

Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades

ANNE D. BJORKMAN^{1,2}, SARAH C. ELMENDORF^{3,4}, ALISON L. BEAMISH^{1,5}, MARK VELLEND⁶ and GREGORY H. R. HENRY¹

¹Department of Geography and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada,

²German Centre for Integrative Biodiversity Research and University of Leipzig, Leipzig 04103, Germany, ³National Ecological

Observatory Network, Boulder, CO 80301, USA, ⁴Department of Ecology and Evolutionary Biology, University of Colorado,

Boulder, CO 80309, USA, ⁵Periglacial Research Unit, Alfred Wegener Institute, Potsdam 14473, Germany, ⁶Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K2R1, Canada

Abstract

Recent changes in climate have led to significant shifts in phenology, with many studies demonstrating advanced phenology in response to warming temperatures. The rate of temperature change is especially high in the Arctic, but this is also where we have relatively little data on phenological changes and the processes driving these changes. In order to understand how Arctic plant species are likely to respond to future changes in climate, we monitored flowering phenology in response to both experimental and ambient warming for four widespread species in two habitat types over 21 years. We additionally used long-term environmental records to disentangle the effects of temperature increase and changes in snowmelt date on phenological patterns. While flowering occurred earlier in response to experimental warming, plants in unmanipulated plots showed no change or a delay in flowering over the 21-year period, despite more than 1 °C of ambient warming during that time. This counterintuitive result was likely due to significantly delayed snowmelt over the study period (0.05–0.2 days/yr) due to increased winter snowfall. The timing of snowmelt was a strong driver of flowering phenology for all species – especially for early-flowering species – while spring temperature was significantly related to flowering time only for later-flowering species. Despite significantly delayed flowering phenology, the timing of seed maturation showed no significant change over time, suggesting that warmer temperatures may promote more rapid seed development. The results of this study highlight the importance of understanding the specific environmental cues that drive species' phenological responses as well as the complex interactions between temperature and precipitation when forecasting phenology over the coming decades. As demonstrated here, the effects of altered snowmelt patterns can counter the effects of warmer temperatures, even to the point of generating phenological responses opposite to those predicted by warming alone.

Keywords: Arctic tundra, Bayesian hierarchical modeling, climate change, flowering time, interval censoring, plant phenology, seed maturation

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Introduction

Synchronization between the timing of seasonal changes and phenological events is of fundamental importance to an individual's fitness (Fox, 1989; Stenseth & Mysterud, 2002; Berteaux *et al.*, 2004). As phenology is often driven by temperature (Rathcke & Lacey, 1985), recent climate warming has led to considerable shifts in phenology across ecosystems and taxa (Parmesan & Yohe, 2003; Root *et al.*, 2003; Menzel *et al.*, 2006; Parmesan, 2006; Høye *et al.*, 2007; Oberbauer *et al.*, 2013; Ovaskainen *et al.*, 2013). In Europe, 78% of 561 plant and animal species studied demonstrated phenological advances over the last three decades of the 20th century (Menzel *et al.*, 2006). Similarly, a global meta-analysis spanning decades to centuries of observations of plant and animal

spring phenology found significant advancement in 62% of species studied (Parmesan & Yohe, 2003).

Both species and individuals within species differ in their phenological responsiveness to year-to-year climate fluctuations, which can have important implications for community composition and population dynamics (Diez *et al.*, 2012). For example, European bird species whose phenology has not tracked changes in temperature in recent decades have experienced significant population declines, while more responsive species have experienced little or no decline (Both *et al.*, 2006; Møller *et al.*, 2008). Similar findings have been reported for plants (Willis *et al.*, 2008; Cleland *et al.*, 2012). In addition, if different populations of the same species respond differently to climate change – either due to genetic differences between populations or to site-specific differences in the magnitude of warming (Primack *et al.*, 2009; Diez *et al.*, 2012) – it could lead to a

Correspondence: Anne D. Bjorkman, tel. +49 170 902 6201, fax +1 604 822 6150, e-mail: anne.bjorkman@idiv.de

reduction or increase in gene flow between these populations (Fox, 2003). Thus, phenological shifts can lead to changes not only in the abundance and distribution of species, but also in the genetic makeup of those species.

Arctic tundra ecosystems provide a particularly compelling setting for investigations of phenological responses to climate change, as warming is happening faster in the Arctic than anywhere else on the planet (Weller *et al.*, 2005; IPCC, 2013). Thus, we might expect to see especially rapid changes in phenology and consequently high potential for out-of-sync phenologies in Arctic systems (Høye *et al.*, 2007). In contrast to temperate systems, where increasing spring temperatures is generally considered the primary driver of advancing plant phenology (Cleland *et al.*, 2006), Arctic and alpine phenology is substantially influenced by the timing of snowmelt (Billings & Bliss, 1959; Billings & Mooney, 1968; Wielgolaski & Inouye, 2013; but see Thórhallsdóttir, 1998). Thus, changes in winter precipitation resulting in altered snowmelt dates may be as or more important than temperature in driving future phenological changes. Future temperature increases are predicted with relatively high confidence for the Arctic, but current projections of precipitation change are much less certain and could be much more variable over space and time (Weller *et al.*, 2005). The most recent projections predict an Arctic-wide increase in winter precipitation (Saha *et al.*, 2006; Bintanja & Selten, 2014). This could lead to very different phenological patterns than would be observed as a response to changing temperatures alone.

