolainen, 2004; Kenta *et al.*, 2011). In the Arctic, small absolute changes in temperature may represent relatively larger increases in the thermal budgets of plants at cold sites (Bliss, 1962; Billings, 1992; Oberbauer *et al.*, 2013); hence, one might expect plants at colder, higher latitude sites to respond more strongly to the same degree of warming than those from warmer, lower latitude sites. Plants growing in high Arctic locations with very short growing seasons could be under strong selective pressure to initiate growth and flowering as soon as temperatures are favorable. Differential sensitivity to temperature at sites with different climatic conditions could, in turn, result in a convergence of flowering times across sites as the climate warms. Many tundra plant species extend over large geographical and elevational ranges, with populations of the same species adapted to local environmental conditions (Chapin & Chapin, 1981; McGraw & Antonovics, 1983; Welker *et al.*, 1997; Bennington *et al.*, 2012). Populations of a species occurring in colder sites have been found to flower later than those of the same species in warmer sites (Lévesque *et al.*, 1997; Riihimäki & Savolainen, 2004; Kenta *et al.*, 2011). Consequently, if warmer temperatures lead to a greater advancement of flowering at colder sites than at warmer sites, overlap in flowering times across sites will likely increase. This, in turn, could lead to increased gene flow among populations, with potentially important consequences for adaptive evolution and the ability of plant species to persist under climate change (Fox, 2003; Phillimore *et al.*, 2010; Sexton *et al.*, 2011). However, few

studies have compared phenological sensitivities between sites, so we have been unable to predict whether reproductive phenology will converge, diverge, or show no change as the climate warms in high-latitude regions.

Climate change influences the phenology not only of flowering, but also of leaf emergence and senescence, and therefore ecosystem processes such as carbon dynamics (Oberbauer *et al.*, 1998, 2007; Welker *et al.*, 2004; Peñuelas *et al.*, 2009; Cahoon *et al.*, 2012). Current process-based vegetation models – which are linked to global carbon models – assume similar temperature sensitivities of plant species responses across the Arctic (e.g., Miller & Smith, 2012). However, if growth initiation of plants from colder regions responds more quickly to warmer temperatures than plants from warmer regions, then the net balance of carbon exchange from Arctic ecosystems might change considerably (Oechel *et al.*, 2000; Welker *et al.*, 2004; Cahoon *et al.*, 2012; Sharp *et al.*, 2013; Myers-Smith *et al.*, 2015). Studies examining differences in the phenological sensitivity of growth to temperature across species' ranges can thus help improve predictions of the cumulative responses of high-latitude ecosystems, and associated ecosystem services, to climate change.

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

Materials and methods

Site and phenological data description

We examined phenological data for flowering and leaf emergence/senescence from 18 sites along a climatic gradient including sub-Arctic, sub-Arctic alpine, and Arctic tundra ecosystems (Table 1, Fig. 1). Eleven of the 18 sites in this analysis were established as part of the International Tundra Experiment (ITEX) network (Webber & Walker, 1991; Henry & Molau, 1997), and observers at all 18 sites collected data following a standardized phenology protocol developed for ITEX (Molau & Molgaard, 1996). The phenological status of plant species within plots was recorded one to three times per week over the snow-free season, and this allowed for the estimation of the average day of year when each phenological event occurred per species per site. Four phenological events were recorded: first flowering, flower senescence, greening, and leaf senescence (Arft *et al.*, 1999). Phenological events were defined differently depending on plant species (Molau & Molgaard, 1996), but were recorded consistently over time for each species in each plot. Depending on the species, 'flowering' was defined as the date when either the first flower was open, the first pollen was visible, or the first anthers were

exposed; 'flower senescence' was when anthers withered, or petals dropped; 'greening' was the date of leaf emergence, when the first new leaf was visible or open; and 'leaf senescence' was when the first color change of a leaf was observed.

