

Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic

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Advancing phenology in response to global warming has been reported across biomes^{1,2}, raising concerns about the temporal uncoupling of trophic interactions^{3,4}. Concurrently, widely reported flower visitor declines have been linked to resource limitations⁵. Phenological responses in the Arctic have been shown to outpace responses from lower latitudes and recent studies suggest that differences between such responses for plants and their flower visitors could be particularly pronounced in the Arctic^{1,6}. The evidence for phenological uncoupling is scant because relevant data sets are lacking⁷ or not available at a relevant spatial scale⁸. Here, we present evidence of a climate-associated shortening of the flowering season and a concomitant decline in flower visitor abundance based on a long-term, spatially replicated (1996–2009) data set from high-Arctic Greenland. A unique feature of the data set is the spatial and temporal overlap of independent observations of plant and insect phenology. The shortening of the flowering season arose through spatial variation in phenological responses to warming. The shorter flowering seasons may have played a role in the observed decline in flower visitor abundance. Our results demonstrate that the dramatic climatic changes currently taking place in the Arctic are strongly affecting individual species and ecological communities, with implications for trophic interactions.

Topographic heterogeneity creates pronounced spatial variability in timing of flowering, particularly in snow-dominated environments^{9–11}. Hence, landscape scale duration of the flowering season is an integration of potentially different local scale flowering times and is sensitive to changes in the spatial variability of flowering times¹². For example, if patches of early flowering individuals advance their flowering time at a faster pace than patches of late flowering individuals in response to climate change then the overall flowering season becomes extended. In contrast, if local patches of late flowering individuals advance their flowering time at a faster pace than local patches of early flowering individuals then the overall flowering season becomes shorter (Fig. 1). In the latter case, a climate-induced reduction of the spatial variation in the timing of flowering translates into an earlier and shorter flowering season. To track such changes in resource availability, flower visitors must simultaneously advance and shorten their flight season^{8,13}. Plants and arthropods are currently undergoing dramatic phenological changes in the High Arctic¹. Combined with the strong seasonality of high latitude ecosystems, this sug-

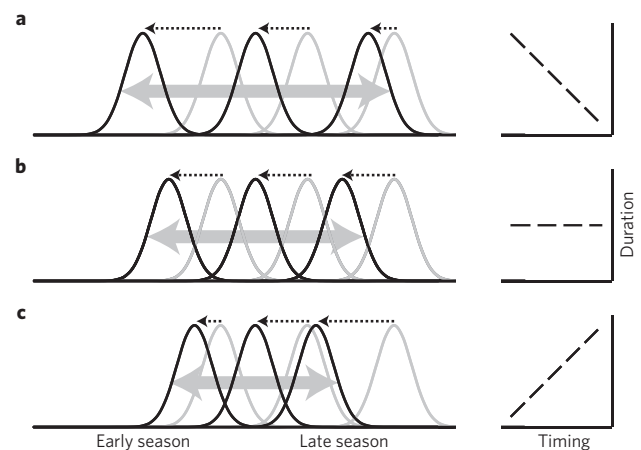


Figure 1 | Conceptual model of how differential changes in timing of a phenological event among local populations may affect the duration of the event at the landscape scale. The model is general for life history events and applies, for instance, to the timing and duration of flowering. In **a**, local populations of early flowering individuals advance faster than local populations of late flowering individuals and vice versa in **c**. In **b**, all populations advance at the same rate. The magnitude of change in early, intermediate or late populations or species under each scenario is given by hatched arrows above each bell-shaped curve. The different scenarios of local population responses result in **a**, longer, **b**, unaltered or **c**, shorter overall flowering seasons in response to earlier flowering (represented by wide grey arrows) at the landscape scale. Grey bell-shaped curves in each panel represent the baseline timing of flowering for each population. Associated x–y plots (right) illustrate this relationship between community-wide timing of flowering and duration of flowering. When applying the conceptual model to assessments of changes in resource availability for flower visitors and regarding each bell-shaped curve as an individual plant species, it is assumed that flower visitors do not discriminate among flower resources provided by each plant species. The distributions can take other forms than the bell-shape presented in the figure (for example, skewed distributions), which would result in more complex responses of the duration at the landscape scale.

gests that interactions between high-Arctic plants and flower-visiting insects may be particularly vulnerable to phenological uncoupling^{1,6,14}.