The relative importance of snowmelt vs. changes in temperature *per se* may affect species differently depending on whether they have relatively early or late phenologies. Early-flowering subalpine plant species in the Rocky Mountains, for example, showed greater phenological advances in response to warming than late-flowering species (Dunne *et al.*, 2003). In the Alaskan subarctic tundra, early-flowering species were more sensitive to snowmelt manipulations than late-flowering species (Wipf, 2010). Winter snowpack might also have an effect on plant phenology through a mechanism other than timing of snowmelt, for example, through freezing damage when the snowpack is too low (Inouye & McGuire, 1991) or by the volume of water released during snowmelt (Høye *et al.*, 2013). Furthermore, because tundra species form leaf and flower buds in the summer prior to flowering (Billings & Mooney, 1968), temperatures during the previous summer of growth might affect flowering in the following summer. Finally, increases in winter (rather than spring) temperatures have been found to be important in delaying phenology in some alpine species, likely due to a delay in chilling requirements (Yu *et al.*, 2010; Cook *et al.*, 2012).

While continuous, long-term records of phenology are relatively common in temperate ecosystems, very few such records exist for Arctic regions (Post & Høye, 2013). Short-term monitoring of phenological responses to experimental warming has demonstrated that Arctic plants flower earlier when warmed (Arft *et al.*, 1999; Hollister & Webber, 2000; Hollister *et al.*, 2005a), but these short-term responses have been shown to overestimate responses to long-term experimental warming and underestimate responses to ambient warming (Chapin *et al.*, 1995; Hollister *et al.*, 2005b; Wolkovich *et al.*, 2012; Kremers *et al.*, 2015). Furthermore, most studies of phenological responses to climate change have focused exclusively on changes in flowering time. Very few studies have specifically examined changes in seed maturation phenology, which can be as important as flowering time to plant fitness (Molau, 1993; Kudo & Hirao, 2006; Cooper *et al.*, 2011). In particular, late-maturing individuals or species may have fewer or less viable seeds if fall freezing occurs before seed maturation is complete (Galen & Stanton, 1991; Kudo & Hirao, 2006; Cooper *et al.*, 2011).

Here, we ask whether flowering time and seed maturation for four common Arctic plant species have advanced in response to both experimental and ambient (natural) warming in two distinct tundra habitat types over a period of 21 years. This study represents the longest record of phenological responses to both experimental and ambient warming in the Arctic to date (but see Høye *et al.*, 2007; Oberbauer *et al.*, 2013; Kremers *et al.*, 2015 for other studies spanning one decade or more). We examine changes in the timing of snowmelt and in winter and spring temperatures over the same time period, as well as snowfall trends from a nearby weather station.

We use this comprehensive data set to test (i) whether flowering phenology and seed set have advanced in response to experimental warming or to ambient warming over the past two decades; (ii) whether these changes vary by habitat type or species; and (iii) what environmental drivers are most closely related to changes in flowering phenology for each species. We predict that both the timing of snowmelt and spring temperature will be related to flowering time across all species. Therefore, if ambient warming at our Arctic field site has been as rapid as elsewhere in the Arctic, and if this warming has led to earlier snowmelt, we would expect strong and consistent advances in flowering time and seed set across sites, species, and treatments. However, if the timing of snowmelt has not changed, or if warmer winter temperatures have led to a delay in chilling requirements, we would expect only a slight advancement or no advancement in flowering time in response to warmer temperatures. In addition to

testing these predictions, we present an improved method for analyzing interval-censored and right-censored phenological data using Bayesian hierarchical modeling, as described in the Methods section.

Materials and methods

Study site and species

The Alexandra Fiord lowland is a ~8 km² area of heterogeneous tundra habitat on Ellesmere Island, Canada, bounded on two sides by low mountains, to the south by the Twin Glacier, and to the north by Alexandra Fiord (78°53'N, 75°55'W). Although the surrounding area is dominated by polar desert due to very low precipitation levels (Freedman *et al.*, 1994), the Alexandra Fiord lowland itself supports a relatively diverse assemblage of species and habitats due in part to spatial variation in soil conditions and to a strong moisture gradient due to microtopographic controls on snow distribution and glacial runoff (Muc *et al.*, 1989; Freedman *et al.*, 1994).

Our study was conducted in two common habitat types, a mesic heath community dominated by the evergreen shrubs *Dryas integrifolia* (mountain avens) and *Cassiope tetragona* (Arctic white heather), and a dry sandy creek bank dominated by graminoids and the deciduous dwarf shrub *Salix arctica* (Arctic willow; Muc *et al.*, 1989). Two of the four focal species – *Dryas integrifolia* and *Papaver radicum* (rooted poppy) – are abundant in both habitat types. The other two focal species, *Oxyria digyna* (mountain sorrel) and *Salix arctica*, also occur in both habitats, but phenological observations were conducted only at the dry site. These four species were chosen because they are abundant at our field site and are widespread throughout the Canadian Arctic and subarctic (Porsild & Cody, 1980). The distribution of *Oxyria* is circumpolar and spreads as far as the alpine areas of the southwestern United States (Mooney & Billings, 1961; Billings *et al.*, 1971).