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

Temperature sensitivity of phenology

Temperature sensitivities of phenological events for each species at each site were calculated as the slope of the relationship between the day of year of a phenological event (flowering,

Table 1 Information on Arctic sites used in this study

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

'Mean summer temp.' is the average June–August temperature for each site from 1981 to 2010. 'Temp. data source' lists the name of the weather station data that mean summer temperature data were obtained from or indicates whether mean summer temperature was estimated from 0.5 gridded CRU data. Superscripts listed after summer temperature data sources correspond to citations and websites listed in Data S1.

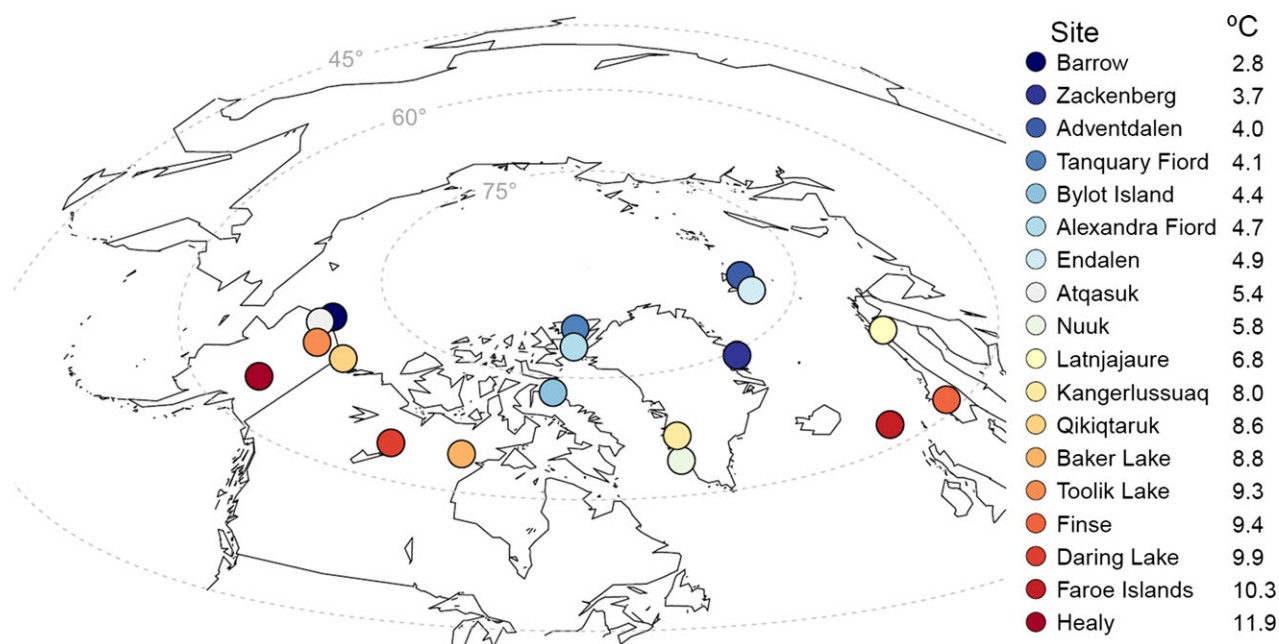


Fig. 1 Locations of the 18 sites used in this analysis. Colors denote the mean summer (June–August) temperature (°C) for each site from 1981 to 2010. [Colour figure can be viewed at wileyonlinelibrary.com].

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

Chilling temperatures over winter (Cook *et al.*, 2012; Clark *et al.*, 2014), extreme events (Phoenix & Bjerke, 2016), and lag effects from temperatures experienced the previous year

(Mulder *et al.*, 2016) can also influence the timing of phenology of plants. However, in this dataset, we found no relationships between winter temperatures or monthly temperatures of the previous year and the timing of phenological events (data not shown).

