

# Increased variance in temperature and lag effects alter phenological responses to rapid warming in a subarctic plant community

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## Abstract

Summer temperature on the Cape Churchill Peninsula (Manitoba, Canada) has increased rapidly over the past 75 years, and flowering phenology of the plant community is advanced in years with warmer temperatures (higher cumulative growing degree days). Despite this, there has been no overall shift in flowering phenology over this period. However, climate change has also resulted in increased interannual variation in temperature; if relationships between phenology and temperature are not linear, an increase in temperature variance may interact with an increase in the mean to alter how community phenology changes over time. In our system, the relationship between phenology and temperature was log-linear, resulting in a steeper slope at the cold end of the temperature spectrum than at the warm end. Because below-average temperatures had a greater impact on phenology than above-average temperatures, the long-term advance in phenology was reduced. In addition, flowering phenology in a given year was delayed if summer temperatures were high the previous year or 2 years earlier (lag effects), further reducing the expected advance over time. Phenology of early-flowering plants was negatively affected only by temperatures in the previous year, and that of late-flowering plants primarily by temperatures 2 years earlier. Subarctic plants develop leaf primordia one or more years prior to flowering (preformation); these results suggest that temperature affects the development of flower primordia during this preformation period. Together, increased variance in temperature and lag effects interacted with a changing mean to reduce the expected phenological advance by 94%, a magnitude large enough to account for our inability to detect a significant advance over time. We conclude that changes in temperature variability and lag effects can alter trends in plant responses to a warming climate and that predictions for changes in plant phenology under future warming scenarios should incorporate such effects.

**Keywords:** Cape Churchill Peninsula, climate change, flower preformation, Hudson Bay lowlands, nonlinear responses, plant flowering phenology, saltmarsh, tundra

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## Introduction

Shifts in plant phenology over the past decades are considered one of the best indicators of effects of climate change on biological communities (e.g., Fitter & Fitter, 2002; Parmesan & Yohe, 2003). However, while many studies have found the patterns of advanced phenology in association with rising summer temperatures, these plant communities often include high proportions of 'nonresponders' (e.g., Bradley *et al.*, 1999; Fitter & Fitter, 2002; Ge *et al.*, 2011), and in some communities, there is no evidence for phenological advance despite a significant warming (Hart *et al.*, 2014; Davis *et al.*, 2015). Such lack of an expected response to temperature may be because plants use cues for flowering or

leaf-out that are not affected by climate change [e.g., photoperiod (Mooney & Billings, 1961; Caffara & Donnelly, 2011)], or it may result from changes in other environmental variables that counteract the impacts of increased temperatures. For example, increased snowfall resulting in delayed snow melt, increased damage from freeze–thaw events following early snow melt, and winter warming to the point where chilling requirements are not met can all lead to a delay in plant phenology (Murray *et al.*, 1989; Augspurger, 2009; Bokhorst *et al.*, 2011; Semenchuk *et al.*, 2013). However, climate change affects not just mean values of temperature and precipitation but also their variability (Trenberth *et al.*, 2007; Hansen *et al.*, 2012). Yet, with the exception of increased occurrence of extreme events such as mid-winter thaws (e.g., Augspurger, 2009; Bokhorst *et al.*, 2011), the potential for altered environmental variability to affect plant communities has

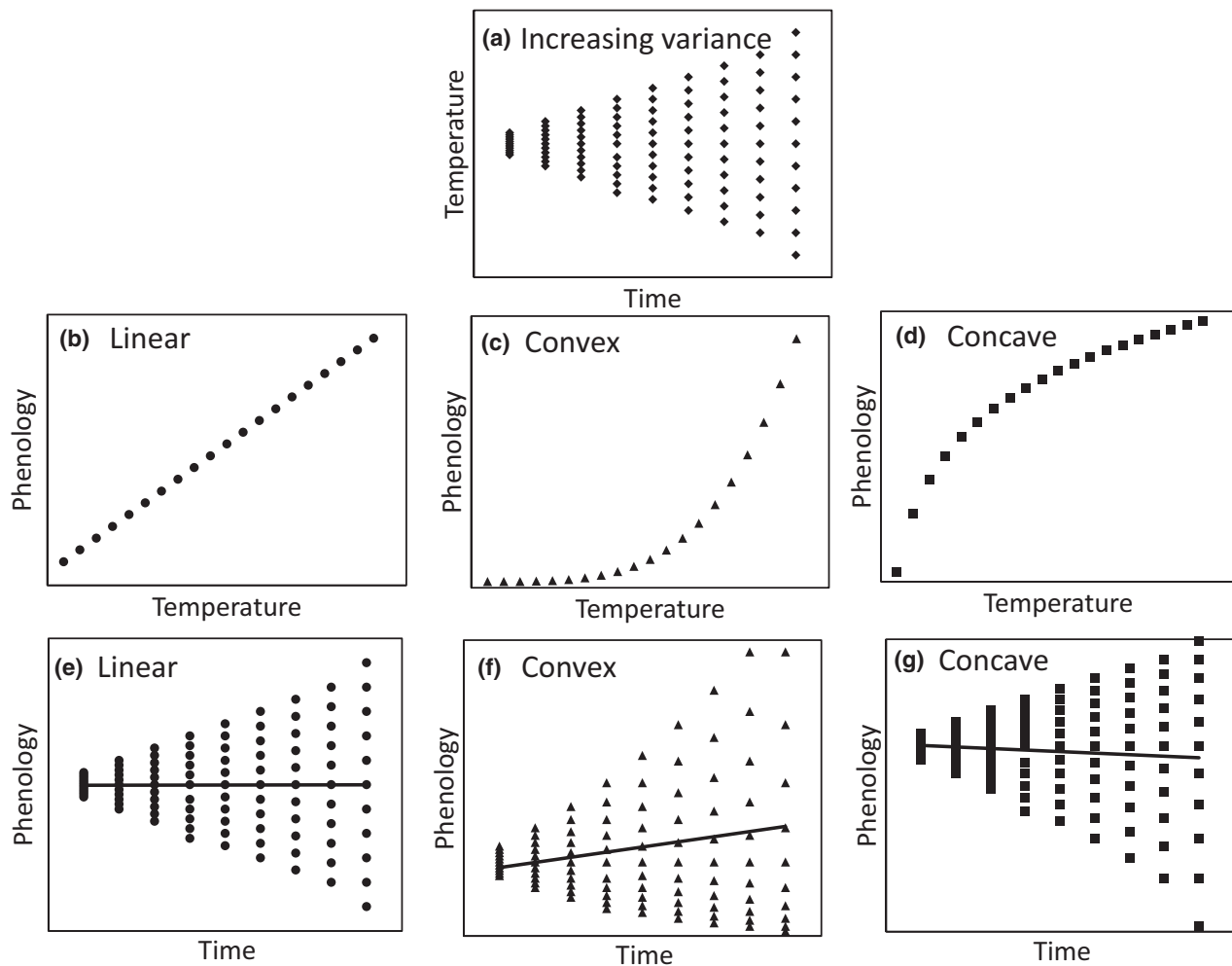
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received little attention, and predictions for changes in plant phenology in the future are usually based on shifts in mean temperature alone (e.g., Morin *et al.*, 2009; Clark & Thompson, 2010).

A change in environmental variance can affect species' responses by exposing individuals to more extreme conditions, but if the relationship between the response variable and the environment is not linear, the mean of the response variable can also be affected (Fig. 1; Ruel & Ayres, 1999). If the relationship between the response variable and the environment is convex (Fig. 1c), greater variance in environmental conditions will result in an increase in the mean of the response variable (e.g., because the effect of a favorable environment is greater than that of an unfavorable one) (Fig. 1f). Conversely, if the relationship is concave

(Fig. 1d), then greater variance in environmental conditions will result in a decrease in the mean of the response variable (Fig. 1g). Thus, we might expect that if phenology does not change linearly with temperature, then a change in interannual variability can exacerbate or dampen the effects of rising temperatures. Several recent studies have demonstrated that plant phenology can respond asymmetrically to increased temperature (Fu *et al.*, 2013; Wang *et al.*, 2014) and date of snow melt (Iler *et al.*, 2013); if such asymmetrical relationships are common, then increased environmental variability may alter the patterns in phenology over time.