Experimental design

In 1992, 20 permanent 1 m² randomly placed plots were established at both the dry and mesic sites. These experimental plots, along with those in several other habitats at Alexandra Fiord, were the first to be established as part of the International Tundra Experiment (ITEX). In 1993, an additional 18 plots were established at the mesic site. Half of the plots were experimentally warmed using clear-sided, hexagonal open-top chambers (OTCs; 1.5 m diameter at the top and 0.5 m tall), according to the established ITEX protocol (Henry & Molau, 1997). An unavoidable consequence of passive warming is the reduction of wind inside the chambers, but CO₂ concentrations are not affected (see Marion *et al.*, 1997 for more about the environmental effects of OTCs). Within each experimental plot, between 2 and 5 individuals of each study species were chosen randomly and tagged for long-term monitoring. When a tagged individual died or tags became detached, a replacement individual of that species was chosen from nearby in the plot. Comprehensive phenological monitoring was conducted

for *Papaver* and *Oxyria* between 1993 and 2013, for *Dryas* between 1993–2009 and 2012–2013, and for *Salix* between 1995–2009 and 2012–2013 (Table S1). From 1995 to 2009, only 12 plots were monitored at the mesic site. Site access constraints prevented monitoring in 1999 and 2006.

Phenological monitoring was generally conducted every 3 days, but in some years, the time between sampling was 6 days or more at the end of the growing season (after most plants had already flowered, but before seed maturation). The day of the year on which the first mature flower was observed was recorded for every tagged individual in every plot. A 'mature' flower was defined as visible pollen (*Oxyria* and male *Salix*) or a receptive stigma (female *Salix*), or when the corolla was fully open (*Papaver* and *Dryas*). We also recorded the date at which mature (dispersing) seeds were first observed for each species. Because seed dispersal in *Dryas* occurs very late in the season, usually after monitoring has ended, we instead monitored the formation of a seed capsule. Seed maturation in *Salix* (a dioecious species) was monitored only in female individuals.

Climate stations were established in both sites; shielded copper–constantan thermocouples measured air temperatures at 10 cm above ground level in four plots of each treatment to assess the warming effect of the OTCs. The thermocouples were connected to a data logger (CR10; Campbell Scientific Canada Corp., Edmonton, AB, Canada), and temperatures were recorded every 5 min. These data were used to estimate the warming effect of the OTCs relative to control plots. Daily average ambient air temperatures (1.5 m) were measured at a third climate station located ~250 m from the mesic and dry sites. Winter temperature (average temperature from day 225 of the previous year to day 150 of the current year), previous summer temperature (average temperature of days 150–225 of the previous year), and spring temperature (defined below) were derived from temperature measurements at this climate station.

Because different species first flower at different times (Table S1), species-specific spring temperatures were calculated as the average temperature between day 150 (~beginning of snowmelt) to the day (averaged across all years) at which 75% of the monitored reproductive individuals had flowered. Day 150 was used as the start date for calculating spring temperature to reduce correlation with date of snowmelt (which generally occurs on or shortly after day 150) and because snow cover substantially buffers plants from air temperature fluctuations that occur while they are still covered by snow (Jones, 1999; Groffman *et al.*, 2001). Snow-depth sensors were also installed in four plots at each site to record snowmelt rates each spring. Early analyses of these data demonstrated no change in snowfall over time (1993–2002) at one site (Hudson & Henry, 2009), but electronic malfunctions at all of the sites, especially after 2002, restricted the reliability of the data. We instead report total winter snow accumulation at the Environment Canada weather station at Eureka, approximately 240 km northwest of Alexandra Fiord. We assess the validity of this substitution by comparing yearly snowfall at Eureka with yearly mean snowmelt dates at Alexandra Fiord, as well as monthly mean and July mean temperatures at both sites.

In addition to phenological monitoring, the timing of snowmelt in each plot (defined as the day on which snow cover in the plot was visually estimated to be $\leq 10\%$) was recorded in every year except 2009, when we arrived at the site after all snowmelt had occurred. In 1993, 1994, 1997, 2004 and 2012, some plots were already snow free upon our arrival (in all cases except 1994, fewer than half the plots were already snow free). In total, across all years, 20% of plot-level snowmelt dates were unobserved. Because these data were not missing at random (i.e., early-snowmelt plots and early-snowmelt years were most likely to be missing), simply excluding these values would bias yearly average snowmelt dates to appear later than they actually were. Instead, we estimated snowmelt dates for these plot-years. Specifically, we modeled snowmelt dates as an interval-censored response variable (as described below), where the upper interval bound was the first date a given plot was observed to be already snow free and the lower bound was 5 days prior to the single earliest snowmelt date observed in each site across all years (= day 150 at the mesic site and day 140 at the dry site). We included predictor variables of total winter snowfall at the Eureka weather station (~240 km to the northwest), early spring (day 120–150) mean temperature at Alexandra Fiord, treatment (warmed/control) and site, with a random effect of plot. A regression of true (observed) vs. model-predicted snowmelt dates had an R^2 value of 0.87.

Statistical analyses

Trends in temperature variables over the 21 years of the study were determined using linear models. The change in snowmelt date was determined using a linear mixed model, where year (a continuous variable), site, and a year \times site interaction were included as fixed effects. Random effects of plot and year (as a factor) were included to account for the nonindependence of the same plot over time and of all plots measured in the same year. Observed snowmelt dates were included when available, otherwise modeled snowmelt dates were used (as described above). We used the R package *lme4* (Bates *et al.* 2015) for mixed model analyses.