To statistically test whether species at colder sites shifted phenological dates more strongly in response to the same degree of warming than those from warmer sites, we then modeled the response of temperature sensitivities (described above) to the mean summer (June–August) temperature of sites from 1981 to 2010 using a Bayesian hierarchical modeling approach (described below). We used a two-level model in which species-level phenological sensitivities to temperature and the associated uncertainties were used to estimate site-level phenological responses and their relationship with mean summer temperature across sites. We chose mean summer temperature over the last 30 years as the main predictor variable at the site level because summer temperatures are strongly associated with growth and phenology of many tundra species (Thórhallsdóttir, 1998; Elmendorf *et al.*, 2012a; Oberbauer *et al.*, 2013; Myers-Smith *et al.*, 2015). Average June–August temperatures at sites ranged from 2.8 to 11.9 °C (Fig. 1). Mean summer temperatures for sites were obtained from local weather stations when available (Table 1; Data S1). For several sites, temperature data were not available for months or years when the phenological events were not recorded. If no long-term (1981–2010) weather data were available near sites, mean summer temperatures were estimated using 0.5° gridded temperature data from the Climate Research Unit (CRU) TS3.21 (Harris *et al.*, 2014; Table 1). June–August CRU data were strongly correlated with local temperature data for those cases where both were available (R^2 from 0.71 to 0.99).

Phenology model description

We assumed that the phenology of a species could vary among different plots within a site due to effects of local topography on microclimate (plot-by-species-combinations are indexed by the letter *i*), but that the phenological response of a species to temperature would not differ among plots within a site (site-by-species-combinations are indexed by the letter *j*). We modeled the date of the phenological event (DOY) as a function of temperature over the summer time-window per site (*s*) in a given year (*y*) ($\text{temp}_{y,s}$), with a_i being the plot-by-species-level intercept, b_j the site-by-species-level slope, and σ_j the variation in observed dates ($\text{DOY}_{i,y}$) around the prediction at the site-by-species level

$$\text{DOY}_{i,y} \sim \text{Normal}(a_i + b_j \cdot \text{temp}_{y,s}, \sigma_j).$$

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

$$b_j \sim \text{Normal}(\beta_s, \sigma_s),$$

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

$$\beta_s \sim \text{Normal}(\gamma_0 + \gamma_1 \cdot \text{avsummertemp}_s, \sigma_\beta).$$

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

$$\text{DOY}_{i,y} \sim \text{Normal}(a_i + \beta_s \cdot \text{temp}_{y,s}, \sigma_j).$$

Slopes of the same species at different sites were assumed to be independent of each other. We tested the normality of the data by running a model where species-by-site slopes were fit independently from each other and by visually assessing the distribution for each site. Our results demonstrated that the assumption of a normal distribution was not violated at any site and that a normal distribution is a good description of site-level variation in species' temperature sensitivity. Additionally, we do not investigate how phenology varies directly with summer temperature between sites; but rather, we investigate how the temperature sensitivity of phenology (i.e., the change in phenology per °C) varies among sites with different mean summer temperatures, so we have not within-subject mean-centered the site-level temperature data as recommended in other similar hierarchical modeling approaches where site is included as a random effect (Van de Pol & Wright, 2009; Phillimore *et al.*, 2013).

For this model, we did not include both plot and year random effects (to account for the nonindependence of plots measured repeatedly over time as well as the nonindependence of observations conducted in the same year at a given site) because some sites had very few yearly observations, and including both plot and year random effects resulted in a model that did not converge. We thus included only the plot effect in the model presented here, and ran a separate version of the analysis including a year random effect (but no plot

random effect), which demonstrated the same overall relationship (Data S2.1). Finally, we also analyzed data using simple linear regressions and a mixed-model framework using the R package lme4 (Bates *et al.*, 2015), which gave similar results (Data S2.2). To investigate whether the variation in the number of years that sites were sampled influenced our results, we also performed two separate analyses for the flowering data, one limited to sites with 10 or more years of data and the other limited to sites with less than 10 years of data. Both analyses gave similar results to the analysis that included all sites (Table S2.3).

