Arctic Science

OPEN ACCESS | Review

Effects of short- and long-term experimental warming on plant–pollinator interactions and floral rewards in the Low Arctic

Roxaneh S. Khorsand [a], **Flavia Sancier-Barbosa** [b], **Jeremy L. May** [c,d], **Toke T. Høye** [e], **and Steven F. Oberbauer** [c]

[a]Department of Organismal Biology and Ecology, Colorado College, Colorado Springs, CO, USA; [b]Department of Mathematics and Computer Science, Colorado College, Colorado Springs, CO, USA; [c]Department of Biological Sciences, Florida International University, Miami, FL, USA; [d]Department of Biology and Environmental Science, Marietta College, Marietta, OH, USA; [e]Department of Ecoscience and Arctic Research Centre, Aarhus University, Aarhus, Denmark

Corresponding author: **Roxaneh S. Khorsand** (email: rkhorsand@coloradocollege.edu)

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Abstract

Plant phenological and growth responses to experimental warming are widely documented, but less is known about warming effects on plant–pollinator interactions. We investigated the effects of short- and long-term passive warming on flowering phenology, insect visitation, fruit production, and floral rewards in the Low Arctic in northern Alaska. To better understand the role of insect visitors in plant reproductive success, we quantified pollen loads on floral visitors and tested for pollen limitation in four species. Long-term warming advanced flowering onset in evergreen shrubs and forbs. Warming, in general, increased the duration of flowering for forbs, evergreen shrubs, and deciduous shrubs. Considering all growth forms together, long-term warming increased floral density. This pattern was primarily driven by deciduous and evergreen shrubs. Dipterans accounted for more visits than Hymenopterans, although Hymenopterans had higher pollen loads. Insect exclusion and warming decreased fruit set in the forb, *Bistorta officinalis Delarbre*. Nectar volume in the deciduous shrub, *Vaccinium uliginosum*, was higher in the warmed plots than the control, but nectar quality did not differ. Advanced flowering onset, longer flowering duration, and increased flower density and nectar volume may have important implications for the pollinator community, warranting further research on long-term warming effects on tundra ecosystems.

Key words: Arctic, floral rewards, phenology, pollen limitation, pollination, warming

Introduction

The disproportionate effect of climate change on Arctic regions is well documented (Post et al. 2009; Ernakovich et al. 2014; Box et al. 2019). A substantial body of research documents phenological shifts of Arctic plants in response to warming, specifically advanced growth and flowering, although these shifts are species-specific (Wookey et al. 1993; Chapin et al. 1995; Oberbauer et al. 2013; Bjorkman et al. 2015; Parmesan and Hanley 2015). Evidence also suggests Arctic arthropod phenology is shifting in response to climate change (Høye et al. 2007; Høye et al. 2013; Forrest 2015), although fewer data exist on arthropods compared to plants (Gillespie et al. 2020). While phenological shifts are evident, less is known about the effects of warming on plant–pollinator interactions and plant reproductive success (Forrest 2015; Urbanowicz et al. 2017). From the plant perspective, understanding the shifting dynamics of plant–pollinator networks (Jordano 1987; Olesen et al. 2006) is particularly important in the Arctic, where plant reproduction is limited by a highly variable environment and short growing season (Grime 1974; Robinson et al. 2018; Høye 2020). Low species diversity in the Arctic may add to the vulnerability of these plant–pollinator networks (Kaiser-Bunbury et al. 2010; Vasiliev and Greenwood 2021). Homogenization of plant phenology can also threaten plant–pollinator networks. In a meta-analysis of tundra plants, Prevéy et al. (2019) reported a contraction of community-level flowering seasons, which could lead to a reduction in floral resources for the pollinator community. Thus, it is important to understand the effects of warming on plants and pollinators in the Arctic.