Phenological responses were estimated using Bayesian hierarchical modeling with an interval-censored or right-censored response variable to account for the varying intervals between survey dates. Censored observations (i.e., those in which the event of interest is not directly observed) are common in survival analyses (Ibrahim *et al.*, 2005), but appropriate analytic techniques developed in other fields have rarely been applied to phenology studies. Typically, researchers assign dates to a phenological transition based on one of two assumptions: the transition occurred on the first day on which it was observed to have occurred (which will lead to late-biased estimates of flowering time), or the transition occurred at the midpoint between sampling days (which systematically underestimates the variance). Both adjustments have the potential to introduce artifacts, particularly when the sampling interval is not consistent over time. For example, if the monitoring intervals vary from year to year or within the same year, failure to account for these differences would lead to late-biased

estimates of phenological events for those years, species, or events that were sampled less frequently (Miller-Rushing *et al.*, 2008). Conversely, if phenological monitoring has become more intensive over time, failure to account for sampling frequency would lead to early-biased estimates and a false trend of phenological advancement over time. Finally, end-of-season events, such as seed maturation, can be strongly early-biased if monitoring ends before all individuals have reached that stage. Hence, we use Bayesian hierarchical modeling with interval-censored and right-censored response variables to account for uneven sampling frequency, ensuring that the patterns presented here reflect actual changes in phenology and not statistical artifacts of variation in sampling effort or duration of monitoring.

We defined the upper interval bound as the day on which flowering was first observed for a given individual and the lower interval bound as the closest preceding survey date on which a plant was observed to be not flowering. This observation model accounts for the realized observation process, wherein the actual date of flowering is known to occur somewhere between the lower and upper bounds. The associated uncertainty is incorporated into the parameter estimates. For those individuals that reached the seed maturation stage before monitoring ended, lower and upper bounds were assigned as described above. If an individual did not reach the seed maturation stage before the end of monitoring, the lower bound was defined as the last day on which monitoring was conducted and no ripe seeds were observed (i.e., we used a right-censored model in this case). Individuals that showed prominent signs of herbivory or fungus on the flower or had aborted/unfertilized flowers were excluded from the analysis.

We used three primary sets of models to determine (i) the direction and magnitude of the experimental treatment (warming) effect for each species in each habitat type, (ii) the change in flowering date and seed maturation date over time (control plots only) for all species within each habitat type, and (iii) the environmental variables most predictive of flowering time for each species (control and warmed treatments together). Flowering responses to variation in snowmelt date were partitioned (Fitzmaurice *et al.*, 2011 see chapter 14) into responses due to spatial variation in snowmelt (differences among plots within a year) and temporal variation in snowmelt (differences in mean snowmelt date across years). Modeled snowmelt dates per plot (as described above) were used only for calculating the yearly mean snowmelt date (temporal variation component); estimates of the relationship between flowering time and spatial variation in snowmelt were based only on observed snowmelt dates per plot.

All models included a random effect of plot to account for nonindependence of plants measured within the same plot and a random effect of year to account for nonindependence of plants measured within the same year. For the third set of models (see above), environmental variables (winter temperature, spring temperature, previous summer temperature, and timing of snowmelt per plot and per year) were incorporated into the model at the level at which they

were measured (e.g., temperature variables at the year level, plot-level snowmelt dates at the plot level). The maximum correlation between any pair of environmental variables was 0.23 (Pearson's correlation coefficient). We refer to environmental predictors as 'significant' in the text when the 95% credible interval for the corresponding parameter in the fitted models did not overlap zero. We used flat priors for all coefficients. All models were conducted in JAGS (v. 3.4.0) called from R (v. 3.0.3) using the programs *rjags* (Plummer, 2014) and *R2jags* (Su & Yajima, 2015). Convergence was assessed both visually and using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992) available in the *coda* package (Plummer *et al.*, 2006). JAGS code for the Bayesian model estimating change in first-flowering date over time is provided (see suppl. mat.).

Results

Treatment effect

Between 1995 and 2011, experimentally warmed plots were 2.14 and 1.56 (± 0.04) °C warmer than the control plots at the dry and mesic sites, respectively, averaged over the entire year. The warming effect of the OTC's was greater during the winter than during the summer, likely due to a snow-trapping effect (increased insulation). Winter temperatures (September–May) were 3.01 and 2.38 °C warmer in OTCs than in control plots, while growing season temperatures (June–August) were 1.78 and 0.91 °C warmer in control plots at the dry and mesic sites, respectively.

Environmental change

Temperatures have increased substantially at Alexandra Fiord over the past two decades (Fig. 1a,b). Winter temperatures increased the most consistently, at a rate of 0.52 °C per decade ($R^2 = 0.234$, $P = 0.026$). Spring temperatures (days 150–200) also increased, but with slightly greater among-year variation than annual temperatures (0.52 °C per decade; $R^2 = 0.181$, $P = 0.055$). Over the same time period, total winter snowfall at Eureka (~240 km northwest of Alexandra Fiord) increased by 10.9 cm per decade ($R^2 = 0.189$, $P = 0.049$), although again with considerable year-to-year variation (Fig. 1c). This snowfall increase is part of a longer trend; long-term data from this same station indicate a slight but steady increase in snowfall at Eureka since 1950 (4.2 cm/decade, $P < 0.001$; Fig. S1).

Snowmelt was slightly delayed over time at the dry site but not at the mesic site (year \times site interaction $P < 0.001$; Figs 1d and S2), although there was again large among-year variation. Snowmelt was delayed by 0.5 days/decade at the mesic site and 1.7 days/decade at the dry site. Overall, snowmelt occurred significantly

earlier at the dry site than at the mesic site (4.2 days earlier; $P < 0.0001$), and there was a slight but not significant effect of treatment on snowmelt (0.96 days earlier in the warm treatment, $P = 0.11$). Similar but slightly weaker patterns were found when repeating the analyses omitting (rather than imputing) data from plot-years in which snowmelt occurred prior to arrival at the site (Table S2).