Bayesian hierarchical modeling allowed us to incorporate the uncertainties of species- and site-level phenological responses in the final correlation of site climate and site-level phenological responses (Data S3, Latimer, 2007). We fit Bayesian models using the program STAN, accessed using the package Rstan (Stan Development Team, 2015). We used flat priors for all parameter estimates. Each model was run with two chains of 20 000 iterations, using Hamiltonian Monte Carlo (HMC) sampling. We checked for convergence of chains for all parameters both visually with trace plots and with the Gelman–Rubin convergence statistic (Gelman & Rubin, 1992). Trace plots showed that chains mixed well and converged to stationary distributions for all parameters estimates. Gelman–Rubin convergence statistics for parameter estimates of all models were <1.02.

Flowering of *Cassiope tetragona*

We additionally tested whether the flowering times of the single most common species in the dataset, the evergreen dwarf shrub *C. tetragona*, showed greater temperature sensitivity in colder vs. warmer locations. We had flowering observations of *C. tetragona* at eight sites, with four or more years of observations per site, so we were able to perform a robust intraspecific analysis using this species. The relatively long time series of *C. tetragona* observations at sites (4–19 years) also allowed us to test whether the flowering dates of *C. tetragona* have advanced more at colder sites than at warmer sites over time. For these analyses, we calculated the temperature sensitivities of flowering of *C. tetragona* to yearly June temperatures, and the change in the day of year of flowering of *C. tetragona* per year at each site. We then compared these temperature sensitivities and temporal changes to the mean summer (June–August) temperature of sites from 1981 to 2010 using the Bayesian modeling framework described above. Stan model specifications for the phenological models used for all species and *C. tetragona* are presented in Data S3.

Temperature change over time

To test whether colder or higher latitude sites have experienced greater changes in spring and summer temperatures over the last 50 years than warmer or lower latitude sites, we analyzed the temperature data for the 18 sites included in these analyses. To identify longer term trends in temperature change, we used CRU 0.5° gridded temperature data (Harris *et al.*, 2014) to examine temperature change over a longer

period (1960–2013) than the period we used to estimate mean summer temperature at each site (1981–2010). To determine how spring and summer temperatures have changed at northern sites over time, we regressed CRU temperature data for each site against year to calculate the change in May, June, July, and August temperatures from 1960 to 2013. Then, to examine whether colder sites at higher latitudes had experienced more warming over time than lower, warmer sites, we compared the temperature changes to both the mean summer temperature of sites from 1981 to 2010, and also to site latitude using simple linear regressions. All statistical analyses were conducted in the statistical program R 3.2.2 (R Core Team, 2015).

Results

Temperature sensitivity of phenology

Overall, the temperature sensitivity of the timing of flowering was greater (i.e., the slopes of the relationship between flowering date and temperature were more strongly negative) at colder sites than at warmer sites (Figs 2a and S1). The temperature sensitivity of greening was also greater at colder sites (Fig. 2c). However, there were no differences between colder and warmer Arctic sites in the temperature sensitivity of either