Since 1992, researchers involved in the International Tundra Experiment (ITEX) have been measuring the phenological and growth responses of Arctic and alpine plants to passive warming using open top chambers (OTCs) (Webber and Walker 1991; Henry et al. 2022). While this work has provided substantial knowledge about plant and ecosystem responses to warming (Henry and Molau 1997; Hollister et al. 2005; Walker et al. 2006; Elmendorf et al. 2012*a*, 2012*b*; Oberbauer et al. 2013; Khorsand Rosa et al. 2015; Prevéy et al. 2021), one major ITEX knowledge gap is biological interactions, specifically the effects of warming on pollination and pollinators (Böcher 1996; Henry et al. 2013). Relatively few ITEX

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

studies have focused on this topic over the past three decades (Henry et al. 2022). While some studies have experimentally manipulated snowmelt and measured responses by pollinators (Hoiss et al. 2015; Gillespie et al. 2016; Kudo and Cooper 2019; Gillespie and Cooper 2021), only a few have taken place at ITEX sites or used OTCs (Gillespie et al. 2016; Robinson and Henry 2018). Quantifying pollinator responses to warmed vegetation in ITEX sites is important as these responses may lead to plant–pollinator asynchrony (Hegland et al. 2009), reduced seed set (Kudo and Cooper 2019), and reduced floral resources (Høye et al. 2013; Schmidt et al. 2016), with cascading effects on foraging resources for primary consumers, plant diversity and cover, and global carbon budget (Totland and Eide 1999; Klady et al. 2011; Settele et al. 2016). This work is especially needed at Low Arctic sites, as few studies have focused on plant–pollinator interactions in the Low Arctic (Williams and Batzli 1982) compared to the High Arctic (Lundgren and Olesen 2005; Olesen et al. 2008; Gillespie et al. 2016; Robinson and Henry 2018; Gillespie and Cooper 2021).

Reproductive strategies of Arctic plants are shaped by snow depth and duration, temperature extremes, a short growing season, and a general lack of pollinators (Kevan 1972; Bell and Bliss 1980; Molau 1993; but see Wookey et al. 1993; Murray 1997). In general, Arctic plants allocate a minor proportion of resources to sexual reproduction compared to vegetative propagation and apomixis (Molau 1993). Some ITEX studies demonstrate that experimental warming has a positive effect on sexual reproduction (Henry and Molau 1997; Molau and Shaver 1997; Klady et al. 2011), while others report no effect (Totland and Alatalo 2002; Robinson and Henry 2018). Extreme temperature fluctuations associated with climate change may counteract the expected positive reproductive responses to warming, although these responses appear to be species-specific (Panchen et al. 2022).

Pollen limitation is a key factor to consider when determining the relationship between warming and plant reproductive success (Ashman et al. 2004). Although pollen limitation is predicted to be most severe in highly variable environments where pollinator services are unreliable (Knight et al. 2005), the empirical evidence from the Arctic is mixed; some studies have reported pollen limitation (Stenström and Molau 1992; Fulkerson et al. 2012; Urbanowicz et al. 2018), while others have found little evidence (Koch et al. 2020). Given this knowledge gap in pollen limitation across biomes (Bennett et al. 2018), site-specific and species-specific investigations are necessary to better understand Arctic plant reproductive responses to warming, as well as the importance of pollinators to plant reproductive success. In addition to experimentally testing for pollen limitation and observing floral visitors in the field, we must also quantify pollen transport by floral visitors (Ne'eman et al. 2010; Schmidt et al. 2016; Richman et al. 2020).

Warming can affect the production of floral rewards and resources (Scaven and Rafferty 2013). Plastic responses to floral traits are important as they may alter the way pollinators perceive and visit plants (Carroll et al. 2001). Few empirical studies quantify the relationship between warming and nectar production, specifically in the Arctic (Scaven and Rafferty 2013; Mu et al. 2015). However, some temperate studies have reported decreased nectar volume and pollen production in response to heat and drought (Zimmerman 1983; Wyatt et al. 1992; Carroll et al. 2001; Waser and Price 2016; Borghi et al. 2019). It is important to expand the focus of pollination studies in the context of climate change from the phenological responses of plants and pollinators to the links between environmental variables, floral resources, and biotic pollination (Waser and Price 2016).