Total winter snowfall at Eureka and raw (not gap-filled) mean snowmelt dates at Alexandra Fiord were significantly correlated over those years for which both measurements were available (19 years in total; Pearson's correlation coefficient = 0.51 for the mesic site and 0.55 for the dry site, P -values = 0.03 and 0.02, respectively; Fig. S3). Monthly mean and July mean temperatures at the Eureka weather station were also highly correlated with those at Alexandra Fiord (Pearson's correlation coefficient = 0.997 and 0.900, respectively, $P < 0.0001$ for both; Fig. S4), suggesting that both locations are affected similarly by regional weather patterns.

Phenological responses

Three of the four species flowered significantly earlier in the experimental warming treatment than in the control plots, as expected. However, the magnitude of the response varied by species and site (Fig. 2a). *Papaver* flowered 2–5 days earlier (95% CI) in the warm treatment at the dry site, but did not respond significantly to warming at the mesic site. *Salix* did not flower significantly earlier in the warm treatment. Experimental warming also led to earlier seed development for three of the four species (Fig. 2b), but the 95% credible intervals excluded 0 only for *Dryas* at the mesic site (1.5–7 days earlier) and *Papaver* at the dry site (2.7–10 days earlier).

Despite more than 1 °C of ambient (nonexperimental) warming over the two decades of observation, none of the four species show the expected trend of earlier flowering over time in the control plots (Fig. 3a). In fact, one species (*Dryas*) showed significantly delayed phenology over time at the dry site (0.58 days/year, CI range = 0.06–1.11). Both *Papaver* and *Oxyria* also demonstrated delayed phenology, although 95% credible intervals for the slope of change over time overlapped zero for both species. The flowering time of the other species, *Salix*, remained constant over the study period. The magnitude of the time trend varied between the two habitat types. The delay in flowering time was greater at the dry site than at the mesic site for at least one species: At the beginning of the study, first flowering of *Dryas* occurred significantly earlier at the dry site than at the mesic site (mean = 8.5 days ear-

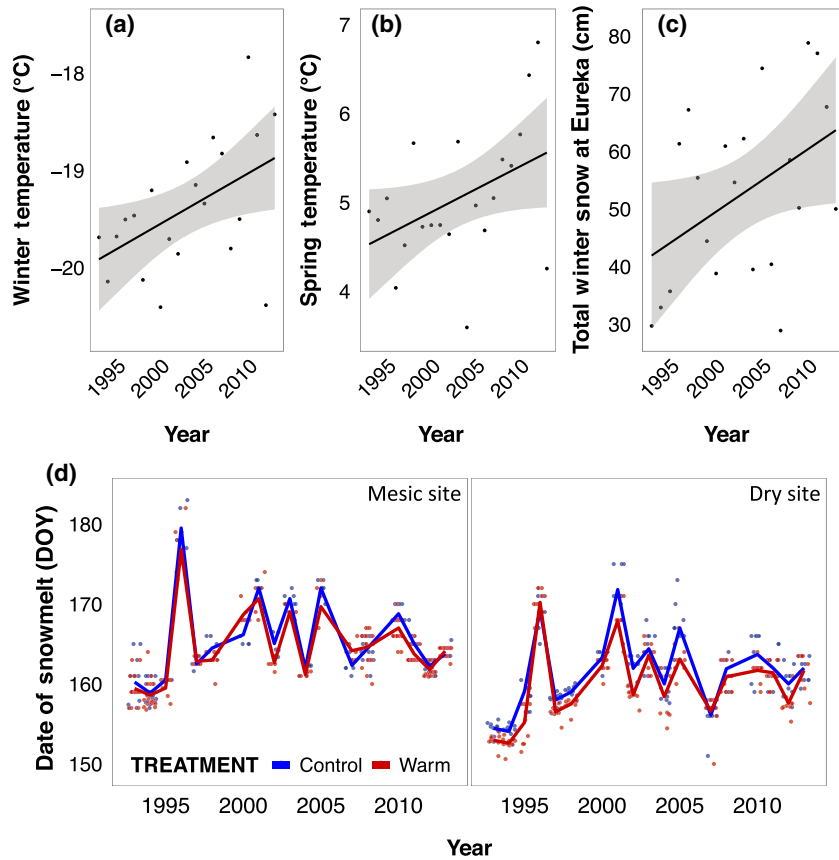


Fig. 1 Change in winter temperature (a) and spring temperature (b) at Alexandra Fiord, and in total winter snowfall at Eureka (c), and mean date of snowmelt (day of the year), where points are snowmelt dates in each plot and lines are means per treatment, per year (d) over the past two decades.