Anthesis (the opening of a flower bud) is the final stage in a long developmental trajectory that can begin several years earlier (e.g., Foerste, 1891; Diggle, 1997;



**Fig. 1** Change in environmental variation can affect the mean of species' responses when the relationship between the response and the environment is not linear. This example shows an environment with a constant mean but increasing variation in temperature over time (a). When the relationship between phenology and temperature is constant (b), mean phenology does not change over time (e). When the relationship between phenology and temperature is convex (c), the mean of phenology increases over time (f); when it is concave (d) the mean decreases over time (g).

Geber *et al.*, 1997). Preformation of flower primordia one or more years prior to emergence is ubiquitous in high-elevation and high-latitude species and common in temperate forest trees, shrubs, and herbaceous perennials (Sørensen, 1941; Hodgson, 1966; Billings & Mooney, 1968). If environmental conditions affect flower developmental rates in the year(s) prior to flower emergence and anthesis ('lag effects'), then the changes in phenology over time will be more difficult to predict. For example, if warm temperatures in one year result in advanced phenology the following year, then several warm years in a row will produce a greater advance in phenology than predicted based on yearly phenology–temperature relationships alone.

Plants in arctic and subarctic regions worldwide have been subject to the greatest amount of climate change to date (e.g., Trenberth *et al.*, 2007; Høye *et al.*, 2013), but historical records for plant phenology in the arctic and subarctic regions of North America are scarce due to low population densities and extremely limited road access. The subarctic tundra and salt-marshes of the Cape Churchill Peninsula on Hudson Bay (58°44'N, 94°28'W) have historically been more accessible than other subarctic locations because of a railroad connection to the town of Churchill that was completed in 1929. As a result, the Cape Churchill Peninsula is well represented among plant specimens in herbaria throughout the United States and Canada. The Cape Churchill Peninsula has experienced rapid warming: Mean temperatures for June–August have increased by 0.25 °C per decade over the past 75 years (our study period) and even faster in more recent decades (e.g., 0.47 °C per decade over the past 50 years and 0.33 °C per decade over the past 25 years; see Climate Data section in Methods for sources of temperature data). Interannual variability in temperature has also increased (see Results Fig. 3; Table S1 in Supporting Information). We used the combination of a long-term observational phenology dataset and herbarium specimens to evaluate the impacts of changing mean and interannual variability in temperature on long-term trends in plant flowering phenology in tundra and saltmarsh communities of the Cape Churchill Peninsula, with a focus on phenological responses at the whole community level, although we also include some results for individual species.

We first asked whether flowering phenology of the plant community responded to temperature and whether it had advanced over time. Upon finding strong responses to temperature but no pattern of change over time, we examined three sets of potential mechanisms to explain this lack of a relationship: (i) opposing effects of other climate variables; (ii) a nonlinear relationship between temperature and plant

phenology coupled with increased temperature variance; and (iii) impacts of temperature in one year on flowering phenology in the following years. Last, we used simulations to evaluate whether the mechanisms for which we found support were sufficient to account for the lack of change in flowering phenology of the plant community over time.

## Materials and methods

We combined flowering phenology data from field observations and herbarium specimens for ericaceous tundra and salt-marsh communities on the Cape Churchill Peninsula (Hudson Bay, Manitoba, Canada). These two habitat types are interspersed, as elevational changes on the order of centimeters drive the large differences in species composition (C.P.H. Mulder, personal observation). Most data (≈90%) were obtained from near Churchill (58.77°N, 94.16°W) or from sites near the La Pérouse Bay field station (58.07°N, 94.05°W). Some herbarium data were obtained from other parts of Wapusk National Park (57.8–58.8°N and 92.4–94.2°W).

### Phenology data

Our dataset was built on a set of phenological observations made by the late R. L. Jefferies at the La Pérouse Bay field station between 1977 and 2008. We selected species for which the most years of data were available, and supplemented these data with our own observations in the same area, observations taken by scientists at the Churchill Northern Studies Center (58.73°N, 93.82°W), and data based on herbarium specimens. This resulted in a dataset containing 39 plant species for which flowering phenology data were available for a large number of years (range: 19–47 years) and that were representative of a wide range of functional groups (16 deciduous forbs, 3 winter-green forbs, 5 graminoids, 9 deciduous shrubs, and 6 evergreen shrubs; Table S2). The Cape Churchill Peninsula is home to a large population of polar bears (*Ursus maritimus*), which has always restricted field data collection in late summer (after July) but especially so in the past decades as bears have been moving onto land earlier in the season (Cherry *et al.*, 2013). Hence, late stages (fruit ripening and fruit loss) are less well represented than earlier stages.

Four sources of data that contributed to the dataset: (i) observations by R. L. Jefferies (1977–2008; 456 raw data points for 39 species); (ii) data obtained from herbarium specimens located at the University of Alaska Museum of the North, Burke Herbarium at the University of Washington, New York Botanical Gardens, University of Manitoba, Royal Ontario Museum, Canadian Museum of Nature, Churchill Northern Studies Center, the George Safford Torrey Herbarium at the University of Connecticut, and the herbarium of the University of North Dakota (1861–2011; 1057 data points for 39 species). Only specimens that had complete dates and at least one reproductive individual were used; (iii) data collected 2–3 times per year by the authors for all species (more frequently for some) on the same individuals (2012–2014, 415 data points

on 39 species); and 4) data collected by observers at La Pérouse Bay and the Churchill Northern Studies Center (2007–2013; 134 data points on 37 species). Because raw data were reduced to a single value per year for analyses of phenological changes over time, years with high sample sizes (e.g., 2012–2014) did not have an undue influence on the outcome of the analyses.

#### *Calculation of mean phenophase scores*

For herbarium specimens and observations made in the field, the number of buds (score = 1), open flowers (score = 2), 'petal-drops' (unfertilized flowers that had dropped their petals or were in very early stages of fruit production, score = 3), unripe fruit (score = 4), and ripe fruit (score = 5) was counted for all reproductive units on the sheet or plant. Phenophase mean was calculated as the mean of these scores (e.g., a plant with 3 buds and 3 open flowers received a score of 1.5). Datasets 1 and 4 consisted almost entirely of observations of first flowering dates. Based on our own experience and the synchronous nature of flower production in this environment, we assigned a score of 1.5 (e.g., an equal number of buds and open flowers) to first flowering observations. To maximize the sample size and the range of years, and because species may differ in which phenophase responds to environmental change (e.g., first flowering vs. peak flowering; CaraDonna *et al.*, 2014), we combined data from all sources. We performed several checks to ensure that the type of data used (observations of first flowering vs. average phenophase score based on live plants or herbarium specimens) did not bias our comparisons between years. First, we calculated our measure of annual advance or delay (phenophase anomalies – see next paragraph) separately by observation type (i.e., dataset 1 or 4 vs. dataset 2 or 3) for all species–year combinations for which we had both types of data available ( $N = 120$ ). There was no detectable difference between the two types of data ( $P = 0.24$ ). Second, we ran our analyses of plant responses to shifts in environmental variables separately for the two types of data; because the results mirror our analyses of early-phenophase plants (first flowering observations) or the entire dataset (scored plant data), they are not reported.