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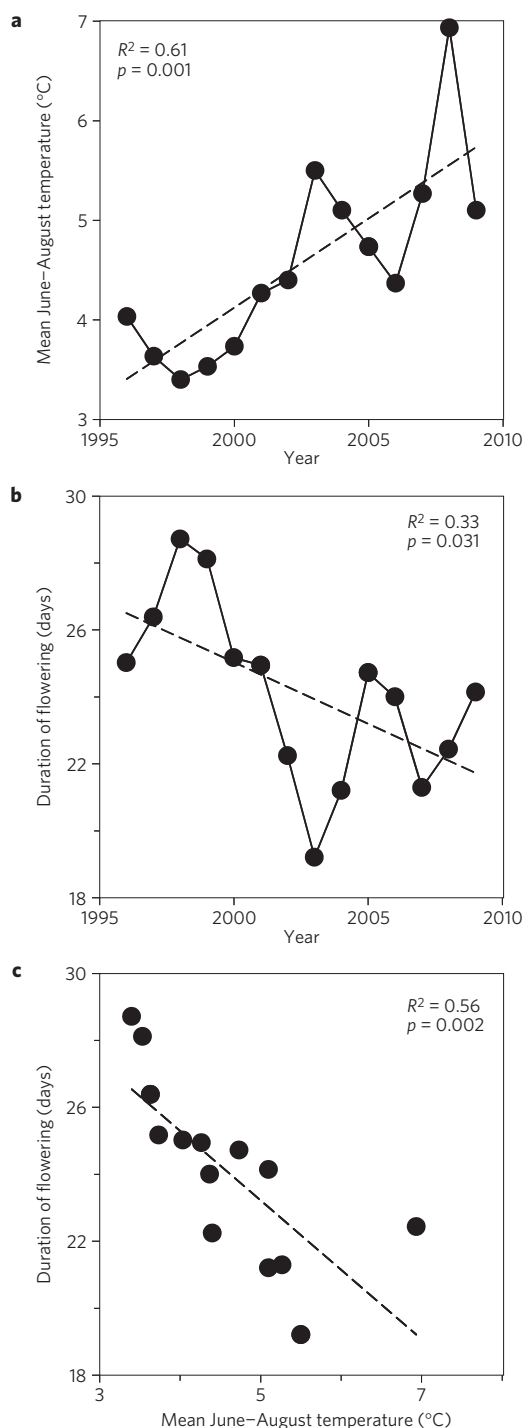


Figure 2 | Temporal trends of temperature, duration of the community-wide flowering season and their relationship. **a**, Average air temperatures in June–August measured at the climate station centrally in the study area during 1996–2009 at Zackenberg, North-East Greenland. **b**, Duration of the community-wide flowering season during 1996–2009. **c**, The relationship between the duration of the community-wide flowering season and average air temperatures in June–August during 1996–2009. For each panel, the hatched line is the regression line. The coefficient of determination (R^2) and p -value of the linear regression models are presented.

The conceptual model in Fig. 1 identifies how local variation in the strength of phenological responses can in theory affect the relationship between the timing and duration of phenological

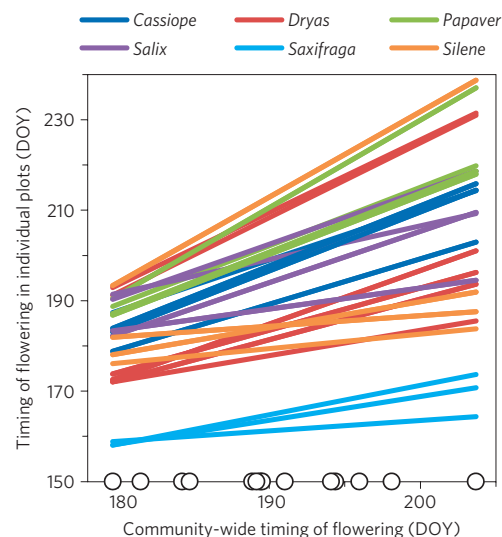


Figure 3 | Relationship between plot-specific timing of flowering and community-wide timing of flowering across years. Regression lines of the relationship between the timing of flowering (mean of onset and end of flowering) for each plot in all six plant species (*Cassiope tetragona*, *Dryas octopetala*, *Papaver radiculatum*, *Salix arctica*, *Saxifraga oppositifolia* and *Silene acaulis*) and the community-wide timing of flowering during 1996–2009. The open symbols on the x axis indicate the annual observations of community-wide timing of flowering on which the regression lines were estimated. When the community-wide timing of flowering is early, the timing of flowering across individual plots is much more temporally synchronized than when community-wide timing of flowering is late. Hence, community-wide flowering seasons are shorter in years with early community-wide timing of flowering. DOY stands for day of the year.

