Phenological decoupling of mortality from wave forcing in kelp beds

De Bettignies, Thibaut, Wernberg, Thomas, Lavery, Paul S, Vanderklift, Mathew A, Gunson, Jim R, Symonds, Graham and Collier, Neil (2015) Phenological decoupling of mortality from wave forcing in kelp beds. Ecology, 96 (3). pp. 850-861. ISSN 0012-9658

Ecology, 96(3), 2015, pp. 775–787

Phenological mismatch with abiotic conditions—implications for flowering in Arctic plants

HELEN C. WHEELER,[1,8] TOKE T. HØYE,[2,3,4] NIELS MARTIN SCHMIDT,[5,3] JENS-CHRISTIAN SVENNING,[1]
AND MADS C. FORCHHAMMER[1,5,6,7]

[1] *Center for Informatics Research on Complexity in Ecology (CIRCE), Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark*
[2] *Aarhus Institute of Advanced Studies, Aarhus University, Høegh-Guldbergs Gade 6B, DK-8000 Aarhus C, Denmark*
[3] *Arctic Research Centre, Aarhus University, C.F. Møllers Allé 8, DK-8000 Aarhus C, Denmark*
[4] *Department of Bioscience, Aarhus University, Grenåvej 14, DK-8410 Rønde, Denmark*
[5] *Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark*
[6] *The Polar Center, Penn State University, University Park, Pennsylvania 16802 USA*
[7] *Greenland Climate Research Centre (GCRC), Greenland Institute of Natural Resources, 3900 Nuuk, Greenland*

Abstract. Although many studies have examined the phenological mismatches between interacting organisms, few have addressed the potential for mismatches between phenology and seasonal weather conditions. In the Arctic, rapid phenological changes in many taxa are occurring in association with earlier snowmelt. The timing of snowmelt is jointly affected by the size of the late winter snowpack and the temperature during the spring thaw. Increased winter snowpack results in delayed snowmelt, whereas higher air temperatures and faster snowmelt advance the timing of snowmelt. Where interannual variation in snowpack is substantial, changes in the timing of snowmelt can be largely uncoupled from changes in air temperature. Using detailed, long-term data on the flowering phenology of four arctic plant species from Zackenberg, Greenland, we investigate whether there is a phenological component to the temperature conditions experienced prior to and during flowering. In particular, we assess the role of timing of flowering in determining pre-flowering exposure to freezing temperatures and to the temperatures experienced prior to flowering. We then examine the implications of flowering phenology for flower abundance. Earlier snowmelt resulted in greater exposure to freezing conditions, suggesting an increased potential for a mismatch between the timing of flowering and seasonal weather conditions and an increased potential for negative consequences, such as freezing damage. We also found a parabolic relationship between the timing of flowering and the temperature experienced during flowering after taking interannual temperature effects into account. If timing of flowering advances to a cooler period of the growing season, this may moderate the effects of a general warming trend across years. Flower abundance was quadratically associated with the timing of flowering, such that both early and late flowering led to lower flower abundance than did intermediate flowering. Our results indicate that shifting the timing of flowering affects the temperature experienced during flower development and flowering beyond that imposed by interannual variations in climate. We also found that phenological timing may affect flower abundance, and hence, fitness. These findings suggest that plant population responses to future climate change will be shaped not only by extrinsic climate forcing, but also by species' phenological responses.

Key words: Cassiope tetragona; *climate change; climatic mismatch;* Dryas octopetala/integrifolia; *flowering; Huisman-Olff-Fresco models; interannual variability;* Papaver radicatum; *phenology;* Salix arctica; *snowmelt; Zackenberg, Greenland.*

INTRODUCTION

Phenological shifts are a pervasive response to climate change, and they are currently occurring across a broad range of systems and taxa (Peñuelas and Filella 2001, Parmesan 2006, Høye et al. 2007*b*). These shifts involve a combination of plastic and genetic responses to climate change (Anderson et al. 2012). Phenological shifts often occur in response to changes in resource availability or in the timing of cues for life history transitions. The consequences of these responses for population growth may be positive, neutral, or negative (e.g., Ozgul et al. 2010, Moyes et al. 2011, Lane et al. 2012).

As the phenologies of different species shift, ecosystem interactions can become altered (Yang and Rudolf 2010). These changes occur when certain events (such as life history transitions) for one species shift at a different rate or in a different direction than other ecosystem

Manuscript received 24 February 2014; revised 17 July 2014; accepted 18 July 2014; final version received 18 August 2014. Corresponding Editor: P. B. Adler.

[8] E-mail: helen.wheeler@bios.au.dk

components (Post and Forchhammer 2008, Post et al. 2008, Yang and Rudolf 2010). Mismatches can occur when cues for life history changes do not correlate precisely with optimal resource conditions, which can have negative fitness effects (Miller-Rushing et al. 2010). Mismatches often occur due to a temporal (e.g., winter emergence of moths and subsequent hatching of eggs; Visser and Holleman 2001) or spatiotemporal (e.g., bird migration; Saino et al. 2011, McKinney et al. 2012) uncoupling of the conditions experienced when decision-making occurs and the conditions that affect the traits on which natural selection acts (Miller-Rushing et al. 2010).

Whereas considerable attention has focused on the biotic mismatch between interacting species (Stenseth and Mysterud 2002, Edwards and Richardson 2004, Visser and Both 2005, Both et al. 2006, Singer and Parmesan 2010, McKinney et al. 2012), less attention has been given to the potential for climatic mismatch under shifting phenologies. Climatic mismatches can occur when the timings of life history events are partially or fully decoupled from the timings of seasonal weather trends (Fig. 1a; see also Miller-Rushing et al. 2010). Phenologically induced changes in weather conditions experienced during a given life history stage or event are most likely to occur when the cues for life history transitions are highly variable interannually and are not directly linked to seasonal weather trends (Fig. 1). Endogenous and temporally fixed external indicators, such as photoperiod, cause limited interannual variation in phenology, whereas cues such as snowmelt, moisture changes, and temperature are more variable interannually (Bernal et al. 2011, Helm et al. 2013). These more variable cues are often influenced by interannual climatic variation and may therefore occur at variable times relative to seasonal weather trends. Interannual climate variation and the timing of events relative to seasonal weather conditions jointly define the weather conditions that species experience.

In arctic and alpine environments, the timing of flowering is highly sensitive to the timing of snowmelt (Dunne et al. 2003, Molau et al. 2004, Iler et al. 2013; but see Thórhallsdóttir 1998). The timing of snowmelt is dependent on winter snow depth and spring temperature (for details of these processes in Zackenberg Research Station, see Appendix A). Snow depth, in turn, is determined by winter precipitation and temperature (Vaganov et al. 1999). Thus, the timing of snowmelt and spring temperature are only partially correlated (Appendix A). The timing of snowmelt is highly variable and drives the phenology of many biotic processes (Høye et al. 2007*b*, Wipf and Rixen 2010, Cooper et al. 2011). In contrast, the seasonal variation in temperature is relatively fixed temporally. The combination of fixed timings of seasonal weather transitions and variable timings of cues for life history transitions should result in a reduced coupling between life history events and seasonal temperature anomalies. Other phenological cues may also decouple phenology from seasonal weather. For example, delayed phenology has been observed in response to winter warming, where development is conditional on a chilling requirement (Yu et al. 2010, Laube et al. 2014).