This raw dataset (using data from all sources) comprised 2062 data points for 39 species collected between 1939 and 2014; the mean of all mean phenophase scores was 2.27, indicating that approximately half of the observations were on plants in bud or peak flower, and half after petals had started to drop. Because different phenophases of plants can differ in their responses to changing temperature (e.g., first flowering vs. peak flowering dates; CaraDonna *et al.*, 2014), we repeated our analyses on two subsets of the data: plants with phenophase mean  $< 2$  ( $N = 1017$ ) and plants with phenophase mean  $\geq 2$  ( $N = 1045$ ).

#### *Calculation of phenophase anomalies and peak flowering dates*

Because our species varied more than twofold in developmental rates (e.g., development from expanding bud to unripe

fruit ranged from 41 to 90 days) and we wanted to compare across species, we expressed advance or delay of species in terms of mean phenophases (Fig. 2). However, because most phenology studies report the changes in date for a particular phenophase rather than the changes in phenophase for a particular date (and changes in date are easier to interpret), we reran analyses using advance or delay in date as the response variables. Because the results were almost identical to those for phenophases, they are summarized in the main text and reported in more detail in the Supporting Information.

To determine the expected phenophase on a given date for each species, we performed a second-order regression of the phenophases against calendar day; this allowed for the incorporation of differences in developmental curves for different species (Fig. 2, middle panel). Next, we calculated the mean value of the residuals in the  $x$ -axis from the regression for each species in each year (Fig. 2, b1 and b2) to generate annual 'phenophase anomalies' for individual species: A positive value indicated that phenophase was advanced in that year compared to that expected under the long-term average. Finally, we calculated means for each year across all species ('community phenophase anomalies'; Fig. 2 right-hand panel); only years with at least 10 species contributing data were included in the final dataset. To determine date anomalies, we performed the same procedure using residuals in the  $y$ -axis ( $\beta_1$  and  $\beta_2$  in Fig. 2 middle panel).

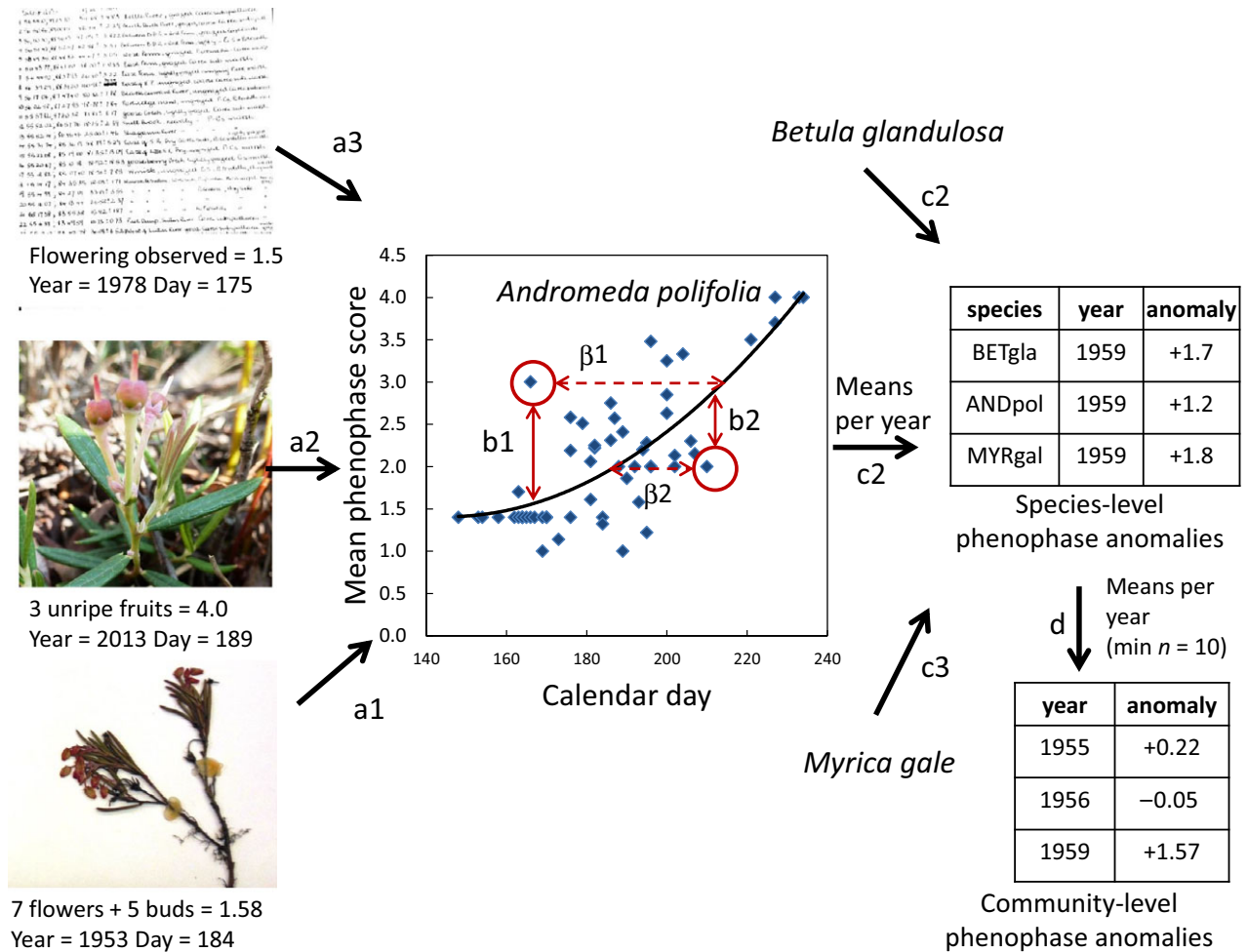
The complete dataset used for community-level analyses included 46 years between 1939 and 2014, with an average of 23.9 species per year contributing to the phenophase anomaly. The dataset using only early-phenophase plants (mean phenophase  $< 2$ ) comprised 28 years between 1950 and 2014 (average of 20.5 species per year), and the dataset using only late-phenophase plants (mean phenophase  $\geq 2$ ) included 28 years between 1939 and 2014 (average of 19.9 species per year).

To estimate mean peak flowering date for each species, we used the developmental curves described above to predict the date on which plants just started to break bud (mean phenophase = 1.1) and the date on which plants were in peak flower (mean phenophase = 2). We then took the means of these dates for the 39 species to produce a community-level bud break date (calendar day 160 = 9 June) and a community-level peak flowering date (calendar day 184 = 3 July).

#### *Climate data*

Weather data for 1939–2014 were obtained from three weather stations near Churchill, Manitoba: Churchill Marine (1933–1945; 58.78°N, –94.18°W), Churchill A (1946–2001; 58.74°N, –94.07°W), and Churchill UA (2002–2014; 58.73°N, –94.07°W). Daily means were calculated as the mean of minimum and maximum values. Cumulative growing degree days (GDD) were calculated by summing all positive mean temperatures using 0 °C as the base temperature because many (sub)arctic species commence activity at very low temperatures (Bliss, 1971; Lundell *et al.*, 2008). We used GDD<sub>160</sub> (GDD for calendar day 160, mean date of first bud break) and GDD<sub>184</sub> (GDD for calendar day 184, mean date of peak flowering) as the basis for temperature analyses.





**Fig. 2** Schematic of the process by which raw data were converted to community-level phenophase anomalies. Left side: Data from herbarium samples (a1), live plants (a2) or recorded field observations (a3) were assigned a mean phenophase score; calendar day and year were also recorded. Middle: A second-order polynomial regression was used to generate a line that estimates the mean phenophase over the course of the growth season for each species. For every data point the ‘phenophase anomaly’ was calculated as the residual from the regression in the x-axis. For example, b1 indicates a date on which *Andromeda polifolia* was more advanced than expected (positive phenophase anomaly) while b2 indicates a date on which it was delayed (negative phenophase anomaly). Right side: The means per year were calculated for phenophases anomalies (c1) and combined with those from other species (c2, c3). These are the species-level phenophase anomalies. Community-level phenophase anomalies were calculated by taking means per year of the species-level phenophase anomalies (d). Data were discarded if there were <10 species contributing data to that year. We calculated ‘date anomalies’ as the residuals in the y-axis. For example, b1 indicates a phenophase that occurred earlier than expected (negative date anomaly) while b2 indicates a phenophase that occurred later than expected (positive date anomaly). These values were processed in the same way as the phenophase anomalies: we calculated means per year for each species, and means per year across all species to generate community-level date anomalies.