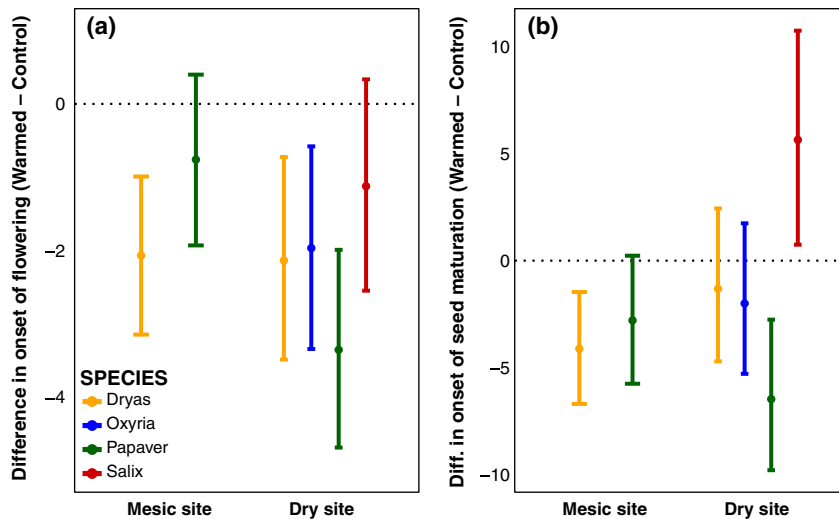


Fig. 2 Modeled difference, in number of days, in flowering time (a) and seed maturation/dispersal (b) between the warmed and control treatment for each species across all years. Negative values (below the zero line) indicate earlier flowering in the warmed treatment. Point estimates and 95% credible intervals are derived from a Bayesian hierarchical model including random effects for plot and year.

lier, CI range = 1.3 to 15.8 days), while at the end of the study, there were no significant differences between the two sites (mean = 2.4 days earlier, CI range = -5.7–

10.4 days). *Papaver* showed a qualitatively similar pattern of more rapid change in the dry site than in the mesic site, but the difference between sites was not sig-

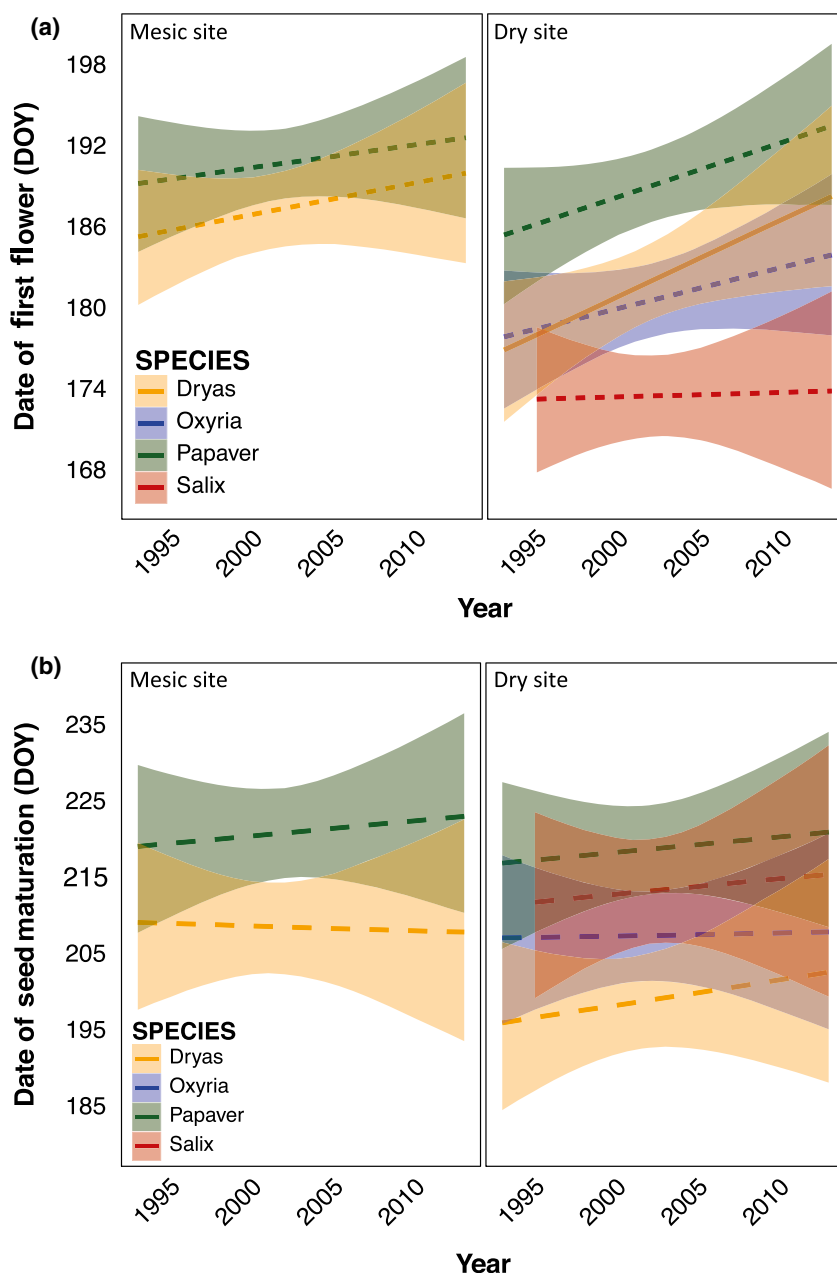


Fig. 3 Change in predicted date of (a) flowering time and (b) seed maturation ($\pm 95\%$ credible intervals) in the control plots over the duration of the study. A dotted line indicates that the 95% CI of the slope parameter overlaps zero. Flowering in *Salix* includes both male and female plants but seed maturation is for female plants only. Seed development, rather than dispersal, is shown for *Dryas* as dispersal usually occurs late in the season after observations have ceased. Modeled results are from a Bayesian hierarchical model with random effects for plot and year. Slopes were allowed to vary by species and site as well as the interaction between the two. DOY = day of the year.

nificant. Similar overall trends were observed in the warm treatment (Fig. S5).