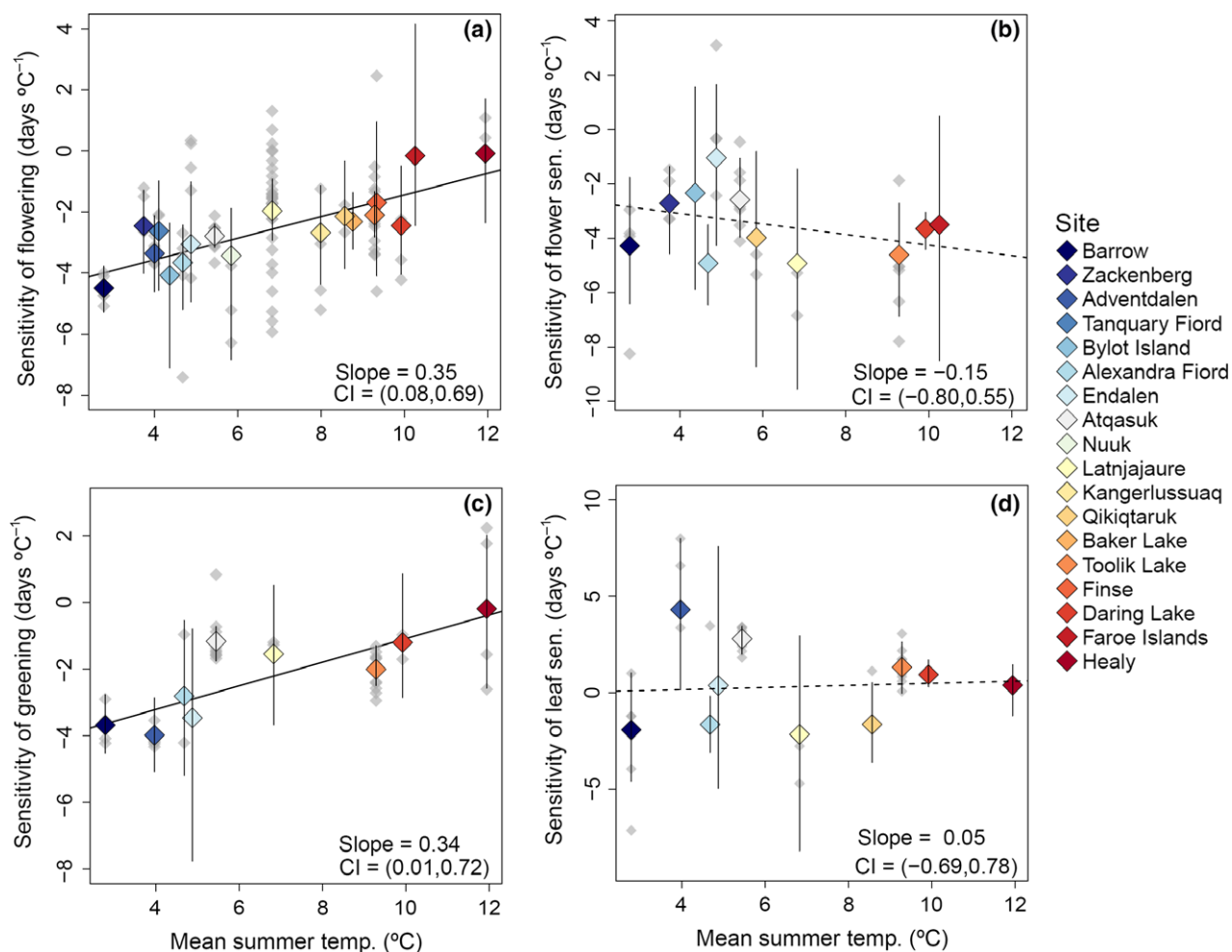


Fig. 2 Relationships between the mean summer (June–August) temperature and the temperature sensitivity of (a) flowering, (b) flower senescence, (c) greening, and (d) leaf senescence at northern latitude sites. Temperature sensitivity is the slope of the relationship between the timing of a given phenological event and temperature and is expressed as the number of days the phenological event changed per 1 °C of warming. Colored points represent the estimated temperature sensitivity for each site (β_s), and vertical black lines span the 95% credible intervals for each site-level estimate. Gray points represent the estimated temperature sensitivity for each species at each site (b_j). The hierarchical model fits for the common slopes across sites and the 95% credible intervals (CIs) are listed in the bottom right of each graph. Site temperature is related to phenological responses when the 95% credible intervals do not overlap zero; overall model slopes that differed from zero are shown with a solid line, while a lack of a relationship is shown with a dashed line. [Colour figure can be viewed at wileyonlinelibrary.com].

flower or leaf senescence dates (Fig. 2b, d). Alternative analyses that calculated slopes for phenological sensitivities using either different summer temperature time-windows for each species and site or using June temperature for all species and sites gave similar results to those presented in the main text (Table S2).