Churchill Marine mean daily temperatures were slightly greater than those from Churchill A (mean annual difference = 0.262 °C, years of overlap: 1943–1951), while those from Churchill UA were slightly lower (mean difference = -0.077 °C, years of overlap: 2006–2008), but there were no detectable differences in temperature variance between stations ( $P > 0.5$  for all comparisons). We corrected for the differences in temperature means between weather stations by calculating the difference in GDD for a given date for Churchill A (the station with the most years of

data) and each weather station for the years of overlap, and then adding this value to the GDD values for the remaining years. Snow melt date (available for 1956–1999 and 2002–2014) was based on daily measurements of snow on the ground. The number of freeze–thaw cycles was calculated by counting the number of times temperatures went from above- to below-freezing following snow melt under two criteria:  $\geq 5$  °C difference between minimum and maximum temperatures (‘small cycles’) and  $\geq 10$  °C difference (‘large cycles’).

### Statistical analyses

Analyses were performed in SAS (v. 9.2) and in R (version 2.15.0). Initially, the relationships between climate variables (e.g., cumulative growing degree days at various times during the growing season, date of snow melt, the number of freeze–thaw cycles), phenophase anomalies (at the community or individual species level), and year were evaluated using simple linear regressions. When we failed to detect the changes in phenology over time despite strong responses to temperature (see Results), we performed additional tests and simulations (see Code S1 for R code for simulations).

*Temporal changes in mean and variance of GDD<sub>160</sub> and GDD<sub>184</sub>.* We created four competing models to test whether the mean and/or variance of GDD<sub>184</sub> changed across the study period (1939–2014): (i) constant mean and constant variance, (ii) temporal trend in the mean but constant variance, (iii) constant mean but temporal trend in variance, and (iv) temporal trend in both the mean and variance. Parameters describing the mean, variance, and any temporal trends in either were estimated using maximum likelihood assuming a normal distribution. We assessed the relative support for the four competing models using AICc (Akaike, 1973; Burnham & Anderson, 2002).

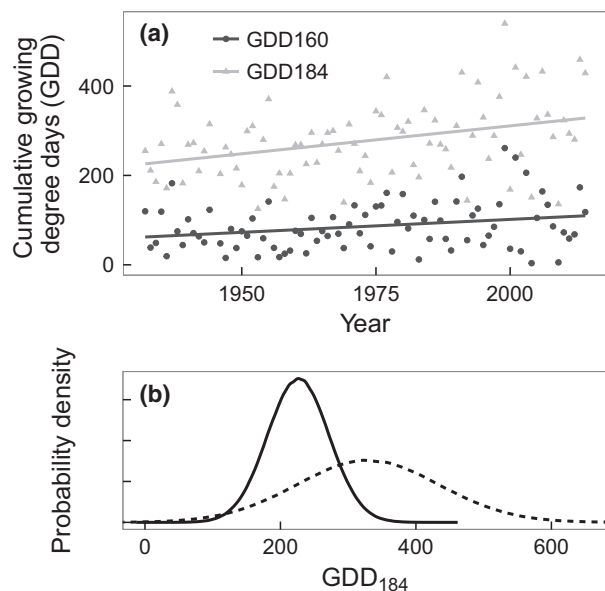
### Changes in community phenology with temperature in the current and previous 2 years

To further explore the relationship between community-level phenology and cumulative degree days, we developed a set of competing models using phenophase anomalies as the response that included plausible additive effects of temperature variables. We first evaluated linear, logarithmic, and quadratic relationships with GDD<sub>160</sub> or GDD<sub>184</sub>. We then took the best model for GDD<sub>160</sub> or GDD<sub>184</sub> and added linear, logarithmic, and quadratic relationships with GDD in the previous year (GDD<sub>160y-1</sub> or GDD<sub>184y-1</sub>) or 2 years previous (GDD<sub>160y-2</sub> or GDD<sub>184y-2</sub>) to account for the potential interannual responses to climate. Relative model support was again evaluated using AICc. These analyses were repeated for the early-phenophase and late-phenophase datasets.

If temperatures affect the development of flower primordia in the year(s) prior to anthesis, we might expect the impact to be the greatest for early-flowering species, which have the most advanced flower buds. We therefore split our dataset into those species flowering prior to the median peak flowering date (calendar day 186; 18 species) and those flowering on or after the mean peak flowering date (21 species; Table S2). Because there were many years with data available for either 8 or 9 species, we set the minimum number of species required for a year to contribute to the community-level datasets to 8 ( $N = 34$  years for early-flowering species,  $N = 40$  years for late-flowering species).

*Simulations to determine the relative contributions of temperature variance and lag effects.* We simulated community

phenology under a series of climate scenarios (i) to determine the relative contribution of temporal changes in the mean and/or variance of temperature and lag effects (the effects of temperature in the previous 2 years) to changes in community phenology and (ii) to determine whether these processes could account for our inability to detect an overall temporal trend in community phenology at our study location. These were performed only for GDD<sub>184</sub> as this variable explained more of the variation in temperature than GDD<sub>160</sub> (see Results). We first obtained the maximum-likelihood estimates of the annual rate of change in the mean and variance of GDD<sub>184</sub> (and, by extension, GDD<sub>184 y-1</sub> and GDD<sub>184 y-2</sub>) across the 75 years of study. We then constructed a suite of climate simulation scenarios (Table S3, Code S1). We repeatedly simulated climate across the 75-year study, either by drawing deviations from the empirically observed distributions and allowing the mean and/or variance of these distributions to change at the empirically observed rate, or by holding them fixed at their initial values. We then calculated the expected community phenology in each year of simulation based on the empirically developed relationship between phenophase and temperature (see *Changes in community phenology with*



**Fig. 3** Change in temperature between 1939 and 2014. (a) Cumulative growing degree days (sum of temperatures  $> 0$  °C) on calendar day 160 (GDD<sub>160</sub>, mean date of first bud break across the 39 plant species), and calendar day 184 (GDD<sub>184</sub>, July 3, the mean date of peak flowering). There was an increase in GDD over time for both dates (GDD<sub>160</sub>:  $R^2 = 0.10$ ,  $F_{1,72} = 7.75$ ,  $P = 0.007$ ; GDD<sub>184</sub>:  $R^2 = 0.15$ ,  $F_{1,72} = 13.01$ ,  $P = 0.0005$ ). (b) The mean and variance of temperature have increased over time, resulting in very different climate distributions at the beginning (solid line) and end (dashed line) of the study. The mean of GDD<sub>184</sub> increased at a rate of 1.35 °C per year (from 228 to 329) while the standard deviation increased by 0.80 °C per year (from 44.7 to 104.9), based on maximum likelihood estimates.