A multi-dimensional approach is necessary to accurately address the question: how does climate change affect Arctic plant–pollinator interactions and plant reproductive success? We used a combination of experimental and observational methods to address plant phenology, floral visitor activity, pollen limitation, pollen transport, and floral rewards in two common plant communities at two Alaskan sites in the Low Arctic (CAVM Subzone E; Walker et al. 2005). Specifically, we tested four questions: (1) How does warming affect flowering phenology and floral visitor activity? (2) Which floral visitors are the most effective pollinators? (3) Does visitor exclusion result in a lower fruit set? and (4) Does experimental warming reduce floral nectar quantity and quality? Our study contributes novel data to better understand the effects of passive warming on floral visitation, plant reproductive success, and floral rewards in the Arctic.

Materials and methods

Study sites

Fieldwork was conducted in the northern foothills of the Brooks Range, Alaska, USA, in the Low Arctic in 2019 and 2020. Mean annual temperatures on the North Slope of Alaska have increased more than other regions of the state (Shulski and Wendler 2007) and at twice the global value, demonstrating polar amplification (Wendler et al. 2017). We worked at two field sites on the North Slope: Imnavait Creek (68°37'N, 148°18'W, elevation 930 m) and Toolik Lake (68°38'N, 149°36'W, elevation 730 m), approximately 12 km from each other (see Walker et al. 1994 for a detailed description of our field sites). The Toolik Lake site is approximately 1.5 km southwest of Toolik Field Station. Site temperature data were acquired from the field station and the Ameriflux network. Mean July temperatures in 2019 for Toolik and Imnavait were 12.3 °C and 12.1 °C, respectively; mean July temperatures in 2020 were 7.6 °C and 7.4 °C. Snowmelt at Toolik occurs in mid- to late-May. Although snowmelt occurs about a week later at Imnavait Creek and foggy conditions are more common, overall climate differences between the sites have been found to be small (Walker et al. 1994). Snowmelt occurred about 10 days later in 2020 compared to 2019.

Experimental design

We worked in a total of 128 1m^2 plots across two plant community types, moist acidic tundra and dry heath tundra ($N = 32$ plots per community type per site) (Fig. S1). This design allowed us to use experiments already established at each site and community type, thus increasing the number of warmed plots. We chose dry heath and moist acidic communities as they are the two most common plant community

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

types in this part of Arctic Alaska. Each community type had 16 control (un-warmed) plots and 16 experimental (warmed) plots. Treatment plots were passively warmed using standard, hexagonal open top chambers (OTCs) (0.35 m tall, 0.6 m opening at the top, and 1.03 m between parallel sides at the base), following protocols established by the International Tundra Experiment (ITEX) (Molau and Mølgaard 1996; Marion et al. 1997). OTCs increase the average near-surface air temperature by 0.6–2.2 °C during the growing season (Hollister et al. 2022). The length of warming varied between sites. One quarter (16 plots) of our treatment plots have been warmed since 1994 at Toolik, one quarter (16 plots) have been warmed at Imnavait since 2016, and half (32 plots) have been warmed since 2019 (spanning both sites). The long-term plots at Toolik constitute the original ITEX plots. Thus, we refer to the following categories of warmed plots for each study year: 2019: 1 y, 4 y, and 26 y; 2020: 5 y and 27 y. The 1 y plots were not used in 2020. Hereafter, 1 y, 4 y, and 5 y constitute short-term warming, and 26 y and 27 y constitute long-term warming. All OTCs, regardless of the warming duration category, were the same size, shape, and material. In 2019, we installed OTCs on experimental plots on 27 May at Imnavait and 28 May at Toolik. In 2020, the COVID-19 pandemic inhibited travel to our field sites, so the Environmental Data Center (EDC) staff at Toolik Field Station installed OTCs on 28 May at both sites. As much as possible, we accessed plots using an elevated boardwalk to minimize effects on the plant community.

Phenology

Between 29 May 2019 and 23 July 2019, we conducted a phenological survey in each plot twice a week to determine the following for 29 species: timing of anthesis, duration of anthesis, number of species in anthesis, and floral density (as an indicator of floral resource availability). We defined anthesis as the period when petals and reproductive structures (stamens, pistils) were intact and/or pollen dispersal occurred by touching the anthers. We considered flowers to be in post-anthesis when petals and reproductive structures wilted and pollen no longer dispersed. Floral density (number of flowers per unit area) was quantified in a sub-plot of each plot by placing a 30.5 cm × 30.5 cm frame in the center of each plot and counting the number of open flowers (not plants) for each species.