events at a larger spatial scale. Here, we demonstrate how observations of flowering phenology fit the theoretical predictions using a comprehensive data set on the dominating plant species from a study site in high-Arctic Greenland. Specifically, we do this by showing how local scale changes in flower phenology affect the duration of the flowering season at the spatial scale relevant for interacting flower visitors. Finally, we extend our analyses to study the effects of such changes in flowering season duration and find concomitant changes in the abundance of two families of important flower visitors¹⁵.

The local climate at our site has changed dramatically during the study period (1996–2009). Near-surface air temperature measured within the study area and averaged across June, July and August increased significantly (slope = 1.8 °C/decade, $F_{1,12} = 14.27$, $R^2 = 0.61$, $p < 0.001$, Fig. 2a) and the timing of snowmelt occurred earlier, although not significantly (slope = –12.8 days/decade, $F_{1,12} = 2.99$, $R^2 = 0.20$, $p = 0.11$). Over the same period, the community-wide duration of flowering (that is, the flowering season) shortened significantly at the landscape scale (slope = –3.7 days/decade, $F_{1,12} = 5.98$, $R^2 = 0.33$, $p = 0.031$, Fig. 2b). Shorter flowering seasons were associated with higher temperatures during June–August across all species (slope = –2.1 days °C^{–1}, $F_{1,12} = 15.23$, $R^2 = 0.56$, $p = 0.002$, Fig. 2c) and similar responses were identified in models of individual species, although the strengths of the responses varied among species (Supplementary Table S1).

We found that variation in the landscape scale duration of flowering was predominantly influenced by the phenology of late flowering plants. The slope of the regression between the timing of flowering in individual plots and the community-wide timing of flowering at the landscape scale increased linearly from early flowering plots to late flowering plots (slope = 0.029, $F_{1,23} = 50.75$, $R^2 = 0.69$, $p < 0.001$, Fig. 3). The duration of flowering