**Table 1** Linear relationships between phenophase anomalies and cumulative growing degree days on calendar day 160 (GDD<sub>160</sub>) and calendar day 184 (GDD<sub>184</sub>). Early-phenophase anomalies are for plants with mean phenophase < 2, and late-phenophase anomalies for plants with phenophase ≥ 2

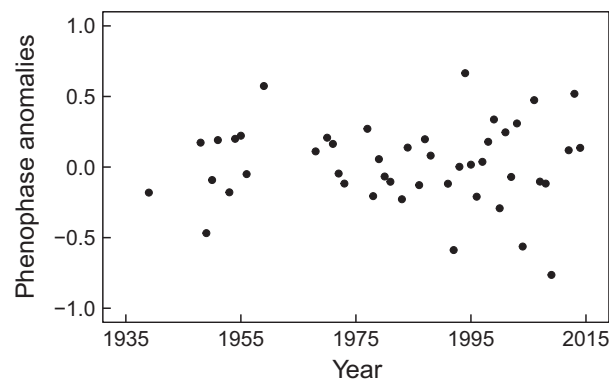
Phenophase anomaly dataset	Explanatory variable	N (# years)	Slope	R <sup>2</sup>	t	P
All	GDD <sub>160</sub>	46	0.003	0.30	4.32	<0.0001
	GDD <sub>184</sub>	46	0.002	0.46	6.16	<0.0001
Early phenophases	GDD <sub>160</sub>	28	0.003	0.44	4.54	<0.0001
	GDD <sub>184</sub>	28	0.002	0.45	4.64	<0.0001
Late phenophases	GDD <sub>160</sub>	28	0.004	0.35	3.76	0.0009
	GDD <sub>184</sub>	28	0.002	0.48	4.94	<0.0001

temperature section above). The overall 'effect size' of each climate variable on phenology was calculated as the slope of the relationship for mean community phenology across the 75-year simulation, averaged across 1000 repeated runs. Finally, to determine the degree to which temporal changes in each climate variable affected our ability to detect a temporal trend in phenology, we calculated the proportion of repeated simulations for which the trend was significantly different from zero ( $P < 0.05$ ).

## Results

Both mean temperature and interannual variation in temperature increased between 1939 and 2014 (Fig. 3, Table S1). Cumulative growing degree days by July 3, the mean flowering date (GDD<sub>184</sub>) increased by 44%, while the standard deviation for temperature doubled over this time period (Fig. 3, Table S1). Plant phenology was advanced in warmer years for the dataset as a whole as well as for the early and late phenophases, and for all three datasets, GDD<sub>184</sub> was a better predictor than GDD<sub>160</sub> (Table 1). When we evaluated individual species' responses, positive phenological responses to greater temperatures were common, with 19 of 39 species showing a positive significant relationship ( $P < 0.05$ ) and an additional 4 showing a marginally significant relationship ( $0.05 < P < 0.1$ ) to the cumulative degree days (GDD) by their species-specific mean peak flowering date (Table S2). Only one species showed a significant negative relationship (Table S2). When we evaluated the community-level date anomalies rather than phenophase anomalies, the results were very similar ( $R^2 = 0.51$ ,  $t_{(46)} = -6.71$ ,  $P < 0.0001$ ; the direction is opposite to that for phenophase anomalies as a negative date anomaly indicates that phenology is advanced). The slope for this model is  $-0.054$  days per degree °C, resulting in a maximum predicted difference of approximately 20 days for the range of temperatures experienced over this period, while the data show a maximum difference of approximately 30 days (Fig. S1).

Despite the increase in temperature by this date over the 75-year time period (Fig. 3), there was no



**Fig. 4** Annual phenophase anomalies between 1939 and 2014. Values are means for all species for which data were available in that year (minimum of 10 species). Positive values indicate advanced flowering phenology in that year and negative values indicate delayed flowering phenology. There was no relationship between phenophase anomalies and year ( $t_{(44)} = 0.00$ ,  $P = 0.999$ ,  $R^2 < 0.0001$ ).

relationship between community-level phenophase anomalies and year for the entire dataset (Fig. 4;  $t_{(44)} = 0.00$ ,  $P = 0.999$ ,  $R^2 < 0.0001$ ) or for the early-phenophase or late-phenophase datasets (early:  $t_{(26)} = 0.16$ ,  $P = 0.51$ ,  $R^2 = 0.017$ ; late:  $t_{(26)} = 0.84$ ,  $P = 0.41$ ,  $R^2 = 0.026$ ). Among individual species, only one showed a significant advance over time ( $P < 0.05$ ) and the remaining 38 species showed no pattern (Table S2). Similarly, when we used date anomalies rather than phenophase anomalies, there was no change over time ( $t_{(44)} = -0.30$ ,  $P = 0.76$ ,  $R^2 = 0.002$ ). This begs the question: If temperatures are increasing and flower phenology advances under higher temperatures, why do we see no advance over time?

We first examined whether the lack of a change in flower phenology over time could result from counteracting effects of other environmental variables. As expected, in warm years, the snow melted earlier (correlation with GDD<sub>160</sub>:  $r = -0.74$ ,  $P < 0.0001$ ,  $N = 55$ ; GDD<sub>184</sub>:  $r = -0.63$ ,  $P < 0.0001$ ) and there were more small freeze-thaw cycles in years with high GDD<sub>160</sub>

( $r = 0.29$ ,  $P = 0.042$ ,  $N = 48$ ), but not  $GDD_{184}$  ( $r = 0.15$ ,  $P = 0.31$ ). Consistent with those results, plants were advanced in years with earlier snow melt (phenophase anomalies vs. snow melt date:  $t_{(33)} = -3.84$ ,  $P = 0.0005$ ) and years with more small freeze–thaw cycles ( $t_{(27)} = 3.33$ ,  $P = 0.0025$ ). However, whereas temperature explained the additional variation in phenology beyond that explained by snow melt date (hierarchical ANOVA with  $GDD_{184}$  entered after snow melt date:  $F_{(32)} = 8.14$ ,  $P = 0.008$ ), snow melt date did not explain any variation beyond that explained by temperature (hierarchical ANOVA with snow melt date entered after  $GDD_{184}$ :  $F_{(32)} = 1.54$ ,  $P = 0.22$ ). Furthermore, neither snow melt date nor the number of freeze–thaw cycles showed a change over time (snow melt date vs. year:  $t_{53} = -0.30$ ,  $P = 0.77$ ; # freeze–thaw cycles vs. year:  $t_{46} = -0.72$ ,  $P = 0.48$ ), and the inclusion of snow melt date and the number of freeze–thaw cycles in the regression model did not result in a significant relationship between phenophase anomalies and year ( $t_{24} = 1.44$ ,  $P = 0.24$ ). The number of large freeze–thaw cycles showed no relationship with phenology, temperature, or year ( $P > 0.3$  for all). Both the early-phenophase and late-phenophase datasets similarly showed advanced phenology in years with early snow melt (early:  $t_{(18)} = -2.50$ ,  $P = 0.024$ ; late:  $t_{(20)} = -2.56$ ,

$P = 0.020$ ), but no relationship or a weak relationship with the number of freeze–thaw cycles (early:  $t_{(14)} = 1.40$ ,  $P > 0.1$ ; late:  $t_{(20)} = 1.91$ ,  $P = 0.074$ ). And again, in neither case did the inclusion of snow melt date and the number of freeze–thaw cycles in the model alter the relationship between phenophase anomalies and year ( $P > 0.5$  for both). We conclude that neither changes in date of snow melt nor changes in freeze–thaw cycles can account for the observed lack of a response in phenology over time.