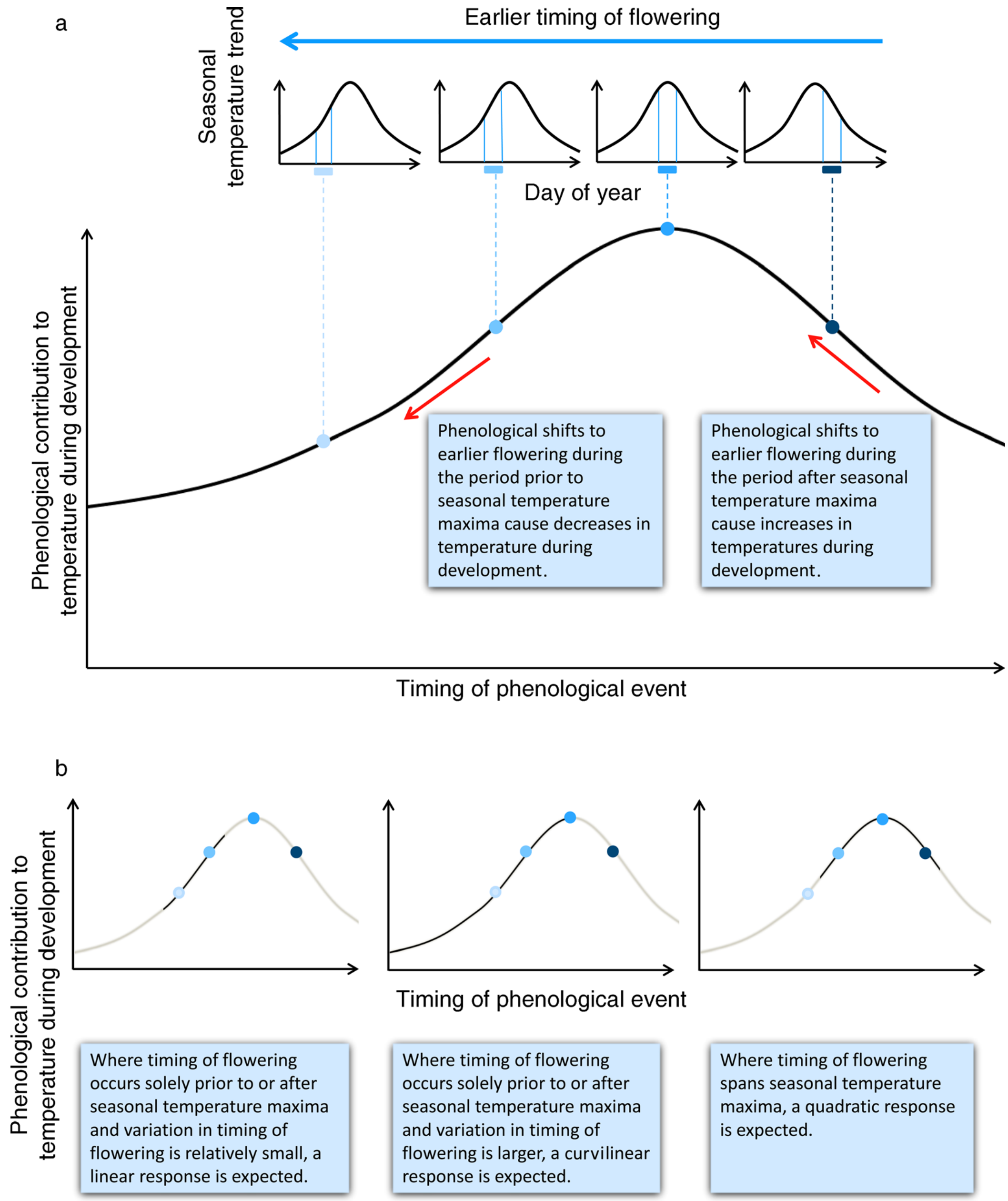
The timing of life history events determines the conditions experienced during a given developmental stage, and as a result, may have consequences for fitness (Molau 1993, O'Neil 1999, Dunne et al. 2003, Inouye 2008, Miller-Rushing et al. 2010, Hulme 2011, Reed et al. 2013). The timing of flowering can affect the abundance of flowers produced and the duration of flowering (Inouye 2008). These changes, in turn, may reduce seed number, altering seed dispersal rates and ultimately seed germination, with potential consequences for plant establishment (Cooper et al. 2011). Therefore, both shifting flowering phenology and altered flower abundance have the potential to substantially alter the fitness of flowering plants.

Here, we assess the extent of phenological contributions to temperature during flower development and the resulting effect of flowering phenology on a plant's reproductive effort. We use a novel application of Huisman-Olff-Fresco (HOF; Jansen and Oksanen 2013) models to characterize seasonal flowering trends in four species of arctic plants. We use interannual and plot-level variation in the timing of flowering to explore the effect of timing of flowering on the conditions experienced during two stages of flower development: pre-flowering and flowering. We hypothesize that in addition to an effect of interannual climate, a phenological signal will be apparent in the temperature conditions experienced during flowering. In particular, we predict that advanced phenology will result in greater-than-average exposure to freezing conditions prior to flowering (e.g., Inouye 2008). In addition, we predict that the temperature during flowering will be associated with timing of flowering. The range of interannual variation in flowering timing relative to the seasonal peak temperature should determine whether the response is quadratic, curvilinear, or linear (Fig. 1b). We then consider whether flowering phenology also has an effect on flower abundance. To this end, we assess the implications of phenological variation on a measure of reproductive effort.

METHODS

Field data

We used long-term data (1995–2011) from monitoring plots at the Zackenberg Research Station, Greenland (74°28′ N, 20°34′ W) to assess state changes between budding, flowering, and senescent developmental stages and to quantify flower abundance in *Cassiope tetragona* (four plots), *Dryas octopetala*/*integrifolia* (six plots), *Papaver radicatum* (four plots), and *Salix arctica* (seven plots; see Plate 1; Schmidt et al. 2012). The plot area varied both within and among species (*Cassiope*, mean 2 m^2, range 2–3 m^2; *Dryas*, mean 24 m^2, range 2–91 m^2;



Phenological shifts to earlier flowering during the period prior to seasonal temperature maxima cause decreases in temperature during development.

Phenological shifts to earlier flowering during the period after seasonal temperature maxima cause increases in temperatures during development.

Where timing of flowering occurs solely prior to or after seasonal temperature maxima and variation in timing of flowering is relatively small, a linear response is expected.

Where timing of flowering occurs solely prior to or after seasonal temperature maxima and variation in timing of flowering is larger, a curvilinear response is expected.

Where timing of flowering spans seasonal temperature maxima, a quadratic response is expected.

FIG. 1. Conceptual diagram of the contributions of interannual climate and phenology to temperature during plant development. Phenological contributions to temperatures experienced during development are defined as the difference in temperature experienced by a plant or population from mean temperatures during a fixed time period (e.g., mean June to August temperature) that is generated by shifts in the timing of the event. (a) The top row of graphs show different flowering windows (between the blue parallel lines), with earlier flowering to the left and later flowering to the right. In the graph below, these windows are linked to the phenological contribution to temperature during development. As a result, we can make (b) several predictions regarding how phenology might influence temperature during development.

Papaver, mean 109 m^2, range 90–150 m^2; *Salix*, mean 136 m^2, range 36–300 m^2). The plots were located in an alpine valley in vegetation types including *Cassiope* heaths, *Salix* snow beds, and *Dryas* heaths. Plots for each species were separated by a minimum of 135 m and a maximum of 2.6 km. From late May/early June to late August/early September, the plots were visited weekly, and the developmental status of 50 randomly selected plants in a budding, flowering, or senescent state was recorded. The plants were selected at each visit and sampled with replacement. The budding state was defined as when the buds were not yet fully open, the flowering state was defined as when the flowers were sufficiently open to allow insects access to the reproductive organs, and the senescent state was defined as when the flowers had either lost all their petals or their petals were largely faded or brown. At approximately peak flowering, the total count of plants in each state in each plot was recorded.