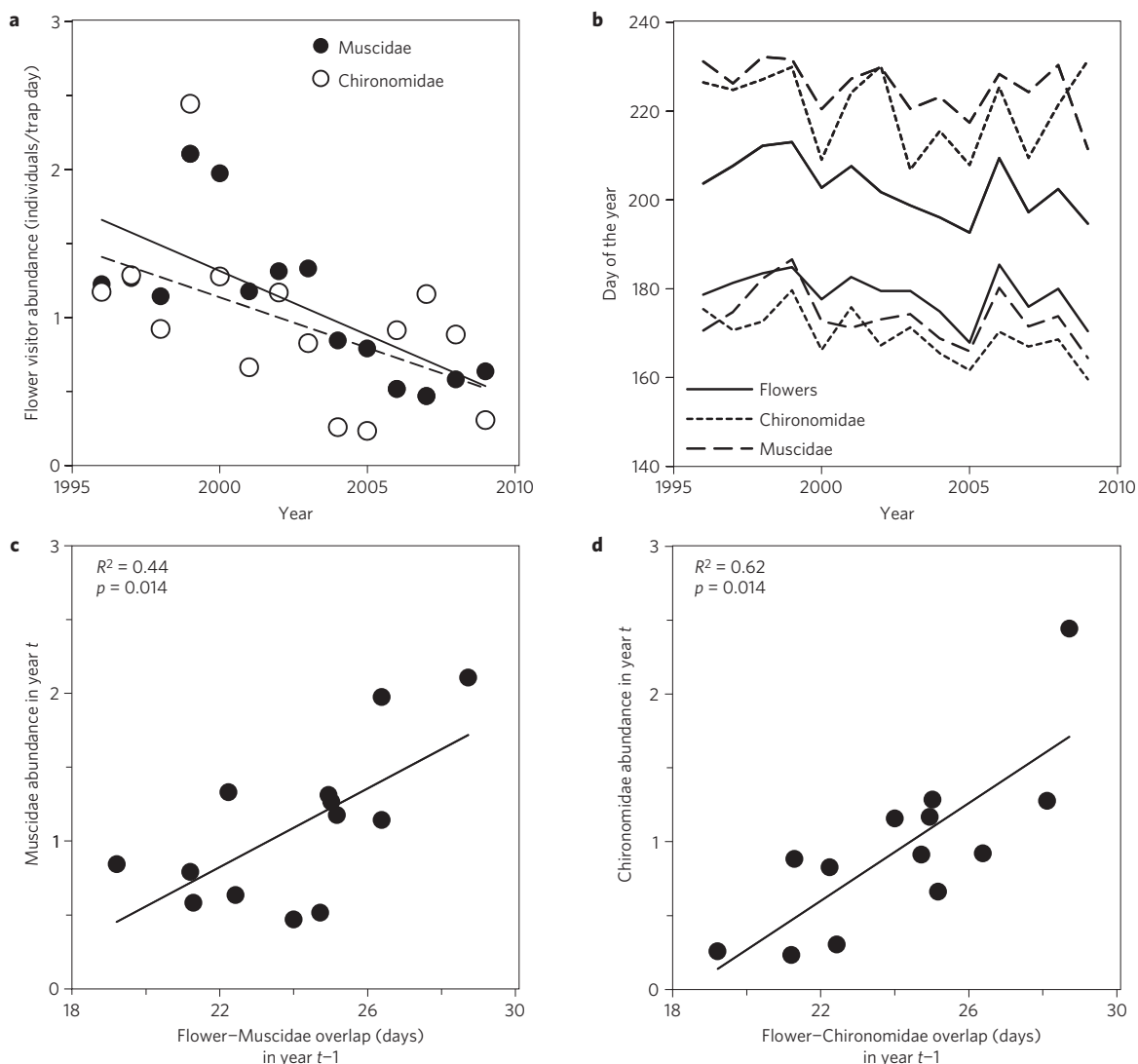


Figure 4 | Interannual variation in flower visitor abundance, plant-flower visitor temporal overlap and relationships between overlap and flower visitor abundance in the following year. a, The abundance of Chironomidae (open symbols and hatched trend line) and Muscidae (closed symbols and full trend line) estimated by the number of individuals per trap per day during the season from four different pitfall trap plots, each consisting of eight (1996–2006) or four (2007–2009) traps. **b**, Onset (bottom lines) and end (top lines) of the Muscidae and Chironomidae flight season and community-wide onset and end of flowering at the landscape scale during 1996–2009. **c**, The relationship between the abundance of Muscidae in year t and the temporal overlap in days between the community-wide flowering season at the landscape scale and the Muscidae flight season in year $t - 1$. **d**, The relationship between the abundance of Chironomidae in year t and the temporal overlap in days between the community-wide flowering season at the landscape scale and the Chironomidae flight season in year $t - 1$.

at the landscape scale was also more sensitive to variation in the end of flowering than to variation in the onset of flowering (Supplementary Tables S2 and S3). Late-flowering plants thus changed their flowering time to a greater extent than early flowering plants as the flowering time of the whole community advanced (Fig. 3). In theory, differential phenological responses to climate change in areas of early and late flowering can result in longer or shorter flowering seasons (Fig. 1), as has been suggested for growing-seasons in general¹⁶. In our study, the duration of the flowering season at the landscape scale was shorter in years of early flowering, in accordance with the conceptual model scenario presented in Fig. 1c. We acknowledge that the duration of flowering at the landscape scale can also be affected by variation in the duration of flowering at the local scale (within each plot). Linear mixed models revealed that, for all six species studied, the duration of flowering at the local scale was shorter when the temperature during flowering was high. In three species, this relationship

was significant (Supplementary Table S4). However, the observed variation in the duration of flowering at the local scale was only weakly related to the community-wide duration of flowering at the landscape scale (Supplementary Table S5).

Alpine studies tend to find stronger advancements of flowering in early flowering plants than in late flowering plants, which, according to Fig. 1, should translate into extended flowering seasons. For instance, decreasing phenological responses to climatic changes from the beginning to the end of the growing season were found in a long-term study from the Rocky Mountains, USA (ref. 17). In contrast, landscape scale spatial variability in timing of flowering at an Arctic site was reduced across a range of species in response to both ambient and experimental warming¹⁸, which according to Fig. 1 should translate into shorter flowering seasons. Duration of flowering in the plant species used in our study has only been quantified in a few cases, where experimental warming apparently had no effect at the local scale in, for example, *Cassiope*

*tetragona*¹⁹ and *Salix arctica*²⁰. Although local and landscape scale estimates of phenological responses are rare, the relationship between the timing and duration of landscape scale flowering seasons seems to follow Fig. 1c in the Arctic, whereas alpine and temperate systems follow Fig. 1a^{17,21}.