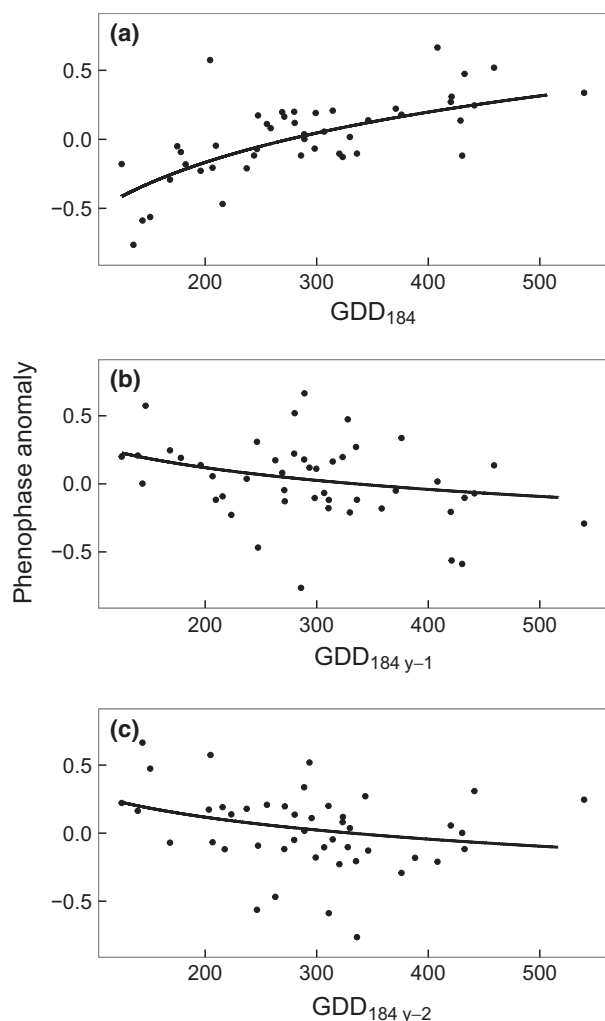
#### *Nonlinear responses to temperature*

We compared the ability of linear, log-linear, and quadratic equations to explain the relationship between phenophase anomalies and GDD (Table 2). For the whole dataset, the best model was a log-linear relationship with  $GDD_{184}$  (Table 2; Fig. 5a). Analyses using only early-stage or only late-stage data similarly also showed the most support for log-linear relationships, although for late-stage data the linear model was indistinguishable from the log-linear model (Table 2). Results were similar when date anomalies instead of phenophase anomalies are used (Table S4, Fig. S1). Because models using  $GDD_{184}$  performed better than those using  $GDD_{160}$  (all data and

**Table 2** Comparing linear, log-linear (base e), and quadratic relationships between phenophase anomalies and growing degree days. Data are for 1939–2014. Temperature is expressed as cumulative growing degree days on calendar day 160 ( $GDD_{160}$ ) or 184 ( $GDD_{184}$ ). Quadratic (second-order) effects are indicated by ‘quad’.  $N = 46$  for the whole dataset, and  $N = 28$  for the early-phase and late-phase datasets. ‘logLik’ refers to ‘log likelihood’, and ‘# par’ refers to the number of parameters in the model

Dataset	GDD used	Relationship	logLik	AICc	$\Delta\text{LogLik}$	$\Delta\text{AIC}_c$	# par	Weight
All data	$GDD_{184}$	Log	7.8	−9.1	15.8	0	3	0.687
	$GDD_{184}$	Quad	7.6	−6.1	15.6	2.9	4	0.158
	$GDD_{184}$	Linear	6.2	−5.9	14.3	3.2	3	0.139
	$GDD_{160}$	Log	4.0	−1.4	12.0	7.6	3	0.015
	$GDD_{160}$	Quad	2.1	4.8	10.1	13.9	4	<0.001
	$GDD_{160}$	Linear	0.2	6.2	8.2	15.3	3	<0.001
	None	–	−8.0	20.3	0	29.4	2	<0.001
Early phenophase	$GDD_{184}$	Log	4.5	−2.1	9.1	0	3	0.359
	$GDD_{160}$	Log	4.0	−0.9	8.6	1.2	3	0.201
	$GDD_{184}$	Linear	3.7	−0.3	8.3	1.8	3	0.149
	$GDD_{160}$	Linear	3.5	0	8.1	2.1	3	0.127
	$GDD_{184}$	Quad	4.6	0.5	9.2	2.6	4	0.100
	$GDD_{160}$	Quad	4.2	1.4	8.8	3.4	4	0.064
	None	–	−4.6	13.7	0	15.8	2	<0.001
Late phenophase	$GDD_{184}$	Log	1.4	4.3	9.6	0	3	0.4009
	$GDD_{184}$	Linear	1.2	4.6	9.4	0.3	3	0.3444
	$GDD_{160}$	Log	0.3	6.4	8.6	2.1	3	0.1425
	$GDD_{184}$	Quad	1.2	7.3	9.5	3.0	4	0.0896
	$GDD_{160}$	Linear	−2.0	10.9	6.3	6.7	3	0.0143
	$GDD_{160}$	Quad	−1.2	12.1	7.1	7.8	4	0.0082
	None	–	−8.2	21	0	17.1	2	<0.001





**Fig. 5** Phenophase anomalies plotted against cumulative growing degree days on calendar day 184 (3 July) in the current and previous two years. Positive values indicate advances; negative values, delays. Relationships in each panel are depicted when the other two variables are fixed at their mean value. Linear-log models were used for all three relationships. (a) Positive nonlinear relationship between phenophase anomaly and temperature in year of flowering ( $GDD_{184}$ ;  $t_{(42)} = 6.65$ ,  $P < 0.0001$ ). (b) Negative nonlinear relationship with temperature in the previous year ( $GDD_{184y-1}$ ;  $t_{(42)} = -2.77$ ,  $P = 0.008$ ). (c) Negative nonlinear relationship with temperature two years earlier ( $GDD_{184y-2}$ ;  $t_{(42)} = -2.67$ ,  $P = 0.011$ ).

late-phenophase data) or equally well (early-phenophase data), we used  $GDD_{184}$  for the remaining analyses.

Phenophase anomalies changed more rapidly with increasing temperature at the colder end of the spectrum than at the warmer end of the spectrum (Fig. 5a). We hypothesized that responses were more similar across all species in a very cold year (when

all species are prevented from flowering because of frozen ground and/or snow cover) than in a warm year (when species may show highly variable responses to temperature). There was no support for this hypothesis: The variance in species' responses was not related to  $GDD_{184}$  ( $t_{(58)} = -0.23$ ,  $P = 0.82$ ,  $R^2 < 0.001$ ).

#### Impacts of temperature in previous years (lag effects)

We next evaluated whether temperature in previous years could explain the variation in the following year. We explored 20 models that included all possible combinations of (i) log-linear or no relationships with  $GDD_{184}$ ; (ii) linear, log-linear, quadratic, or no relationship with  $GDD_{184}$  in the previous year (denoted  $GDD_{184y-1}$ ); and (iii) linear, log-linear, quadratic, or no relationship with  $GDD_{184}$  2 years previously (denoted  $GDD_{184y-2}$ ). The top four models (those with  $\delta AICc < 2$ ) all included  $GDD_{184}$  in the year in which data were obtained plus temperature in each of the previous 2 years (Table 3). However, unlike for  $GDD_{184}$ , there was no clear difference in model fit for linear vs. log-linear relationships with  $GDD_{184y-1}$  or  $GDD_{184y-2}$  (Table 3). Results were very similar when we used date anomalies instead of phenophase anomalies (Table S4, Fig. S1).