The percentage snow cover in each plot was also recorded at weekly or more frequent intervals. The day of the year in which 50% snowmelt occurred in each plot each year was extracted using linear interpolation from a time series of weekly snow cover at each plot following Høye et al. (2007*a*). Where dates with more than and less than 50% snowmelt were not recorded for a given plot (>17% of plot-by-year combinations) because of early snowmelt, the date of 50% snowmelt was estimated based on a linear model estimating the effects of plot and year on snowmelt timing.

Phenological characteristics and floral abundance

As symmetric or skewed unimodal trends in flower abundance over a growing season are common, we applied HOF models to model changes in flower abundance over a season for each plot. HOF models are a series of hierarchical logistic regression models of increasing complexity. These models are most commonly used to assess species responses in terms of probability of occurrence in relation to environmental gradients (Huisman et al. 1993, Jansen and Oksanen 2013). At the lowest complexity, we applied a flat linear model (model 1)

$$y = \frac{1}{1+e^{a}} \tag{1}$$

followed by models with an increasing or decreasing trend with the given gradient (models 2 and 3, respectively)

$$y = \frac{1}{1+e^{a+bx}} \tag{2}$$

$$y = \frac{1}{1+e^{a+bx}}\,\frac{1}{1+e^{c}} \tag{3}$$

and finally, models of unimodal symmetric, skewed, and bimodal responses (models 4, 5, and 6, respectively)

$$y = \frac{1}{1+e^{a+bx}}\,\frac{1}{1+e^{c-bx}} \tag{4}$$

$$y = \frac{1}{1+e^{a+bx}}\,\frac{1}{1+e^{c-dx}} \tag{5}$$

$$y = \frac{1}{1+e^{a+bx}}\,\frac{1}{1+e^{c-b(x-d)}} + \frac{1}{1+e^{a+b(x-d)}}\,\frac{1}{1+e^{c-b(x-d)}} \tag{6}$$

where y is the proportion flowering, x is the timing of flowering (scaled between 0 and 1) and a, b, c, and d are constants (Jansen and Oksanen 2013).

These more complex unimodal and bimodal responses (models 4, 5, and 6) probably characterize the temporal transition of a population into and out of flowering states. Model selection was performed on bootstrapped data resampled with replacement until the original sample size was achieved. For each bootstrapped data set, the most parsimonious model for the flowering curve was selected using $\mathrm{AIC_c}$. After 100 iterations of this procedure, the most frequently selected model type was selected as the best model (Jansen and Oksanen 2013). These methods were implemented using the eHOF R package (functions: HOF and predict; Jansen and Oksanen 2013).

Using HOF models to model temporal transitions between flowering and nonflowering states achieves several objectives. Because the known start and end points of floral development are nonflowering states, these models first provide a means of verifying that the flowering period is fully characterized by the sampling: if lower-order models than the unimodal response (model 4) were selected, it would indicate that the full transition into and out of flowering was not fully sampled (e.g., the start or end of flowering was insufficiently captured due to late initiation or early cessation of sampling, respectively). In these cases, data were excluded from further analysis. Second, HOF models allow for the full estimation of state changes over a growing season, enabling the assessment of multiple phenological characteristics (e.g., onset of flowering, timing of peak flowering, end of flowering, flowering duration, skew in flowering) in each plot in a given year. The timing of peak flowering was defined as the time at which the first derivative of the flowering curve equaled zero. The onset of flowering was defined as the time at which the proportion of individuals flowering first rose to $e^{0.5}$ of the maximum proportion observed flowering for a given species in a plot in the focal year. This threshold was considered appropriate because it is unlikely to be biased by a few early-flowering individuals but still captures the majority of the flowering period. According to Jansen and Oksanen (2013), uneven sampling can affect accuracy of HOF model estimation. Therefore, when logistical constraints caused uneven sampling across the temporal gradient (defined here as greater than 10 days between state samplings), we excluded such curves from analyses; this pattern occurred infrequently (*Cassiope*, one case; *Dryas*, three cases; *Papaver*, eight cases; *Salix*, one case).

The annual flower abundance per plot was calculated to represent the total sum of flowers open across all days of flowering (i.e., population-level flower days) incorporating both the number of flowers and the number of days that the flowers were open. The seasonal flower abundance across plots was calculated by integrating to find the area under the curve and scaling by the number of flowers in all states in the plot census. This process gave an estimate of the total number of flowering days across the population. Because plots differed with respect to species cover, these estimates of seasonal flower abundance were standardized for each plot according to their mean and variance across years in each plot to create seasonal flower abundance indices that were comparable among plots for each species.

Phenology and temperature conditions during development

The effect of phenology on the temperature conditions experienced during a particular stage of development was investigated. To separate the effects of correlations between climate in a given year and phenology from any residual contribution of timing of flowering upon conditions, generalized additive models with a Gaussian error structure and an identity link function were used to assess the effect of interannual variation in climatic conditions and the timing of peak flowering on the weather conditions experienced during the flowering period. We tested for a relationship between mean spring temperature (March and April, interannual effect) and the timing of peak flowering (phenological effect) on the intensity of exposure to freezing conditions prior to flowering:

$$y = a + bt + f(p) + e$$

where y is exposure to freezing, a and b are constants, t is the mean spring temperature, $f(p)$ is a smoothed function of timing of flowering, and e is an error term. This model was compared to one with only an effect of spring temperature, one with only an effect of timing of flowering, and a null model:

$$y = a + bt + e, \quad y = a + f(p) + e, \quad \text{and}$$
$$y = a + e, \quad \text{respectively.}$$

The models were compared using Akaike's information criterion (AIC) corrected for small sample size ($\mathrm{AIC_c}$; Burnham and Anderson 2002). The effect of spring temperature was modeled as a linear relationship, whereas smoothing was allowed for the effect of timing of flowering to allow for potential linear, curvilinear, and humped responses. To prevent overfitting, we limited the number of basis functions for smoothing to four. An analogous analysis was performed for the effect of mean summer temperature (June to August) and the timing of peak flowering on mean temperature during flowering (here, y represents the mean temperature during flowering and t represents summer temperature).

The intensity of exposure to freezing conditions was an index based on the addition of absolute temperature values when the temperature fell below 0°C from hourly temperature records from the 20 days before the snowmelt reached 50% (when plants were deemed sufficiently uncovered from snow to be exposed to ambient temperature; Pedersen et al. 2012) until the onset of flowering divided by the duration of this period. The mean temperature during flowering was estimated as the mean temperature between the onset and end of flowering at the plot level for each plot in each year. All temperature variables just described were extracted from data of hourly air temperature 2 m above the ground obtained from an automatic climate station located within 2 km of all plots.

Phenological characteristics and flower abundance

We used generalized linear models to assess the effect of phenology on flower abundance at the plot level. We investigated the relationship between the timing of peak flowering and seasonal flower abundance for each species. We evaluated three alternative hypotheses: no relationship, a linear relationship, and a quadratic relationship between flower abundance and the timing of flowering. The relative support for each model was evaluated using model selection with $\mathrm{AIC_c}$ (Burnham and Anderson 2002). All analyses were performed using R version 3.0.1 (R Development Core Team 2013), packages gamm4, AICcmodavg, MuMIn, and nlme.