Flowering of *Cassiope tetragona*

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

Temperature change over time

Over the period 1960–2013, May and June temperatures increased slightly more at colder sites than warmer sites (May: $F_{1,16} = 2.98$, $P = 0.10$; June: $F_{1,16} = 5.07$, $P = 0.04$, Fig. 4a, b) and at higher latitudes than at lower latitudes (May: $F_{1,16} = 8.62$, $P = 0.01$; June: $F_{1,16} = 10.59$, $P = 0.005$ Fig. S2a, b). Changes in July and August temperatures over the last 40 years showed no significant trends with mean summer temperature or latitude of sites (all $F_{1,16} < 0.45$, $P > 0.51$, Figs 4c, d and S2c, d).

Discussion

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

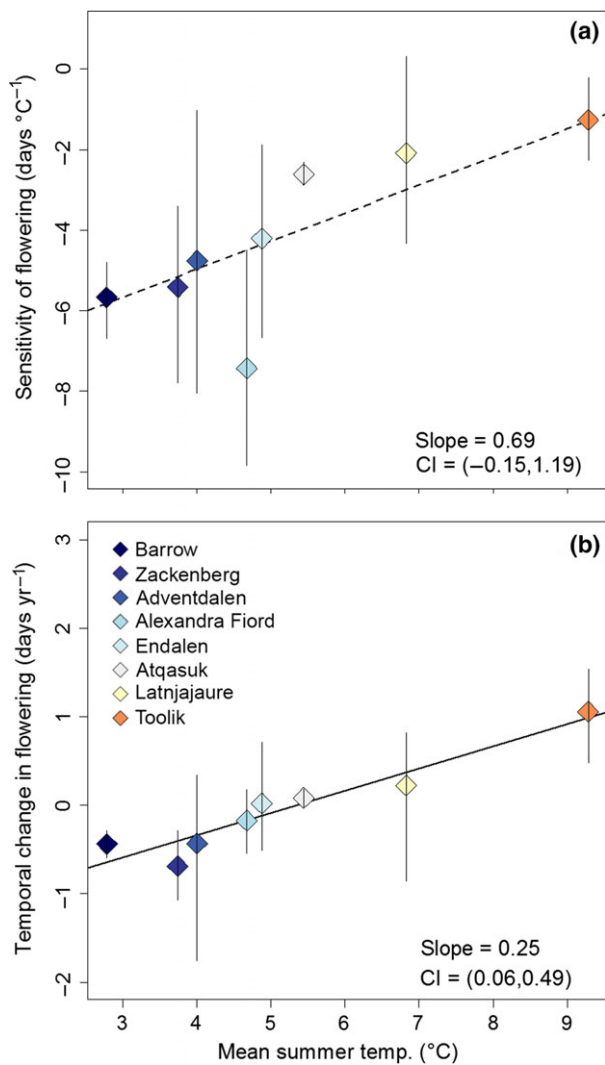


Fig. 3 Relationships between the mean summer (June–August) temperature and (a) the temperature sensitivity of flowering of *Cassiope tetragona* and (b) the temporal change (days per year) of flowering of *C. tetragona* across northern latitude sites. Temperature sensitivity is expressed as the number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

The greater temperature sensitivity of flowering phenology we observed at colder, more northern sites contrasts with other individual- and population-level responses of tundra plants to warming (Elmendorf *et al.*, 2012a,b; Myers-Smith *et al.*, 2015). Specifically, previous studies have found greater plant abundance changes with warming (Walker *et al.*, 2006; Elmendorf