The effect of temperature in each of the two previous years on phenophase anomalies was negative, indicating that warm temperatures result in delayed phenology in the following year(s) (Fig. 5b, c). Slopes for the two regressions were similar ( $GDD_{184y-1}$ :  $-0.230$ ;  $GDD_{184y-2}$ :  $-0.232$ ) and approximately half the slope for  $GDD_{184}$  (0.528), but in the opposite direction. These negative relationships were not the result of confounding between years, as temperature was not correlated between years ( $r \leq 0.1$  and  $P \geq 0.35$  for all pairwise comparisons of  $GDD_{184}$ ,  $GDD_{184y-1}$ , and  $GDD_{184y-2}$ ). When we examined responses for individual species, we found significant negative relationships with temperatures in the previous year ( $GDD_{184y-1}$ ) for 4 species and marginally significant negative relationships for an additional 4 species (Table S2), more than the 2 negative (or 4 total) relationships expected by chance under  $\alpha = 0.1$ . For  $GDD_{184y-2}$ , we found 3 significantly negative and 3 marginally negative relationships (Table S2). To evaluate whether these negative relationships were driven by temperature prior to fruit development or by late-season conditions, we reran the models using cumulative degree days through the end of the growth season (30 September,  $GDD_{273}$ ) for each of the previous 2 years. The ability of this model to explain phenophase was almost identical to using that temperature by July 3 ( $R^2 = 0.62$  for both models),

**Table 3** Comparisons of model fit for the relationship between phenophase anomalies and temperature. Data are for 1939–2014. Temperature is expressed as cumulative growing degree days on calendar day 184 (GDD<sub>184</sub>). Lagged effects of GDD<sub>184</sub> on phenophase anomalies are indicated by GDD<sub>184y-1</sub> (one year lag) and GDD<sub>184y-2</sub> (2 year lag). Quadratic (second-order) relationships are indicated by 'quad'

Effects in model (‘-’ denotes no effect)								
GDD184	GDD184y-1	GDD184y-2	logLik	AICc	dLogLik	dAICc	df	Weight
Log	Log	Log	14.3	-17.2	22.4	0	5	0.3404
Log	Log	Linear	13.9	-16.3	21.9	0.9	5	0.2177
Log	Linear	Log	13.8	-16.2	21.9	1	5	0.2033
Log	Linear	Linear	13.4	-15.3	21.4	1.9	5	0.1322
Log	Log	-	10.8	-12.5	18.8	4.7	4	0.0333
Log	Linear	-	10.5	-12.1	18.5	5.1	4	0.0263
Log	-	Log	10.5	-12	18.5	5.2	4	0.0251
Log	-	Linear	10	-11.1	18	6.1	4	0.016
Log	-	-	7.8	-9.1	15.8	8.1	3	0.0059
-	Log	Log	-2.1	13.3	5.9	30.4	4	<0.001
-	Linear	Log	-2.2	13.3	5.8	30.5	4	<0.001
-	-	Quadratic	-3.1	15.2	4.9	32.4	4	<0.001
-	Linear	Linear	-3.1	15.3	4.9	32.5	4	<0.001
-	Log	Linear	-3.2	15.3	4.9	32.5	4	<0.001
-	Linear	-	-5.2	16.9	2.9	34.1	3	<0.001
-	Log	-	-5.3	17.2	2.7	34.4	3	<0.001
-	-	Log	-5.6	17.7	2.5	34.9	3	<0.001
-	Quadratic	-	-5.1	19.2	2.9	36.4	4	<0.001
-	-	Linear	-6.5	19.6	1.5	36.8	3	<0.001
-	-	-	-8	20.3	0	37.5	2	<0.001

indicating that temperatures prior to fruit development drove these negative relationships.

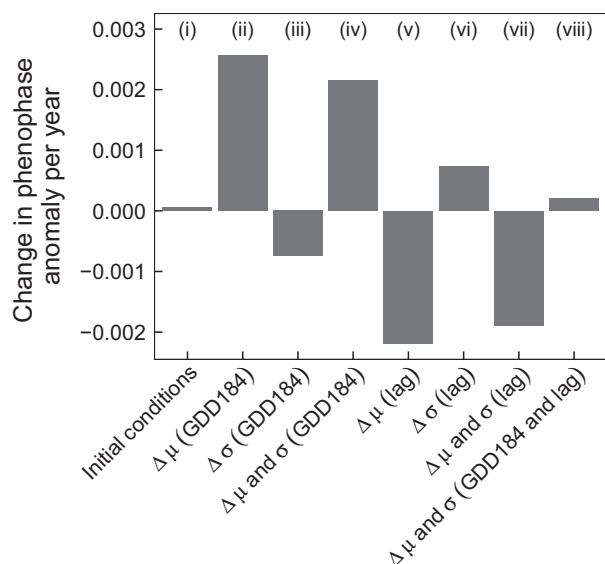
When analyses were run for the early-phenophase and late-phenophase datasets, relationships with temperature in the previous year were negative in both cases, but not statistically significant (early stage:  $\ln(\text{GDD}_{184y-1})$ : slope = -0.14,  $t_{(24)} = -1.11$ ,  $P = 0.28$ , late stage:  $\ln(\text{GDD}_{184y-1})$ : slope = -0.21,  $t_{(24)} = -1.55$ ,  $P = 0.13$ ). Neither early- nor late-phenophase data showed a relationship with temperature 2 years previously ( $P > 0.45$  for both).

We next examined whether early-flowering species differed from late-flowering species in relationships with temperature. Early-flowering species showed stronger relationships with temperature in the year of flowering than late-flowering species (early flowering:  $\ln(\text{GDD}_{184})$  slope = 0.64,  $t_{(34)} = 6.79$ ,  $P < 0.0001$ ; late flowering:  $\ln(\text{GDD}_{184})$  slope = 0.44,  $t = 4.68$ ,  $P < 0.0001$ ). Furthermore, early-flowering species showed a strong negative relationship with temperature in the previous year ( $\ln(\text{GDD}_{184y-1})$  slope = -0.34,  $t_{(34)} = -3.35$ ,  $P = 0.002$ ), but no relationship with temperature 2 years earlier ( $P = 0.59$ ). In sharp contrast, late-flowering species showed a weak negative relationship with temperature in the previous year ( $\ln$

( $\text{GDD}_{184y-1}$ ) slope = -0.18  $t_{(36)} = -1.76$ ,  $P = 0.087$ ), but a very strong negative relationship with temperature 2 years earlier ( $\ln(\text{GDD}_{184y-1})$  slope = -0.44,  $t_{(36)} = -3.73$ ,  $P < 0.001$ ).

#### *Can increased variance and lag effects explain the lack of a trend in phenology over time?*

To evaluate whether the increase in temperature variability coupled with the nonlinear responses of phenology to temperature and combined with the negative lag effects were sufficient to explain why we saw no changes in phenology over time, we performed a suite of climate/phenology simulations in which we manipulated the mean and variance of temperature in the current and previous years in a factorial design (Table S3). Allowing only mean temperature to change resulted in an advance in phenology (positive slope over time; Fig. 6ii), while both an increased standard deviation and negative lag effects resulted in delays (Fig. 6iii, v). The combination of increased standard deviation and lag effects reduced the positive effects of increased mean temperature by 94% (Fig. 6viii). Under that last scenario, the proportion of simulation runs (of 1000) with a slope significantly different from zero (at



**Fig. 6** Results of simulation experiments incorporating shifts in the mean and standard deviation (SD = square root of the variance) of cumulative growing degree temperature by July 3 (GDD<sub>184</sub>). Slopes of the regression for phenology across 75 years under various climate scenarios: (i) Base model (no change in mean and no lag effects). (ii) Change in temperature mean only for the current year. (iii) Change in temperature SD only. (iv) Change in temperature mean and SD. (v) Change in temperature in the previous two years (lag effects). (vi) Change in SD of temperature in the previous two years. (vii) Change in mean and SD of temperature in the previous two years. (viii) Change in mean and SD of temperature in the current year and the previous two years.

$\alpha = 0.05$ ) was 0.043, demonstrating that together these effects are of a magnitude large enough to account for our inability to detect phenological change through time at our study site.