We used both plot-level and temporal replication for our analyses because both plot and year can affect the timing of flowering. An important question is whether to model plot and year as random effects. We found a strong association between plot and year and timing of flowering for all species (Appendix C: Table C1). Random effects models are based on the assumption that main effects and random effects are not correlated. High correlation of this nature can lead to biased parameter estimates (Ebbes et al. 2004, Gelman and Hill 2007, Kim and Frees 2007); see Appendix C: Fig. C1. We therefore focus primarily on the results of fixed-effect models with timing of flowering as a predictor. We believe that this is the best approach, given that plot-based and interannual variation in the timing of snowmelt are the key factors controlling timing of flowering and there is a clear potential for a mechanistic link between timing of flowering and our response variables (exposure to freezing, temperature during flowering, and flower output), but no direct mechanistic link via plot or year. However, for further reference we also present results for each plot separately for each analysis (Appendix B), as well as analogous models with random effects of plot and year (Appendix C). We also provide further discussion of this modeling approach (Appendix C).

Here we briefly describe any differences between our fixed-effects analysis described in the *Results* and the random effects analysis in Appendix C. In all cases, inclusion of random plot and year effects reduces our ability to discern between models as a result of covariation with timing of flowering and shrinkage to the mean, which decreases the observed effects. However, in the case of our assessment of contribution of timing of flowering to temperatures during development, similar trends are maintained in most cases (for further discussion, see Appendix C and Table C2). In the case of our analysis of the association between timing of flowering and flower abundance, where trends are much weaker, this shrinkage causes a reversion to null models

Table 1. Summary of generalized additive models of exposure of four Greenland plants (*Cassiope tetragona*, *Dryas octopetala/integrifolia*, *Papaver radicatum*, and *Salix arctica*) to freezing spring temperature (left) and mean summer temperature during flowering (right).

	Spring (freezing) temperature			Summer (flowering) temperature		
Species and model	$\mathrm{AIC_c}$	Deviance explained	Spring temp. (degree-h < 0°C/°C)	$\mathrm{AIC_c}$	Deviance explained	Summer temp. (°C during flowering/°C)
Cassiope						
Temperature	435.32	5.7%	0.92 ± 0.52	173.84	40.3%	0.96 ± 0.16
Temperature + timing of flowering	387.29	65.2%	0.33 ± 0.33	**165.95**	**50.6%**	**1.13 ± 0.16**
Timing of flowering	**385.75**	**64.7%**		201.30	0.8%	
Null	436.24	0.0%		199.46	0.0%	
Dryas						
Temperature	785.27	0.0%	0.05 ± 0.95	320.60	23.8%	0.99 ± 0.20
Temperature + timing of flowering	**678.87**	**74.9%**	**−0.98 ± 0.49**	**267.62**	**65.4%**	**1.03 ± 0.15**
Timing of flowering	680.89	73.5%		305.36	41.9%	
Null	783.12	0.0%		340.45	0.0%	
Papaver						
Temperature	398.37	0.8%	0.24 ± 0.36	164.20	43.1%	1.47 ± 0.24
Temperature + timing of flowering	333.61	73.8%	−0.09 ± 0.18	**158.20**	**55.0%**	**1.33 ± 0.28**
Timing of flowering	**331.40**	**73.6%**		175.97	31.7%	
Null	396.56	0.0%		192.36	0.0%	
Salix						
Temperature	760.21	0.0%	−0.25 ± 1.86	155.24	64.7%	1.03 ± 0.09
Temperature + timing of flowering	717.28	49.1%	−1.40 ± 1.37	**120.61**	**78.8%**	**0.96 ± 0.07**
Timing of flowering	**716.14**	**48.1%**		206.51	40.6%	
Null	758.04	0.0%		230.22	0.0%	

Notes: Models with the lowest $\mathrm{AIC_c}$ values for each model set are indicated in bold. The percentage of deviance explained by each model is shown. For each model, estimates (± SE) for the effects of spring and summer temperatures are also shown, respectively, as the degree-hours below 0°C for each °C change in spring temperature, and as the temperature (°C) during flowering per °C change in summer temperature.

(Appendix C: Table C3). However, we assert that the strong influence of plot and year on timing of flowering compromises the validity of estimates from these random-effects models.

Results

Phenology and temperature during flower development

Interannual variation in spring temperature did not substantially affect freezing conditions experienced prior to flowering in *Cassiope*, *Papaver*, or *Salix* (Table 1). In *Dryas*, spring temperature was included in the best model under $\mathrm{AIC_c}$; however, the improvement in deviance explained by this model compared to the improvement explained by the model involving solely the timing of flowering was very small (difference = 1.4%). For all species, there was a curvilinear relationship between the timing of flowering and exposure to freezing temperatures. This relationship was characterized by an acceleration of exposure to freezing temperatures with earlier timing of flowering (Fig. 2).

In all species, the interannual variation in summer temperature had a strong positive effect on the mean temperature during flowering (Table 1, Fig. 3). A contribution of the timing of flowering to temperature during flowering was also evident in all four species (Table 1, Fig. 3). The mean temperature over the flowering period showed a positive linear relationship with the date of peak flowering for *Cassiope* and *Salix* (Table 1, Fig. 3). In *Dryas* and *Papaver*, the relationship between the mean temperature over the flowering period and the timing of peak flowering was more humped. In *Dryas*, both early and late flowering were associated with a cooling effect, whereas in *Papaver*, this cooling effect was most evident during late flowering (Table 1, Fig. 3).

Phenological characteristics and flower abundance

For all species, seasonal flower abundance was related quadratically to the date of peak flowering (Fig. 4, Table 2); the most parsimonious model selected by $\mathrm{AIC_c}$ was that with a quadratic relationship between the timing of flowering and flower abundance. We found no evidence of plot effects; however, plots did differ in the range of the timing of flowering, such that when evaluated individually, certain trends appeared to differ among plots. For example, late-flowering plots were sometimes observed to exhibit a negative effect of flowering timing on flower abundance, whereas early-flowering plots sometimes appeared to exhibit a positive association between the two variables; this latter pattern was particularly evident in *Dryas* (Appendix B: Figs. B9–B12).

The estimated date of peak flowering associated with maximum flower abundance differed among species. The date was similar for *Cassiope*, *Dryas*, and *Salix* but much later for *Papaver* (*Cassiope* day of the year, DOY = 195 or 14 July, *Dryas* DOY = 196 or 15 July, *Papaver* DOY = 213 or 1 August, *Salix* DOY = 189 or 8 July). *Cassiope* and *Papaver* exhibited advancement of the