Despite delayed flowering times for at least one species, the timing of seed maturation remained relatively constant over the study period (Fig. 3b). The credible intervals for the slope of seed maturation date over time overlapped zero in all cases.

Environmental drivers

For all four species, flowering time was delayed when snowmelt was later, regardless of whether the delay in snowmelt was due to landscape positioning of a particular plot (spatial variation) or the late snowmelt years (temporal variation; Fig. 4). Flowering time of *Dryas*,

Oxyria, and *Papaver* (but not *Salix*) was negatively related to spring temperature (i.e., warmer spring temperatures led to earlier flowering), independently of snowmelt. Winter temperature was positively related to flowering time for *Papaver*, indicating that warmer winter temperatures led to later-flowering in this species. The temperature of the previous summer was not a significant predictor of flowering time for any species.

Discussion

The results of this study are in marked contrast to many prior studies demonstrating advanced flowering phenology in recent decades. As expected, experimental warming led to significantly earlier flowering phenology across species and habitat types. However, despite more than 1 °C of ambient warming during the course of the study, flowering phenology of all four species in unmanipulated plots remained constant over time or was even delayed. These seemingly contradictory results can best be explained by disparate effects of warming and snowfall on the timing of snowmelt. Winter snow accumulation increased substantially between 1993 and 2013 at the nearest permanent weather station (Fig. 1c), likely as an indirect effect of atmospheric warming (Bintanja & Selten, 2014). Snowmelt date is a function of the quantity of snow and the available thermal energy to melt it, such that increases in both temperature and snowfall should have countervailing effects on snowmelt date, and thus on temporal trends in plant phenology. An alternative explanation for delayed phenology is a delay in chilling requirements due to

warmer winters (Yu *et al.*, 2010), but as winter temperature was a significant predictor of flowering time for only one species, (*Papaver*) this is likely not the primary driver here.

The disparity between phenological responses to experimental warming and the observed temporal trend in phenology concurrent with ambient warming highlights the importance of interpreting phenological responses to experimental warming with care. Several studies have demonstrated advanced phenology in response to experimental warming (Arft *et al.*, 1999; Hollister *et al.*, 2005a), and these experimental responses can sometimes underestimate true responses to climate warming (Wolkovich *et al.*, 2012). The results from our study, however, indicate that responses to experimental warming can, in some cases, actually overestimate the phenological advances we are likely to see with climate warming, as they do not sufficiently account for altered precipitation or other environmental changes that occur simultaneously with warming temperatures. The significant influence of snowmelt timing on phenology emphasizes the major importance of understanding potential precipitation changes in Arctic ecosystems to accurately forecast plant phenology (Richardson *et al.*, 2013; Rumpf *et al.*, 2014).

Phenological responses to ambient warming differed among species within the same habitat type, likely due, in part, to the different environmental variables driving flowering phenology in each species. Date of snowmelt was significantly and strongly related to flowering time for all species, suggesting that the timing of snowmelt is consistently a critical driver of flowering phenology

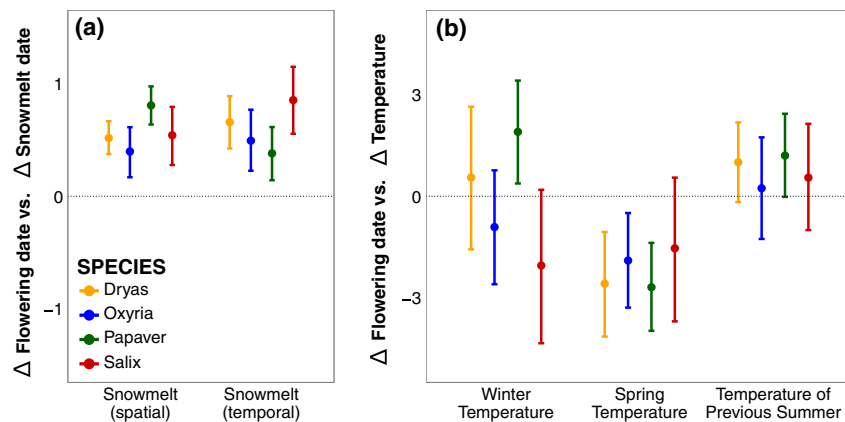


Fig. 4 Coefficients from a Bayesian hierarchical model of flowering time in both treatments ($\pm 95\%$ credible intervals). Coefficients represent the slope of the relationship between flowering time and the different environmental variables for each species. Positive coefficients indicate a positive relationship between that variable and flowering time. Model coefficients reflect the effect of each variable (e.g., a 1-day delay in snowmelt leads to a ~ 1 -day delay in flowering for *Salix*) in the presence of all other variables in the model (including site and treatment, not shown).

in Arctic and alpine species, as has been previously shown (Inouye & McGuire, 1991; Inouye *et al.*, 2002; Wielgolaski & Inouye, 2013). The relationship between snowmelt and flowering was especially strong for *Salix*, the earliest flowering species, which typically flowers only ~15 days after snowmelt. Conversely, spring temperature was most strongly negatively related to flowering time for the two species, *Dryas* and *Papaver*, that flower later in the summer, generally 20–30 days after snowmelt. This pattern suggests that species may differ in their responses to future climatic changes depending on whether they are early-flowering (and thus driven primarily by the timing of snowmelt) or late-flowering (and thus temperature driven; Molau, 1993), although it is not possible to explicitly test this relationship at our site with only four species. Studies of temperate plants have found that early-flowering species are more responsive to changes in temperature than late-flowering species (Rathcke & Lacey, 1985; Mazer *et al.*, 2013). This pattern has been attributed to positive physiological effects of warmer temperatures early in the season (i.e., more rapid development) but a negative physiological effect of extreme heat at mid-summer (Sherry *et al.*, 2007). Plants at our study site show the opposite relationship to temperature; that is, early-flowering plants respond almost exclusively to the timing of snowmelt, while later-flowering plants flower earlier when temperatures are warmer, even after accounting for the effect of differences in snowmelt. This implies that current levels of warming at our field site lead to accelerated plant development.