Whereas the duration of flowering is primarily determined by temperature, the onset of flowering is related to snowmelt at our site¹. Melt water tends to accumulate in snow beds after snowmelt (T. T. Høye, personal observation), ostensibly owing to the prevention of drainage by the continuous permafrost underlayer. Cold melt water may delay flowering in snow beds to a greater extent than on well-drained soils, particularly following winters with deep snowpack. Little is known about the role of permafrost in shaping spatial variation in phenology, but stronger phenological advancements in areas of late snowmelt compared with areas of early snowmelt could be common in tundra ecosystems with continuous permafrost¹. We predict that such spatial variation in plant phenological responses to climate change may differ between environments with and without continuous permafrost²².

Flower visitor declines at lower latitudes have been linked to changes in resource availability⁵. Diptera species dominate among flower visitors in the Arctic, and the multiple benefits they may gain through flower visitation (for example, basking, nectar and pollen feeding, mating and ovipositioning) indicate the importance of this association to their reproductive and population ecology^{23,24}. Both families of flower visitors included in our study declined during the study period (Fig. 4a). Muscidae declined significantly (slope = -0.086 (individuals/trap day)/year, $F_{1,12} = 12.59$, $R^2 = 0.51$, $p = 0.004$), while the negative trend was almost significant for Chironomidae (slope = -0.068 (individuals/trap day)/year, $F_{1,12} = 4.18$, $R^2 = 0.26$, $p = 0.064$). Systematic recordings of flower visitors are virtually absent from the Arctic, and this is the first report of changes in the abundance of insects from the High Arctic we are aware of^{23,25}. Flower visitor abundance could change either by the emergence of fewer individuals or because the adult stage of each individual is shortened, but distinguishing between these mechanisms would be challenging. However, testing if the decline is primarily driven by changes in the abundance in a subset of species within each flower visitor family would be possible through species identification of existing samples and a quantification of changes in the species composition through time.

The temporal overlap (Fig. 4b) of the flowering season with the flight season of the two families of flower visitors (Muscidae and Chironomidae) was significantly positively associated with their population size in the following year (Muscidae: slope = 0.13 individuals per trap day/overlap in days, $F_{1,11} = 8.47$, $R^2 = 0.44$, $p = 0.014$, Fig. 4c; Chironomidae: slope = 0.17 individuals per trap day/overlap in days, $F_{1,11} = 18.01$, $R^2 = 0.62$, $p = 0.0014$, Fig. 4d). Although both Muscidae and Chironomidae are diverse families, including species that are not commonly visiting flowers, many species of both families have been identified as frequent flower visitors at our site¹⁵. It is known that some species of Chironomidae have very short adult life stages and may not require any energy intake during this stage for successful reproduction, but it is not known whether the availability of flower resources for basking or foraging enhances reproductive output. Although the link between shorter flowering seasons and flower visitor declines is not necessarily causal, the relationships are sufficiently strong to warrant further study. We provide extra support for the possibility of a causal link in the Supplementary Information.

In our study, Muscidae and Chironomidae are present during a larger part of the season than flowers of the plant species studied. There could be other plant species that are important flower resources at the tail of the flowering season. If this is the case, the degree of resource limitation in flower visitors is dependent on the phenological response of such late flowering plant species relative

to the subset of the plant community we studied here. However, the significant relationship between flower visitor abundance in one year and the overlap between flowering seasons and flight seasons of flower visitors in the previous year indicates either a causal relationship or a common driver of both phenomena. Spatial synchrony in capture numbers of flying insects at our study sites suggests that mobility roughly equals the extent of our study area²³. Hence, shortening of the flowering season happens at a spatial scale which is relevant to flower visitors and may pose a hitherto unappreciated challenge to plant–animal interactions in a warmer Arctic²⁶. This group of flower visitors could potentially suffer from reduced resource availability late in seasons with shorter and earlier flowering^{8,13}. Hence, we anticipate that negative consequences are most likely for late emerging flower visiting insect species, although this remains to be tested. We emphasize that future studies of the role of phenology for consumer–resource interactions should focus on the spatial scale at the foraging horizon of the consumer¹⁸.