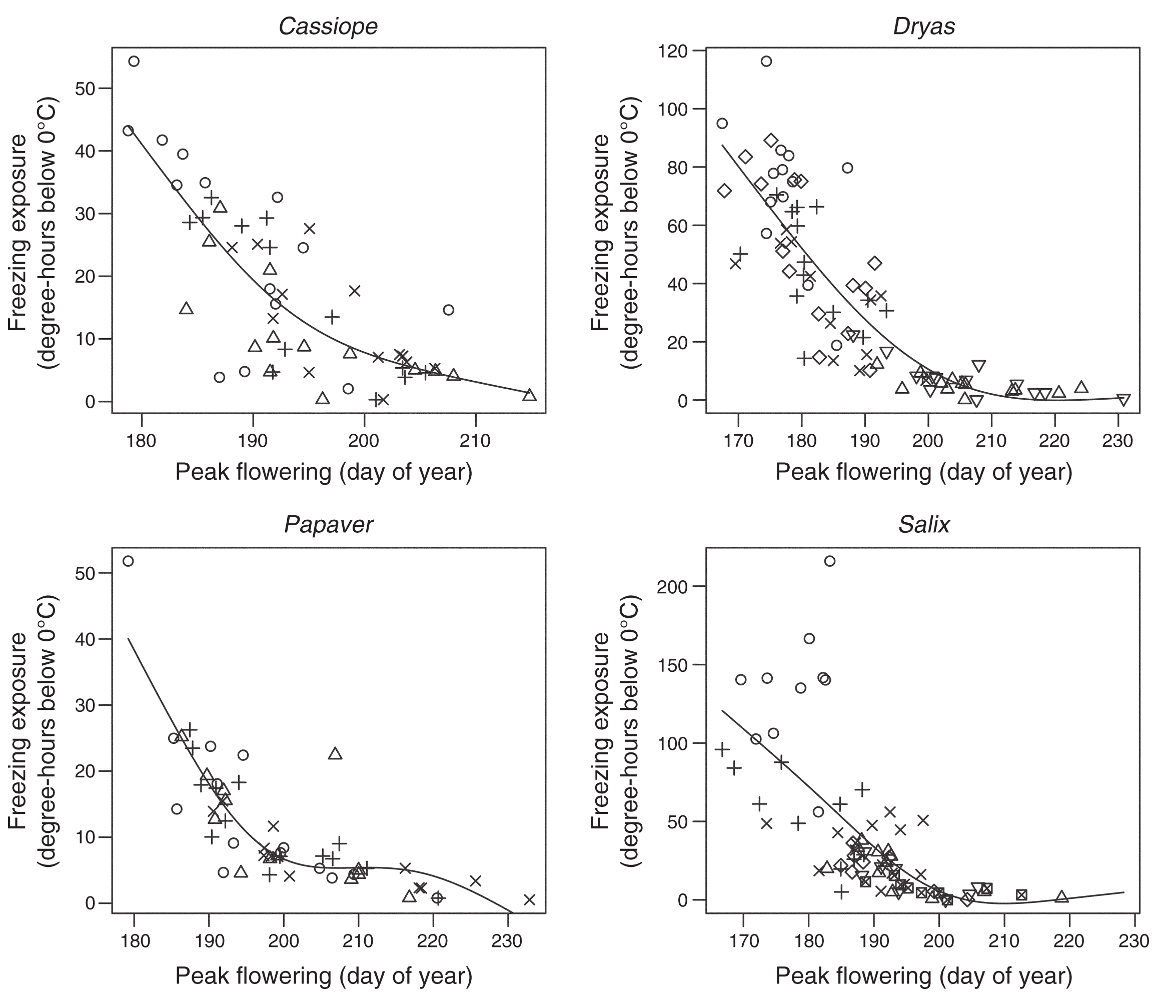


Fig. 2. Relationship between the date of peak flowering (day of year, where day 1 is 1 January) and exposure to freezing conditions (degree-hours below 0°C prior to flowering onset) in four flowering species from Zackenberg, Greenland: *Cassiope tetragona*, *Dryas octopetala/integrifolia*, *Papaver radicatum*, and *Salix arctica*. Different symbols denote different plots. The line shows the smoothed relationship fitted using a generalized additive model.

timing of flowering, increasingly ahead of the date predicted to cause maximal flowering (Appendix D: Fig. D1). In *Dryas*, although a general advancement in the date of peak flowering was observed, some plots consistently flowered later than our predicted timing of flowering where flower abundance should be maximal (Appendix D: Fig. D1). In *Salix*, fluctuations in timing of flowering around the date predicted to result in maximal flower abundance were observed.

Discussion

Our results demonstrate that the timing of flowering can affect the temperature conditions experienced by plants during flower development. Here we briefly summarize these results before discussing their broader implications. Earlier flowering was associated with an increased exposure to freezing conditions early in flower development. This suggests that advancements in flowering may increase risk of freezing damage. We also found humped relationships between the timing of flowering and the temperature during flowering. These results suggest that the influence of phenology on the weather experienced during flowering is likely to depend on context, depending on whether events occur prior to or after seasonal temperature maxima. Both increased exposure to freezing temperatures and altered temperatures during flowering may influence how reproductive effort is affected by climate change. We found a weak association between flowering abundance and phenology, with reduced abundance associated with both early and late flowering. This result suggests that the net effect of advancement of flowering may be reduced flower abundance, possibly due to increased frost damage, particularly in areas where flowering already occurs relatively early.

In the Arctic, there are potentially two contrasting effects of climate change on the timing of snowmelt. In the first scenario, warming temperatures instigate more