Further illustrating the complexity of snowmelt–temperature interactions, the most snowmelt-sensitive species (*Salix*) was the only species to show no evidence of a delayed flowering trend over the course of the study period – despite a delay in snowmelt over the same period, while the two temperature-sensitive species flowered later – despite an overall warming trend. This seeming paradox is likely due to a combination of factors. First, observations for *Salix* at the dry site are available only from 1995; thus, there are no data for this species in the early-snowmelt years of 1993 and 1994. Secondly, several years (including 2004 and 2013) were warm early in the spring, leading to early or normal snowmelt, but then colder than normal shortly after snowmelt. In these years, the snowmelt-driven species, *Salix*, flowered relatively early, while the temperature-driven species, *Papaver* and *Dryas*, flowered relatively late. Thus, a combination of cold springs in some years and later snowmelt in others likely led to the overall pattern of delayed flowering in the latter two species. Such interactions can also have substantial consequences for plant fitness; several studies have shown that early snowmelt can be beneficial in a warm year

(likely due to the longer growing season) but can be detrimental if early snowmelt increases the likelihood of spring freezing events and frost damage (Inouye *et al.*, 2002; Kudo & Hirao, 2006; Wipf *et al.*, 2009). As species vary in their responses to changes in snowmelt (Walker *et al.*, 1999; Wipf *et al.*, 2009), these differences can lead to substantial shifts in community composition (Walker *et al.*, 1999).

The combined responses of flowering time and seed/fruit development to climate change could have important implications for future shifts in species composition at this site. A failure to optimally track climate warming has been shown to lead to reduced fitness in several other species (Both *et al.*, 2004; Cleland *et al.*, 2012) and can lead to changes in species' abundances (Møller *et al.*, 2008) and distributions (Chuine & Beaubien, 2001). In high Arctic ecosystems, where the growing season is often only 6–8 weeks long, delayed flowering could have serious implications for fitness if seeds do not reach maturity before the onset of winter (Molau, 1993; Cooper *et al.*, 2011). Despite the delay in flowering time observed here, however, the timing of seed set was not delayed. This suggests that the rate of seed development may have increased slightly over time due to warming, which could at least partly compensate for the effects of delayed snowmelt. Whether the speed of seed development can have direct consequences for an individual's fitness is unknown for these species, but a prior study at this site showed increased germination success in the seeds of experimentally warmed individuals relative to those in control plots, suggesting that warming improves seed viability in general (Klady *et al.*, 2011).

Differing phenological responses between the two habitat types could also have important implications for gene flow between populations in each habitat (Fox, 2003). While in the early years of the study *Dryas* at the dry site flowered significantly earlier than at the mesic site, the change in flowering over time was also greater at the dry site, so that by the end of the study period plants in both sites flowered concurrently. This difference could be due to differences in microtopography at the two sites and, as a result, differences in snowmelt trends, or to differences in soil moisture. The different responses could also be due to genetic differences between populations at the two sites (Weis & Kossler, 2004). A reciprocal transplant study involving populations of *Oxyria* and *Papaver* from both habitat types found evidence of local adaptation in these populations despite their close proximity to each other (~500 m; A.D. Bjorkman, E.R. Frei, M. Vellend and G.H.R. Henry, unpublished data). Whether local adaptation has also occurred in *Dryas* is not known, but the differential phenological responses to climate warming at the two sites could lead to increased gene flow and thus

increased genetic similarity between the populations of this species.

The results of this study are a striking contrast to most prior studies of phenological responses to climate change in temperate systems. All four species in our study demonstrated unchanged or delayed flowering, despite significant ambient warming at the site over the 21-year period. Changes in flowering time varied by species and by habitat type, indicating that no single prediction will accurately describe future phenological changes for all species and locations. The timing of snowmelt, however, is a universally important driver of phenology in Arctic and alpine ecosystems (Billings & Bliss, 1959; Billings & Mooney, 1968; Wielgolaski & Inouye, 2013; this study). Our results thus highlight the general importance of considering changes in both temperature and precipitation, as well as the interaction between the two, when predicting future responses to climate change.

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Supporting Information

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

Table S1. Growth form, mean flowering date of each species at each site, the number of tagged individuals of each species at each site, and the total number of years each species was surveyed between 1993 and 2013.

Table S2. Change in snowmelt date, imputed vs. observed.

Table S3. Results (modeled means and 95% credible intervals) from Bayesian analyses.

Figure S1. Change in total winter snowfall at the Eureka weather station since 1950.

Figure S2. Modeled change in snowmelt date over the duration of the study.

Figure S3. Regression of yearly mean snowmelt dates at Alexandra Fiord against total winter snowfall at Eureka.

Figure S4. Comparison of monthly mean and July mean temperatures at Eureka and Alexandra Fiord, 1990–2012.

Figure S5. Change in flowering time in both treatments over the duration of the study.

Document S1. JAGS code for change in flowering date over time.