Methods

Study area and data. Data was collected at Zackenberg, Northeast Greenland (74° 28' N, 20° 34' W) as part of the Zackenberg Basic monitoring program²⁷. Temperature was recorded hourly by a weather station located centrally in the study area throughout the study period (Supplementary Fig. S1). We used phenology data on six plant species (*Cassiope tetragona*, *Dryas octopetala*, *Papaver radiculatum*, *Salix arctica*, *Saxifraga oppositifolia* and *Silene acaulis*) from 25 permanent plots. Each plant species was monitored in 3–6 plots (Supplementary Fig. S1). The six plant species were chosen to represent the plant community at Zackenberg because of their dominance in the most common vegetation types at our study site²⁸, their wide distributions in the Arctic and because they are focal species in the International Tundra Experiment ITEX (<http://www.geog.ubc.ca/itex/>). Furthermore, identification of pollen sources carried by flower visitors at our study site was largely restricted to these six plant species²⁹ and they are among those most frequently visited by insects—predominantly of the order Diptera¹⁵. Two Diptera families, Muscidae and Chironomidae, were sampled in four pitfall trap plots. Muscidae (48.1%) and Chironomidae (30.1%) comprised 78.2% of a total of 150,914 individuals of flying insects caught during 30,202 trap days across the 14-year period. All other families of flying insects were less frequent, with Sciaridae (5.5%), Ichneumonidae (3.6%), and Phoridae (3.4%) forming the three most abundant families. Both plant and insect plots were located within a 2 km² study area.

Plant and insect plots were visited at weekly intervals from late May to early September every year during 1996–2009. At each census, the phenological stage (bud, open flower or senescent flower) of at least 200 randomly chosen inflorescences within each plant plot was recorded (see ref. 1 for details). The plots were placed to cover the snowmelt gradient over which each species occurs²⁷. Insect plots each consisted of eight (1996–2006) or four (2007–2009) pitfall traps.

Data analysis. Following ref. 1, we defined the onset of flowering of a species at each plot as the date at which 50% of the buds had opened. Likewise, the end of flowering was defined as the date where 50% of the flowers were senescent within each plot. The dates for onset and end of flowering were estimated by linear interpolation between weekly observations for each plot separately. At the landscape scale, onset and end of flowering were calculated as the mean of the local scale estimates of onset of flowering minus its standard error, and as the mean of the local scale estimates of end of flowering plus its standard error, respectively. In this way, we used information on both mean and variability across all plots whilst ensuring that landscape scale onset and end of flowering occurred approximately at the same time as onset of flowering in the earliest plot and end of flowering in the latest plot, respectively. We defined the duration of flowering as the number of days between onset and end of flowering, and the timing of flowering as the average of onset and end of flowering. The duration and timing of flowering was calculated for each species separately and for all species combined to characterize the community-wide flowering season.

We used the average number of individuals per trap day in each year as an index of flower visitor abundance. The onset and end of the flight season of flower visitors in each plot were characterized by the date when 5% and 95% of the annual catch of each family of Diptera had been reached, respectively. At the landscape scale, we used the same approach as for the flowering data to calculate the onset and end of the flight season. Temporal overlap between the flowering season and the flower visitor flight season was calculated as the number of days when both flowers and flower visitors were present. We used mean monthly temperatures during June–August to explain the variation in the duration of flowering at the landscape scale. Timing of snowmelt was estimated as the first date when the snow depth sensor at the climate station measured less than 10 cm of snow. This threshold was used because the infrared sensor is inaccurate for shallow snow packs³⁰. We used general linear models to examine if temperature, timing of snowmelt or their

interaction could explain variation in the duration of the flowering period. 15 out of 350 observations of onset and end of flowering from individual plots in individual years were excluded because end of flowering took place after the end of the field season or because onset and/or end of flowering were based on observations of less than ten individual flowers in a given plot.

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Author contributions

T.T.H. performed the statistical analyses, created the figures and wrote the first draft of the manuscript. E.P., M.C.F., N.M.S. and K.T. collaborated in writing the manuscript. N.M.S. and K.T. collaborated in planning the study, N.M.S. coordinated the field work and K.T. performed the preliminary analyses. All authors read and approved the final version of the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to T.T.H.

Competing financial interests

The authors declare no competing financial interests.