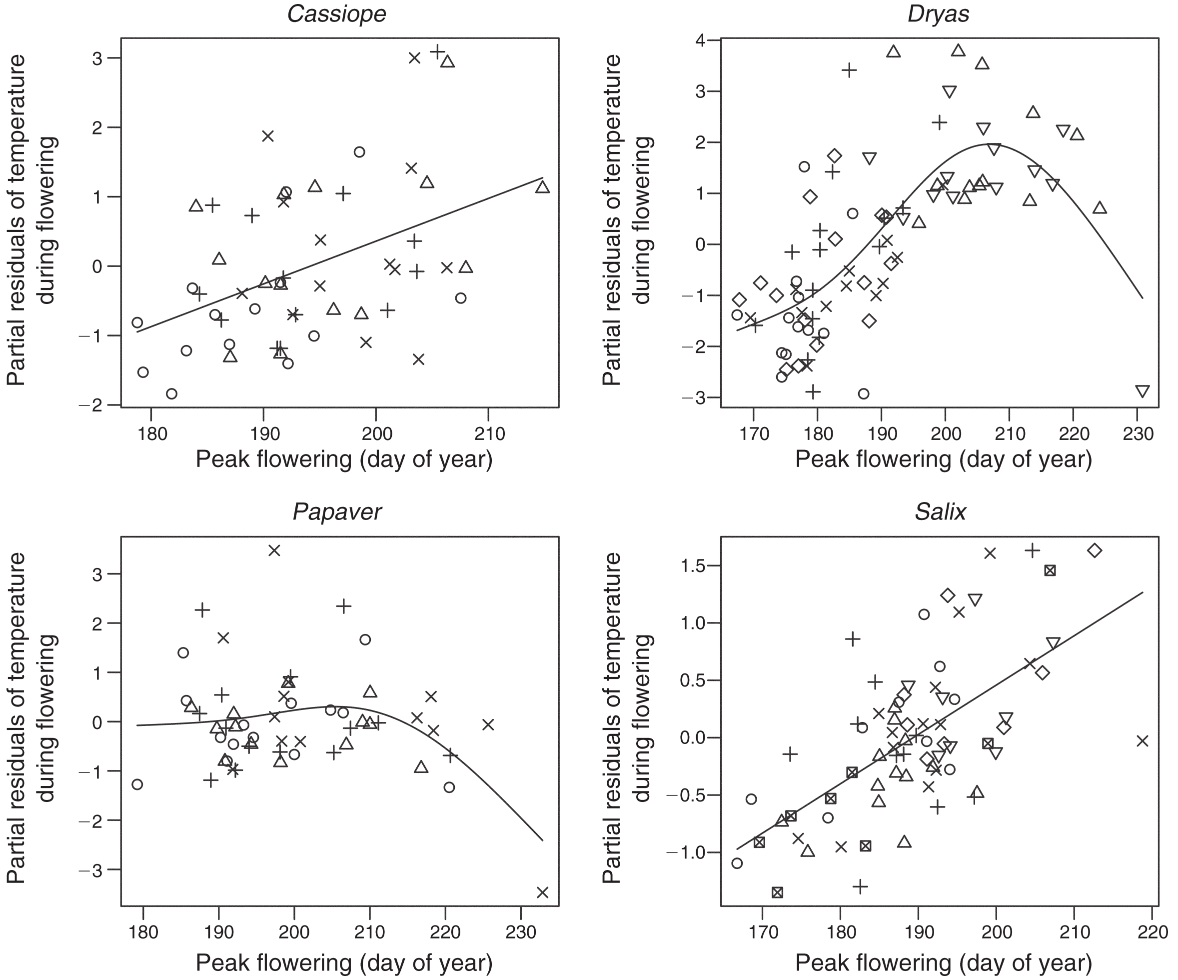


FIG. 3. Effect of the date of peak flowering on mean temperature during flowering in four species of flowering plants from Zackenberg, Greenland. The relationship between the timing of peak flowering and partial residuals is shown, with the linear regression effect of mean summer temperature on mean temperature during flowering removed. Different symbols denote different plots. The line shows the smoothed relationship fitted using a generalized additive model.

rapid and advanced snowmelt. In the second, increased precipitation during the winter, falling as snow, creates a deeper snowpack, resulting in delayed snowmelt. The predominant current trend is toward earlier melt (Dye 2002, Stone et al. 2002, Hinkler et al. 2008), although considerable regional variation is observed (Liston and Hiemstra 2011). In areas with substantial increase in precipitation, the balance between snow depth and temperature may result in delayed snowmelt (Hinkler et al. 2008). Our results indicate that either advances or delays in snowmelt might affect the weather conditions that many species experience during life history events via their effects on the timing of flowering. Although both advanced- and delayed-snowmelt scenarios might occur, we focus on the implications of the predominant trend (i.e., advancing phenology) currently observed at our study site.

There are two key implications of the temperature experienced during development for the species in the present study. The first is that earlier flowering should increase the likelihood of exposure to freezing temperatures prior to flowering. When phenology is advanced to earlier in the spring, frost damage or cold effects may cause damage to vegetation as a result of the combination of advanced phenologies and increasing variance in temperature (Augspurger 2013). In snow-dominated ecosystems, snow cover provides insulation and moderates sub-nivean temperatures, reducing exposure to climatic extremes. Increased frost damage to buds and flowers can occur as a result of advanced snowmelt and early exposure to freezing ambient temperatures (Inouye 2008); however, other cold-related processes, such as desiccation in the absence of protective snow cover and in largely frozen soils (Billings and Mooney 1968), may also contribute to the costs of early exposure to the elements. In mountain habitats, increased frost damage has been observed as a result of advanced phenology associated with snowmelt and has been identified as

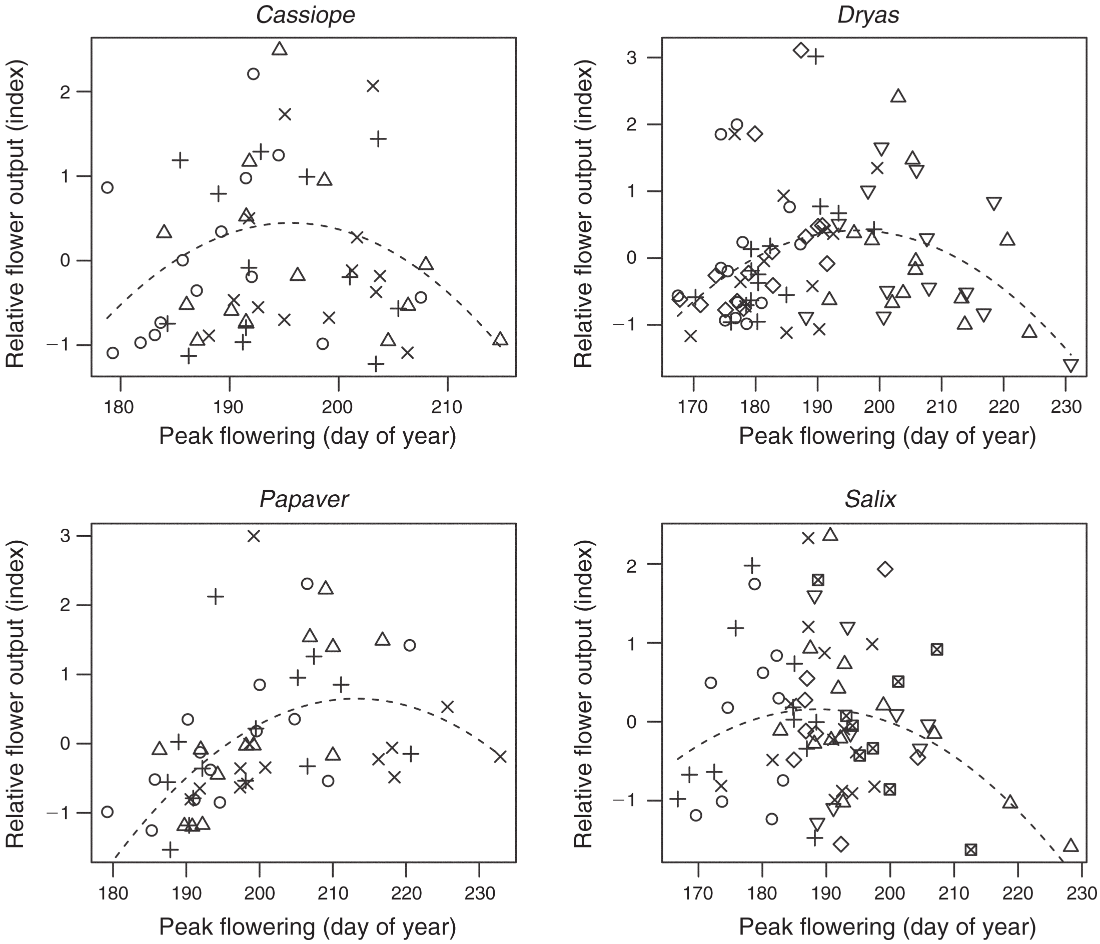


FIG. 4. Effect of the date of peak flowering on seasonal flower abundance in four arctic flowering plant species in Zackenberg, Greenland. Standardized scores reflect the number of standard deviations in flower abundance in a given year that are above the plot mean. The stippled line shows the response across all data from a quadratic regression. Different symbols represent different plots.

TABLE 2. Summary and comparison of alternate models of the association between the timing of flowering and flower abundance for four Greenland plants; effect sizes are given.

Species and model type	Quadratic term	Linear term	Intercept term	AIC_c	ΔAIC_c
Cassiope					
Quadratic	**−0.0040 ± 0.0017**	**1.5532 ± 0.6504**	**−151.47 ± 63.46**	**151.33**	**0.00**
Linear		0.0005 ± 0.0162	−0.10 ± 3.15	154.71	3.39
Null			−0.01 ± 0.13	152.47	1.14
Dryas					
Quadratic	**−0.0015 ± 0.0004**	**0.6074 ± 0.1717**	**−59.17 ± 16.68**	**222.55**	**0.00**
Linear		0.0038 ± 0.0077	−0.69 ± 1.46	232.26	9.71
Null			0.02 ± 0.11	230.36	7.81
Papaver					
Quadratic	**−0.0021 ± 0.0007**	**0.9065 ± 0.3039**	**−95.98 ± 31.00**	**142.62**	**0.00**
Linear		0.0372 ± 0.0109	−7.42 ± 2.18	148.33	5.71
Null			0.03 ± 0.14	157.05	14.42
Salix					
Quadratic	**−0.0013 ± 0.0005**	**0.4955 ± 0.1970**	**−46.59 ± 19.02**	**200.46**	**0.00**
Linear		−0.0115 ± 0.0102	2.18 ± 1.93	204.84	4.38
Null			0.00 ± 0.11	203.98	3.51

Note: For each species, the best model, based on AIC_c, is indicated in boldface.