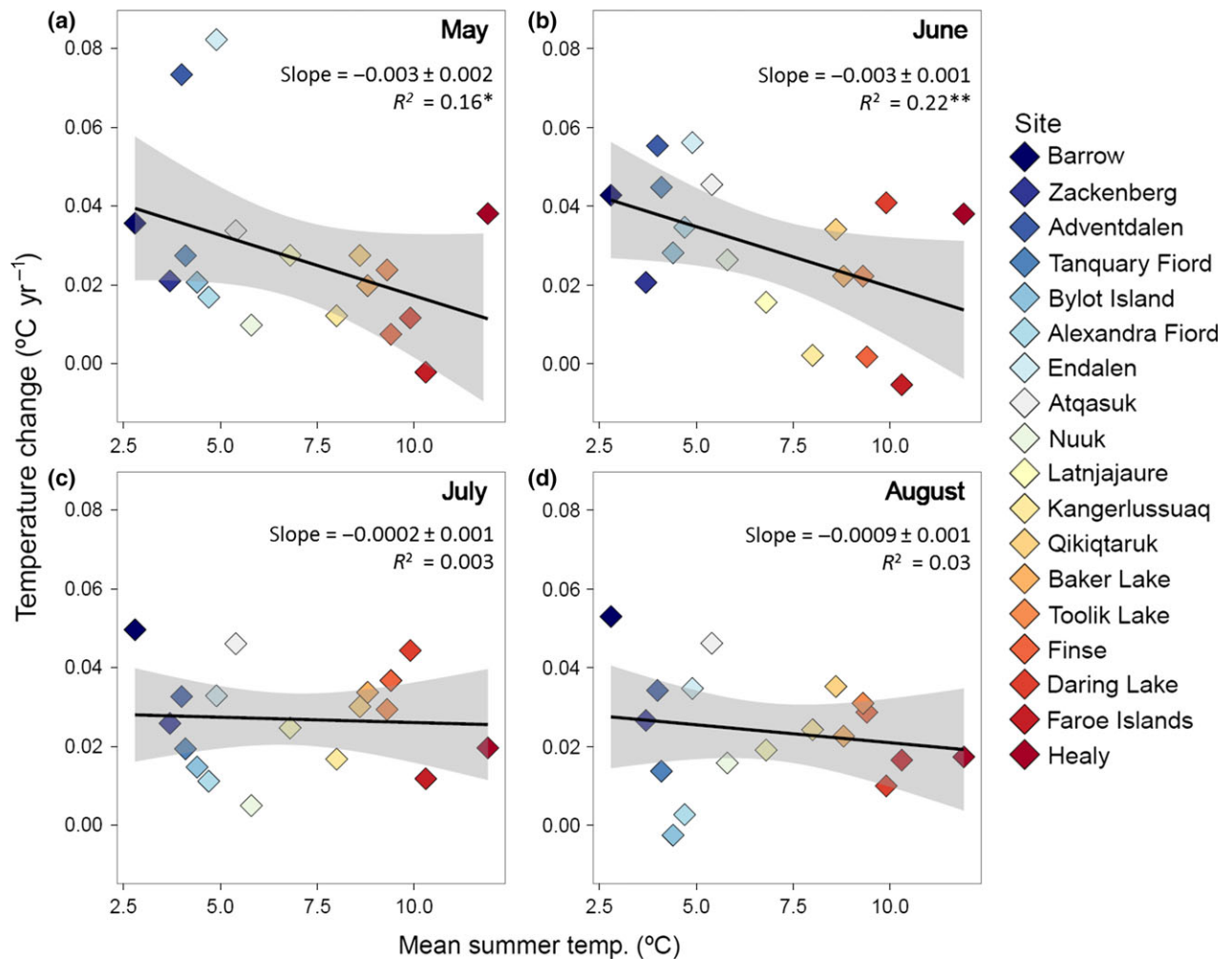


Fig. 4 Comparisons between the mean summer (June–August) temperature of sites from 1981 to 2010 and the average annual change in temperature from 1960 to 2013 for the months of May (a), June (b), July (c), and August (d). Lines and gray shading represent slopes and 95% confidence intervals of simple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

et al., 2012a,b) and greater climate sensitivity of shrub growth rings (Myers-Smith *et al.*, 2015) in warmer, low- and mid-Arctic rather than high Arctic ecosystems. Temperature sensitivity of flowering phenology may be greater in higher latitude ecosystems because reproductive strategies involving flowering and seed development may be more important where there is often more bare ground for seeds to successfully colonize (Wookey *et al.*, 1993; Welker *et al.*, 1997; Klady *et al.*, 2011). Conversely, temperature sensitivity of vegetative growth may be greater at lower Arctic sites because reproductive strategies involved in vegetative growth may be under stronger selection in sub- and low-Arctic ecosystems with dense, closed canopies (Wookey *et al.*, 1993; Parsons *et al.*, 1994). The differences between our results and those of previous syntheses indicate that

not all plant traits will respond in the same way to environmental change (Shaver & Kummerow, 1992; Arft *et al.*, 1999; Barrett *et al.*, 2015; Kremers *et al.*, 2015).