In 2020, we relied on time-lapse photography to document flowering phenology because of COVID-19 travel restrictions. We monitored three control and three warmed plots in each community type and site ($N = 24$ total) (Table S1). EDC staff set up OTCs at the end of May, shortly after the snowmelt. Cameras (Meidase SL122 Pro Trail Camera, www.Meidase.com; Shenzhen Meidasi Technology, Shenzhen, China) were raised 65 cm above plots and fixed to a metal quadropod structure (Fig. S2). Cameras were programmed to take images every 5 s each day between 5 June and 2 September, between 11:00 and 15:00. We originally intended to use images for floral visitor observations and floral density; however, image resolution proved insufficient to identify the smallest insects, as well as distinguish the individual flowers of some species. Thus, daily images taken of each plot were only used to quantify the onset, end, and duration of flowering for each of the 19 species present.

Floral visitor observations

In 2019, between 30 May and 18 August, we performed a total of 355 5-min observations spanning both sites and both community types (Table S2). Repeated observations were made on plots throughout the season, once to twice per week. An average of 28 plots were observed per day, and no more than three observations were made on a single plot per day. We attempted, to the best of our ability, to observe the same number of warmed and controlled plots each day. Given that our field sites are 12 km apart, we focused our observations on one site per day, ensuring that we conducted observations at each site on at least two non-consecutive days per week. Observations were made between 7:00 and 19:00. We did not record floral visitor observations during rain or wind, as unfavorable weather could decrease floral visitor activity. We observed floral visitors at 1.2–1.8 m away from the plot to minimize potential interference with pollinator behavior. During each observation period, we recorded the following: plant species in bloom, number of individuals of each visitor morphotype by order (Coleoptera, Diptera, Hymenoptera, Lepidoptera, or “other”), common name of visitor and physical description, as could be determined from the observing distance (ex. Syrphid fly, non-Syrphid fly, mosquito, bumblebee, non-bumble bee, wasp, moth, butterfly, etc.), number of visits made by each floral visitor, plant species visited, and visitor behavior, including if the visitor entered the flower and appeared to contact floral sexual structures. We defined a visit as when an insect landed on and/or entered the flower (depending on the floral morphology). We only performed visitor observations on plots that had flowers. If marked control plots lacked flowers, we made additional visitor observations in unmarked control plots within the site (Robinson and Henry 2018; Gillespie and Cooper 2021).

In 2020, we relied on the Toolik EDC staff to collect visitor observation data. Field station staff were properly trained to carry out observations. Between 17 June and 21 August, staff conducted a total of 276 floral visitor observations, following the same protocol we used in 2019 (Table S2). In both years, we conducted more observations on control plots than warmed plots because the additional observations in unmarked plots were always control. No floral visitor observations were conducted on warmed plots after 23 July (2019) and 30 July (2020) because of a lack of flowering in these plots.

Insect collection and pollen analysis

In 2019, we collected insect and pollen samples from all treatments at both sites. Collections were not made in 2020. After a floral visitor observation had concluded, we collected a sub-sample of floral visitors ($N = 76$) and euthanized them using ethyl acetate in a killing jar (Kearns and Inouye 1993). Insects were placed in the freezer for at least 12 h and then pinned. A minority of specimens ($N = 21$) were stored in individual vials of 70% ethyl alcohol. We also collected flowers from each species visited by insects, stored them in 70% alcohol, and then removed pollen from the anthers to make

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

pollen reference slides following the methods of Kearns and Inouye (1993). For the dry insect specimens, we removed pollen grains from each visitor's body by swabbing the abdomen with a small cube of fuchsin jelly, which was then placed on a ruled microscope slide (containing 64 2-mm squares), heated, and covered with a cover slip to be viewed under a compound microscope. Pollen grains were quantified and identified by species. We specifically focused on pollen from the head, thorax, and abdomen, not the corbiculae and hind legs, as pollen on these structures may not be available for pollination (Parker 1981; Alarcón 2010; Schmidt et al. 2016). For wet specimens, we sampled both the insects and the suspended alcohol for pollen. Insect voucher specimens will be deposited in the Entomology Collection in the Museum of the North at the University of Alaska, Fairbanks.