PLATE 1. Photographs of the four study species in Zackenberg, Greenland: (top left) *Cassiape tetragona*, (top right) *Dryas integrifolia/octopetala*, (bottom left) *Papaver radicatum*, and (bottom right) *Salix arctica*. Photo credits: T. T. Høye.

impacting floral abundance (Mølgaard and Christensen 1997, Inouye 2008, Wipf et al. 2009). Evidence of frost sensitivity has been reported in the species assessed in the present study (Jones et al. 1997, Mølgaard and Christensen 1997, Semenchuk et al. 2013). Although direct evidence of frost damage on flowers has not been observed at our study site (N. M. Schmidt, *personal observation*), the budding life history stage may also be frost sensitive (Bokhorst et al. 2010). The present study highlights the potential for freezing conditions in early floral development under advanced phenology, which may have similar negative effects on fitness. Indeed, we found earlier flowering to be associated with lower floral abundance in all species. It is during this pre-flowering period that the potential for phenologically driven climatic mismatches (due to frost damage) appears to be most pronounced.

The second implication is that for the species in the present study, earlier flowering should increasingly shift the temporal window during which flowering occurs ahead of the seasonal temperature maxima. The seasonal maximum temperature in Zackenberg is reached approximately on day 200–210 of the year (Pedersen et al. 2012). In species such as *Cassiope* and *Salix*, most peak flowering dates occurred prior to the seasonal temperature maxima (Appendix D: Fig. D2), and we observed a positive linear relationship between the timing of flowering and the realized mean temperature during flowering. This should result in lower temperatures experienced during flowering under advanced phenology, and it may have a moderating effect, reducing the experienced warming relative to that predicted from interannual temperature increases alone. In *Dryas* and *Papaver*, most flowering occurred after the seasonal temperature maxima; therefore, the advancing phenology initially shifted the flowering window closer to the seasonal temperature maxima, a pattern that should exacerbate warming. In *Dryas* in particular, further advancement of the timing of flowering ahead of the seasonal temperature maxima had a cooling effect similar to that observed in *Cassiope* and *Salix*. The one species excepted from this cooling effect might be *Papaver*, for which earlier flowering does not yet appear to substantially reduce the phenological contribution to temperature during flowering. For species that generally flower after the seasonal temperature maxima (i.e., later than the species in the present study), a shift to earlier flowering should exacerbate any increases in temperature, leading to warmer temperatures during flowering than expected from interannual temperature alone.

Given that the net temperature experienced during development is a combination of the effects of the interannual temperature trends and the timing of flowering, projecting how these will change in the future will depend on both the extent of future increases in temperature and the rate of advancement in timing of flowering. We found the exposure to freezing conditions to be much more strongly associated with the timing of flowering than to spring temperature; thus, provided that the timing of flowering continues to advance, we expect increases in exposure to freezing temperatures prior to flowering. However, with sufficient interannual temperature rise, or an end to advancements in the timing of flowering (e.g., due to a limit to phenological change; Iler et al. 2013) this relationship may change. Temperatures experienced during flowering were affected by both summer temperature and timing of flowering, and therefore should be more sensitive to trends in both interannual temperature and timing of flowering.

Altered temperatures during flowering might have fitness effects on plants. Temperature may affect flower abundance, and both increased and decreased flower abundance have been reported in response to warming (Arft et al. 1999, Inouye 2008). The temperature experienced during flowering can affect flower longevity. Pollinator-excluded flowers warmed with open-top chambers were found to exhibit reduced longevity, which should reduce opportunities for pollination (Arroyo et al. 2013). Pollinator activity also may be affected by temperature. In the subarctic, cooler temperatures led to reduced pollinator activity (Bergman et al. 1996), which may reduce pollination success. The ways in which such processes are affected by the phenological contributions to conditions during flowering that we describe will depend on the net effect of interannual temperatures and phenological contributions to temperature during flowering. The effects will depend on the timing of flowering (preceding or following the seasonal temperature maxima), and the amplitude of seasonal temperature trends.

At larger scales, phenological shifts to different seasonal climate windows will also affect the climate associations of species, both spatially and temporally. Currently, most species distribution models do not account for the potential effects of shifting phenology on species' spatial climate interactions. Although phenology is starting to be incorporated into mechanistic species distribution models (e.g., Chuine 2010), we are not aware of any models that incorporate phenology–weather feedbacks. When projecting future distributions, it may also be important to consider how species' climatic niches may change temporally as phenology shifts.

Within the range of phenologies observed, both early and late flowering were associated with lower flower abundance, suggesting that further advancements in flowering should reduce flower abundance (Fig. 1). In these species, the flowering abundance is probably a response to a range of complex weather-related and physiological factors. Within the current range of flowering phenologies, there may be an ideal (generally intermediate) timing of flowering associated with maximizing flower abundance. Increased exposure to freezing temperatures is the most likely cause of reduced flower abundance under earlier flowering, and we found these conditions in our study. Alternative explanations include the potential for a correlation between early flowering and midwinter snowmelt. Extreme winter warming events have been associated with low flower abundance in the following summer in some arctic species (Semenchuk et al. 2013). Following extreme winter warming, low snowpack and early flowering is likely. As such, early flowering and low floral abundance might be correlated due to winter warming effects. In both cases, we would predict an increasing tendency toward lower flower abundance under warming temperatures. However, predictions may differ slightly between these two mechanisms of damage to buds, depending on future shifts in phenology. Some evidence suggests that advances in the timing of flowering may reach a limit beyond which no further advances in flowering timing would occur (Iler et al. 2013). In such a scenario, we would predict that freezing exposure during the spring may lessen as temperatures warm without further advancements in flowering. However, in the case of winter warming, negative effects on flowering would be expected to continue regardless of whether phenological advances continue.

The combined effects of extrinsic climatic forcing and phenological responses in communities are likely to have strong effects on ecosystem processes and community composition, in particular by inducing or mitigating climatic mismatches in climate-sensitive processes such as reproduction. Contingent effects on fitness, population dynamics, and interspecific interactions are likely. The timing of flowering and flower abundance can determine the success of species that rely on floral resources. Pollinators and herbivores are often dependent upon the timing of flowering, with phenological mismatches having the potential to alter the functioning of the pollinator community (Memmott et al. 2007, Aldridge et al. 2011, Rafferty and Ives 2012). Floral abundance also affects pollinator densities and flower visitation rates (Essenberg 2013), and changes in flower abundance can have long-term effects on community composition via effects on plant reproductive success and pollinators and floral consumers. Here, we demonstrate that phenology contributed to temperature conditions experienced during floral development, and we find phenology-related variation in reproductive effort. Our results indicate that under climatic change and shifting phenology, the realized climatic niche of species and the associated population dynamics may be modified by how phenological timing contributes to the weather conditions that species experience.