## Discussion

In our system, plants showed strong positive responses in flowering phenology to temperature (expressed as cumulative growing degree days by calendar day 160 or calendar day 184), and temperature has increased significantly over the 75-year study period. Consistent with earlier studies (e.g., Fitter & Fitter, 2002; Wolkovich *et al.*, 2013), these relationships were stronger for early-flowering species than for late-flowering species, but unlike CaraDonna *et al.* (2014) we did not find the differences between responses of plants at early vs. late phenophases. Yet despite the strong responses to temperature, there was no evidence for changes in flowering phenology over this time period at either the whole community or species level. Furthermore, we found no support

for the hypothesis that changes in timing of snow melt or in the number of freeze–thaw cycles could explain the lack of a change over time. We therefore focused on two other explanations: (i) nonlinear relationships between phenology and temperature combined with increases in temperature variability and (ii) lag effects of temperature in previous years. We found support for both explanations and demonstrated that together they are large enough to account for our inability to detect a shift in phenology over time. However, lag effects had a much larger impact than did the increase in temperature variance in reducing the shift in phenology (Fig. 6iii vs. v).

### *Nonlinear responses to plants to temperature and consequences under increased temperature variability*

Phenology showed a nonlinear response to temperature, with stronger responses at the cold end of the spectrum than at the warm end of the spectrum. Our results are consistent with other studies that have found a reduction in sensitivity to warming at higher temperatures in alpine species (Wang *et al.*, 2014) and some temperate tree species (Fu *et al.*, 2013), and a limit to the ability to respond to earlier snow melt in alpine plants (Iler *et al.*, 2013). Because temperature can have both direct effects on flower and fruit development and indirect effects (e.g., by affecting the availability of resources such as water and nutrients, or the activity of pollinators), nonlinear responses are likely to vary between systems. Our study reinforces the need to evaluate plant phenological responses for nonlinearity, particularly given the potential consequences under the increased environmental variability.

In our simulations, a change in the mean and the standard deviation of temperature interacted to reduce the response of plant flowering phenology over time substantially (by about 24% by itself, and by 13% when taking into account the interaction with a shifting mean; Fig. 6iii and iv vs. ii). Our study is not the first ecological study to demonstrate that altered environmental variability may affect the mean of a response: In a number of demographic studies, concave relationships between growth rate and the environment resulted in reduced population growth under the increased environmental variability, although the effects were weak, affecting long-term growth rates by <1% (Lawson *et al.*, 2015). Given that environmental variability is already changing and is predicted to continue changing (Trenberth *et al.*, 2007; Hansen *et al.*, 2012; Huntingford *et al.*, 2013), we suggest that increased (or decreased) environmental variability may substantially affect the trends in phenology of a range of organisms in any location where climate is rapidly changing.

*Negative effects of temperature in previous years on phenology*

Surprisingly, there was a strong negative relationship between phenology in a given year and temperature 1 or 2 years earlier for the whole dataset. This was driven by different relationships for early- vs. late-flowering plants: Early-flowering plants were delayed by temperatures one year (but not 2 years) previously, while for late-flowering plants the reverse was true. For late-flowering plants, the effect of the lag effect was of equal magnitude (but in the opposite direction) as of temperature in the year of flowering, suggesting that for these species a warm year resulted in an advance in flowering in that year but an equivalent delay 2 years later (no impact when evaluated over a 3-year time span). For early-flowering plants, the magnitude of the lag effect was only about half that of effect of temperature in the year of flowering.

These results suggest that temperature in years prior to anthesis affects the flower development. Leaf and floral bud primordia of the majority of high-latitude and high-altitude plants are initiated in the previous year or earlier (Sørensen, 1941; Hodgson, 1966; Bliss, 1971; Diggle, 1997; Meloche & Diggle, 2001). There are several mechanisms through which warm temperatures could result in delayed (or apparently delayed) flowering the following year. First, warm temperatures in late summer may induce early bud set and dormancy, as has been shown for *Populus* and *Betula* in experimental studies (Tanino *et al.*, 2010; Hänninen & Tanino, 2011). This would result in less developed flower primordia that take longer to mature the following spring. Second, warm temperatures may induce some flower primordia to mature in late fall, either by accelerating development or by delaying bud set (premature maturation). Although this would actually represent an advance in flowering phenology, it would result in an apparent delay because the remaining buds would be less advanced and mature later in the following year. Our understanding of the development of preformed buds is currently insufficient to determine which of these hypotheses (if any) is most likely responsible for the negative relationships between temperature and phenology in later years observed in this study.

An alternative hypothesis is that warm temperatures in fall increase chilling requirements for bud burst, as has been found for birch and alder saplings in temperature systems (Heide, 2003). However, this is not a likely explanation for the negative relationship in our system. First, the winter chilling capacity of the subarctic probably greatly exceeds chilling requirements (Murray *et al.*, 1989; Heide, 1993). Second, models that included temperature accumulation during fall (through September)

were not better at predicting phenology in the following year(s) than ones that included temperature through the middle of summer, indicating that temperature at time of flowering captured the impact of a warm summer on phenology in the following years.

Our hypothesis for this Cape Churchill Peninsula dataset is based on correlations only, but support for the notion of premature maturation of flowers exists from other locations. Ge *et al.* (2011) documented an increased frequency of second blooms associated with warming temperatures for seven species in China, and the expansion of this phenomenon into northern China in warm years. In late August and early September of 2015, following a very warm spring (mean temperatures for April and May were 2.4 °C and 3.3 °C, respectively, above long-term averages), we observed the production of a new cohort of flowers and leaves in a subset of individuals of several boreal plant species near Fairbanks, Alaska (C. Mulder, personal observation). Several species also included in this study were affected: *Vaccinium vitis-idaea* produced a second cohort of flowers and *V. vitis-idaea*, *Rhododendron groenlandicum* and *Shepherdia canadensis* produced a second cohort of leaves.

The impact of temperature on flower development in years prior to (anticipated) anthesis deserves further attention. First, the maturation of flower buds toward the end of the growing season may be maladaptive, as it is unlikely that there will be sufficient time for fruit maturation. Premature bud maturation therefore may have negative consequences under a rapidly changing climate. Second, our simulations suggested that the effects of negative relationships between temperature and phenology in the following years on phenological trends over time were large: By themselves, they reduced the slope of the expected relationship between year and phenology by approx. 89% for the entire dataset (Fig. 5v vs. ii), although the negative concave relationship combined with the increase in variance mitigated this effect somewhat (Fig. 5vi). While these effects might be greatest at high altitudes or latitudes because of the almost ubiquitous preformation of inflorescence buds in previous years (Billings & Mooney, 1968; Bliss, 1971), many temperate perennials species also preform leaf or inflorescence buds (e.g., Geber *et al.*, 1997; Diggle, 2002; Magnin *et al.*, 2012). We hope these results will motivate other researchers, particularly those who work in high-altitude and high-latitude systems, to examine their datasets for lag effects. Our results also suggest the need for experiments in which temperature is manipulated and bud initiation and maturation are tracked for several years in order to improve our understanding of how environment affects the development of flower (and leaf) primordia.



### Relevance of results to patterns found in other systems

Impacts of a change in variance and negative lag effects may help explain the lack of directional change over time in other communities in which temperatures are rapidly rising and plants show strong responses to interannual variation, as was found in two recent studies (Hart *et al.*, 2014; Davis *et al.*, 2015). Our results also suggest that experiments in which communities under consistently elevated temperatures are compared to those under ambient temperatures are unlikely to adequately mimic the impacts of climate change on phenology; this may help account for differences between results from such experiments and observational datasets (Wolkovich *et al.*, 2012; Marchin *et al.*, 2015). Our findings suggest that the incorporation of interannual variability in temperature (or other environmental variables) and tests for lag effects may improve predictive models for phenology under climate change and unmask responses to temperature in species in which they currently appear to be lacking.

### Acknowledgements

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### Supporting Information

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

**Table S1.** Support for a shift in mean and standard deviation of temperature between 1939 and 2014.

**Table S2.** Results for individual species.

**Table S3.** Descriptions of simulation scenarios.

**Table S4.** Comparisons of model fit for the relationship between date anomalies and temperature.

**Figure S1.** Date anomalies plotted against cumulative growing degree days on calendar day 184 (GDD<sub>184</sub>, 3 July) in the current and previous two years.