Pollen limitation experiments

To determine how warming and visitor exclusion affect reproductive output, we performed a bagging experiment in 2019 on four focal species: *Cassiope tetragona* (Ericaceae), *Rhododendron tomentosum* (Ericaceae), *Dryas octopetala* (Rosaceae), and *Bistorta officinalis* (Polygonaceae). Experiments on *C. tetragona* and *B. officinalis* were located at Imnavait, *D. octopetala* were located at Toolik, and *R. tomentosum* were evenly split between both sites. Individuals of each species were located in warmed and control plots, and about half were bagged to exclude floral visitors (Table S3). We used individuals in any of the three warming treatments to meet basic sample size requirements. *Bistorta officinalis* had fewer individuals in the warmed plots compared to the control plots (Table S3). For *D. octopetala* that produces singular, apocarpous flowers, we covered each unopened and undamaged floral bud with a nylon mesh bag. For *C. tetragona* that produces several unicarpellate flowers towards the terminus of the flowering branch, we verified that all floral buds were unopen and undamaged, then covered a single branch with a mesh bag. For *R. tomentosum* and *B. officinalis* that produce inflorescences, we removed any open flowers along the inflorescence before covering the entire inflorescence with the mesh bag. Mesh bags had 0.1 mm holes and contained a Velcro seal to ensure insects could not enter. Bags were removed and fruits were collected six to eight weeks later. We defined fruit set as fruit to flower ratio. Ratios for each individual were calculated as the proportion of the number of capsules (for *C. tetragona*, *R. tomentosum*, and *B. officinalis)* or plumed achenes (for *D. octopetala*) over total number of flowers or flower scars.

Nectar measurements

In 2019, we quantified nectar quantity (volume) and quality (Brix or % sucrose) in *Vaccinium uliginosum* (Ericaceae) to understand how warming affects floral rewards in this species. We focused on this species because it is abundant in our plots and is also monitored for phenology in our study. In addition, this species offers an important fruit resource for wildlife and native communities throughout Alaska (Parkinson and Mulder 2020). To our knowledge, no published study addresses nectar production in this species. At the Toolik site, we measured nectar volume and Brix (% sucrose) across 20 warmed (10: 26 y, 10: 1 y) and 20 control plots. Although the 1 y plots had only been passively warmed for a few weeks when nectar measurements were made, we still took these measurements to compare with control plots and 26 y warmed plots, as well as to have baseline data for our future research on this species. We randomly sampled one flower per plant and three to five flowers per plot. In the case that plots did not contain enough flowers, we sampled from unmarked control plots (see explanation in Floral visitor observations section). Each day, we sampled from control and warmed plots, and we randomized the order of plot sampling. We measured nectar from 7 June to 15 June, between 7:30 and 14:00. Volume (μL) of nectar was calculated by measuring the length of the nectar column in 1–5 μL Drummond microcapillary tubes. We used a low-volume hand-held refractometer (Bellingham and Stanley Ltd., Tunbridge Wells, Kent, UK) to quantify Brix.

Statistical analyses

All data analyses were conducted using R (R Core Team 2020). We used the following packages: coin (Hothorn et al. 2008) to perform Exact Wilcoxon–Mann–Whitney tests, MASS (Venables and Ripley 2002) to fit negative binomial GLMs, dplyr (Wickham et al. 2023) to summarize data, and ggplot2 (Wickham 2016) to create plots. The R code for the more complex statistical analyses can be accessed at Rpubs (https://rpubs.com/fsancier/warming).