Acknowledgments

This article is a contribution by the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by the Aarhus University Research Foundation under the AU Ideas program. We thank David Inouye and an anonymous reviewer for helpful comments on the manuscript. Monitoring data for this paper were provided by the BioBasis and ClimateBasis program run by Department of Bioscience, Aarhus University, Denmark and Asiaq, Greenland. The programs are part of the Greenland Environmental Monitoring (GEM) Program (www.g-e-m.dk) and financed by the Danish Environmental Protection Agency, Danish Ministry of the Environment, and the Greenland Government.

Literature Cited

Aldridge, G., D. W. Inouye, J. R. K. Forrest, W. A. Barr, and A. J. Miller-Rushing. 2011. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. Journal of Ecology 99:905–913.

Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of the Royal Society: B 279:3843–3852.

Arft, A. M., et al. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. Ecological Monographs 69:491–511.

Arroyo, M. T., L. S. Dudley, G. Jespersen, D. A. Pacheco, and L. A. Cavieres. 2013. Temperature-driven flower longevity in a high-alpine species of *Oxalis* influences reproductive assurance. New Phytologist 200:1260–1268.

Augspurger, C. K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. Ecology 94:41–50.

Bergman, P., U. Molau, and B. Holmgren. 1996. Micrometerological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. Arctic and Alpine Research 28:196–202.

Bernal, M., M. Estiarte, and J. Peňuelas. 2011. Drought advances spring growth phenology of the Mediterranean shrub *Erica multiflora*. Plant Biology 13:252–257.

Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biological Reviews 43:481–529.

Bokhorst, S., J. W. Bjerke, M. P. Davey, K. Taulavuori, E. Taulavuori, K. Laine, T. V. Callaghan, and G. K. Phoenix. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. Physiologia Plantarum 140:128–140.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Chuine, I. 2010. Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B 365:3149–3160.

Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science 180: 157–167.

Dunne, J. A., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. Ecological Monographs 73:69–86.

Dye, D. G. 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. Hydrological Processes 16:3065–3077.

Ebbes, P., U. Böckenholt, and M. Wedel. 2004. Regressor and random-effects dependencies in multilevel models. Statistica Neerlandica 58:161–178.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884.

Essenberg, C. J. 2013. Scale-dependent shifts in the species composition of flower visitors with changing floral density. Oecologia 171:187–196.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Helm, B., R. Ben-Shlomo, M. J. Sheriff, R. A. Hut, R. Foster, B. M. Barnes, and D. Dominoni. 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. Proceedings of the Royal Society B 280: 20130016.

Hinkler, J., B. U. Hansen, M. P. Tamstorf, C. Sigsgaard, and D. Petersen. 2008. Snow and snow-cover in central Northeast Greenland. Pages 175–195 *in* H. Meltofte, T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch, editors. High-Arctic ecosystem dynamics in a changing climate. Advances in Ecological Research. Volume 40. Academic Press, New York, New York, USA.

Høye, T. T., S. M. Ellebjerg, and M. Philipp. 2007*a*. The impact of climate on flowering in the High Arctic: The case of *Dryas* in a hybrid zone. Arctic, Antarctic, and Alpine Research 39: 412–421.

Høye, T. T., E. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007*b*. Rapid advancement of spring in the High Arctic. Current Biology 17:R449–R451.

Huisman, J., H. Olff, and L. F. M. Fresco. 1993. A hierarchical set of models for species response analysis. Journal of Vegetation Science 4:37–46.

Hulme, P. E. 2011. Contrasting impacts of climate-driven flowering phenology on changes in alien and native plant species distributions. New Phytologist 189:272–281.

Iler, A. M., T. T. Høye. D. W. Inouye, and N. M. Schmidt. 2013. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? Philosophical Transactions of the Royal Society B 368:20120489.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Jansen, F., and J. Oksanen. 2013. How to model species responses along ecological gradients—Huisman–Olff–Fresco models revisited. Journal of Vegetation Science 24:1108–1117.

Jones, M. H., C. Bay, and U. Nordenhall. 1997. Effects of experimental warming on arctic willows (*Salix* spp.): A comparison of responses from the Canadian high Arctic, Alaska Arctic and Swedish Subarctic. Global Change Biology 3(S1):55–60.

Kim, J. S., and E. W. Frees. 2007. Multilevel modelling and correlated effects. Psychometrika 47:505–533.

Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489:554–557.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20:170–182.

Liston, G. E., and C. A. Hiemstra. 2011. The changing cryosphere: Pan-Arctic snow trends (1979–2009). Journal of Climate 24:5691–5712.

McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resource. Ecology 93: 1987–1993.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10:710–717.

Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B 365: 3177–3186.

Molau, U. 1993. Relationships between flowering phenology and life history strategies in tundra plants. Arctic and Alpine Research 25:391–402.

Molau, U., U. Nordenhäll, and B. Eriksen. 2004. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. American Journal of Botany 92:422–431.

Mølgaard, P., and K. Christensen. 1997. Response to experimental warming in a population of *Papaver radicatum* in Greenland. Global Change Biology 3:116–124.

Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton, L. E. B. Kruuk, and T. H. Clutton-Brock. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. Global Change Biology 17:2455–2469.

O'Neil, P. 1999. Selection on flowering time: An adaptive fitness surface for nonexistent character combinations. Ecology 80: 806–820.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466: 482–485.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Pedersen, M. R., et al. 2013. Zackenberg Basic: The ClimateBasis and GeoBasis programme. Pages 13–29 *in* L. M. Jensen, M. Rasch, and N. M. Schmidt, editors. Zackenberg Ecological Research Operations, 18th Annual Report, 2012. Aarhus University, DCE–Danish Centre for Environment and Energy, Roskilde, Denmark.

Peñuelas, J., and I. Filella. 2001. Responses to a warming world. Science 294:793–795.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B 363:2367–2373.

Post, E., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proceedings of the Royal Society B 275:2005–2013.

R Development Core Team. 2013. R Version 3.0.1. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rafferty, N. E., and A. R. Ives. 2012. Pollinator effectiveness varies with experimental shifts in flowering time. Ecology 93: 803–814.

Reed, T. E., S. Jenouvrier, and M. E. Visser. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. Journal of Animal Ecology 82:131–144.

Saino, N., et al. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278:835–842.

Schmidt, N. M., L. H. Hansen, J. Hansen, T. B. Berg, and H. Meltofte. 2012. BioBasis Manual. Conceptual design and sampling procedures of the biological monitoring programme within Zackenberg Basic. 15th edition. Zackenberg Ecological Research Operations. Department of Bioscience, Aarhus University, Roskilde, Denmark.

Semenchuk, P. R., B. Elberling, and E. J. Cooper. 2013. Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. Ecology and Evolution 3:2586–2599.

Singer, M. C., and C. Parmesan. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philosophical Transactions of the Royal Society B 365:3161–3176.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match–mismatch to the environment. Proceedings of the National Academy of Sciences USA 99:13379–13381.

Stone, R. S., E. G. Dutton, J. M. Harris, and D. Longenecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research: Atmospheres 107:ACL 10-1–ACL 10-13.

Thórhallsdóttir, T. E. 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114:43–49.

Vaganov, E. A., M. K. Hughes, A. V. Kirdyanov, F. H. Schweingruber, and P. P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400:149–151.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B 272:2561–2569.

Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society B 268:289–294.

Wipf, S., and C. Rixen. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29:95–109.

Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94:105–121.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 13:1–10.

Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proceedings of the National Academy of Sciences USA 107:22151–22156.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/14-0338.1.sm