Phenological responses to climate change have been well studied, either on their own (e.g., Fitter *et al.*, 1995; Miller-Rushing & Primack, 2008) or in the context of phenological synchrony between interacting species and potential feedbacks to fitness (Both *et al.*, 2009; Kharouba & Vellend, 2015; Kharouba *et al.*, 2015). Here, we focus on phenological synchrony both among different species, and of one species situated at different sites along a temperature gradient. Our results point to an important, yet often overlooked, consequence of phenological synchrony: variation in the temperature sensitivity of phenology among populations – as demonstrated here with *C. tetragona* – could alter the

potential for pollen transfer and therefore gene flow, which could either promote adaptive evolution and persistence via increased genetic variation and reduced inbreeding depression (Alleaume-Benharira *et al.*, 2006), or counteract adaptive evolution via the introduction of locally maladapted alleles (Lenormand, 2002; Sexton *et al.*, 2011). Although many of the sites in this study are too distant for pollen transport by pollinators, the variation observed in the temperature sensitivities of flowering from these sites can inform the manner in which flowering times in regions with strong elevational or continental climatic gradients may converge with warmer summer temperatures. Specifically, our results suggest that increased summer temperatures will shift the flowering times of plants from colder, higher latitude sites earlier to overlap more with those of populations from warmer sites, thus potentially increasing gene flow between populations across latitudes.

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

There was no relationship between the phenological sensitivity of flower or leaf senescence and summer temperature across sites, similar to results of an earlier synthesis of tundra plant phenology (Oberbauer *et al.*, 2013). Non-temperature-related cues, such as successful pollination, may exert a greater influence on the timing of flower senescence than temperature (Stead, 1992). Multiple factors, such as photoperiod, soil moisture, frost, and insect damage may be more important cues than temperature for leaf senescence (Körner, 2003; Panchen *et al.*, 2015). Growing seasons are predicted to expand in polar ecosystems as temperatures increase, snow melt occurs earlier, and snow fall occurs later

(Oberbauer *et al.*, 1998). Our findings suggest that growing season duration may extend due to earlier greening or flowering in warmer years, but not as a result of a longer period of photosynthetic activity in the fall in the aboveground parts of plants (Macias-Fauria *et al.*, 2012; Rumpf *et al.*, 2014; Khorsand Rosa *et al.*, 2015). However, belowground phenology might differ, as longer growing seasons could occur with later freeze-up due to an extended period of root growth (Blume-Werry *et al.*, 2016; Radville *et al.*, 2016; Sloan *et al.*, 2016).

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

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

with fine-grained climate scenarios will allow us to predict where and when plant phenology will change most rapidly in the future.

Data accessibility

The data used in this synthesis are archived at the Polar Data catalog (www.polardata.ca/pdsearch/?doi_id=12722).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Names and websites for sources of temperature data used to estimate the mean summer (June–August) temperatures for each site from 1981 to 2010.

Data S2. Results from alternative models used to analyze how mean summer temperatures at sites influence the temperature sensitivity of phenological events.

Data S3. Stan model specifications for hierarchical Bayesian analyses presented in the main text.

Figure S1. Relationship between the mean summer temperature at sites and the temperature sensitivity of flowering only for species that occurred at three or more sites.

Figure S2. Comparisons between the latitude of sites in the analyses and the average annual change in temperature from 1960 to 2013 for the months of May (a), June (b), July (c), and August (d).

Table S1. List of all plant species and phenological measurements used in analyses.

Table S2. Results of Bayesian hierarchical analyses using different summer temperature windows.