Definitions

We separated phenological data into temporal windows of 7 days, which we labeled "week 1" through "week 13". We defined the beginning of week 1 as the first day of our field observations. Data collection began on 29 May in 2019 and on 5 June in 2020. To keep the dates of each 7-day window consistent between years, we started 2020 with week 2. The first day, last day, and duration of flowering for each species were calculated as the mean for each particular treatment across community type and site (Table S1), thus reducing the disproportionate sensitivity of single, early- or late-flowering individuals. We used the mean first day of year (DOY) and mean last DOY of flowering for each species to place species into seasonal categories. We defined "early-flowering" as weeks 1–3 (29 May through 18 June), "mid-flowering" as weeks 4–7 (19 June through 9 July), and "late-flowering" as weeks 8 and onward (10 July–19 August). We recognize that a few species may bloom before 29 May or after 19 August, but our observations account for the majority of flowering at our sites. As expected, some species flowered in more than one seasonal category. If 90% or more of the range between the mean first DOY of flowering and the mean last DOY of flowering fell within one category, the species was assigned to that category. Otherwise, the species was assigned to both categories. The later start date in 2020 could potentially affect seasonal classification, particularly for early-flowering species. Thus, we used the 2019 data for the classification of early-flowering species. For each species in a plot, we recorded the onset of flowering as the first DOY anthesis was observed and the termination of flowering as the last DOY anthesis was observed. The

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

duration of flowering for each species in a plot was defined as the difference between the onset and termination of flowering. We also recorded the DOY on which maximum floral density occurred for each species in each plot. Peak floral density for each species was calculated as the mean DOY within each particular treatment (Table S1). We used the weekly temporal window to determine peak flowering, which was defined as the maximum number of species in bloom per plot.

Phenology

To account for species-specific effects in response to warming, we analyzed phenological variables (first, last, duration, and floral density) for each individual species, as well as all species together. We also analyzed these response variables according to growth form by grouping species into forbs, evergreen shrubs, deciduous shrubs, and graminoids (Chapin et al. 1996). To test the effect of experimental warming on flowering phenology for each species and growth form, we performed Exact Wilcoxon–Mann–Whitney tests for first, last, duration, and peak floral density days. An exact test was used because most species appeared in a small number of plots (Tables S4 and S5), and exact tests are appropriate for small sample sizes and skewed distributions (Hothorn et al. 2008). We note that the exact tests did not consider the effects of community type and site. We also tested if the temporal patterns were different between control and warmed plots in the number of species in anthesis, floral density, and floral visits (see details in Floral visitor observations).

To understand how warming affects the diversity of floral rewards, we calculated the number of different plant species that flowered within a plot throughout the entire field season. We compared the average number of species that bloomed in control and warmed plots via a generalized linear mixed model (GLMM) with a random effect for community type and a quasi-poisson family to account for underdispersion in the number of different plant species. Nesting community type within the site did not improve any of the models that considered only community type as a random effect, according to Akaike's information criterion (AIC). Therefore, seeking the most parsimonious model given the sample size, we considered only community type as a random effect. To account for the effects of long-term versus short-term warming, we compared the number of species that bloomed in plots warmed for 1, 4, and 26 years versus control plots.

Floral visitor observations

Although we conducted a total of 632 floral visitor observations on a total of 27 plant species in both 2019 and 2020, we only included results for plant species that received at least five observations and at least one visit. To determine which plant species received the most insect visits, we calculated the mean number of visits per five-minute observation per plant species per treatment (Tables S1 and S2). We also examined weekly patterns in control and warmed plots for the number of visits per observation, species in anthesis, and floral density. Tests of significance for each week were conducted through GLMMs with community type as a random effect and quasi-Poisson (for number of species in bloom) and negative binomial (for floral density and visits per observation) families. Nesting community type within the site did not improve the models (assessed by AIC). This analysis was performed considering all species together, as well as by growth form.

Pollen analyses

We used non-parametric tests to compare counts of pollen grains by insect order (Hymenoptera, Diptera, and Lepidoptera). Coleoptera and Araneae were excluded from analyses because of the small sample size. Exact *p*-values (calculated via permutation) were used for pairwise comparisons. Because insect specimens were stored using different methods (wet or dry), we used a Mann–Whitney U test to check if wet and dry specimens could be analyzed together. Because we found no evidence that pollen counts for the two storage methods came from different distributions (Diptera: $U = 127.5$, $p = 0.12$; Lepidoptera: $U = 11.5$, $p = 0.95$), we analyzed the wet and dry specimens together.

Pollen limitation

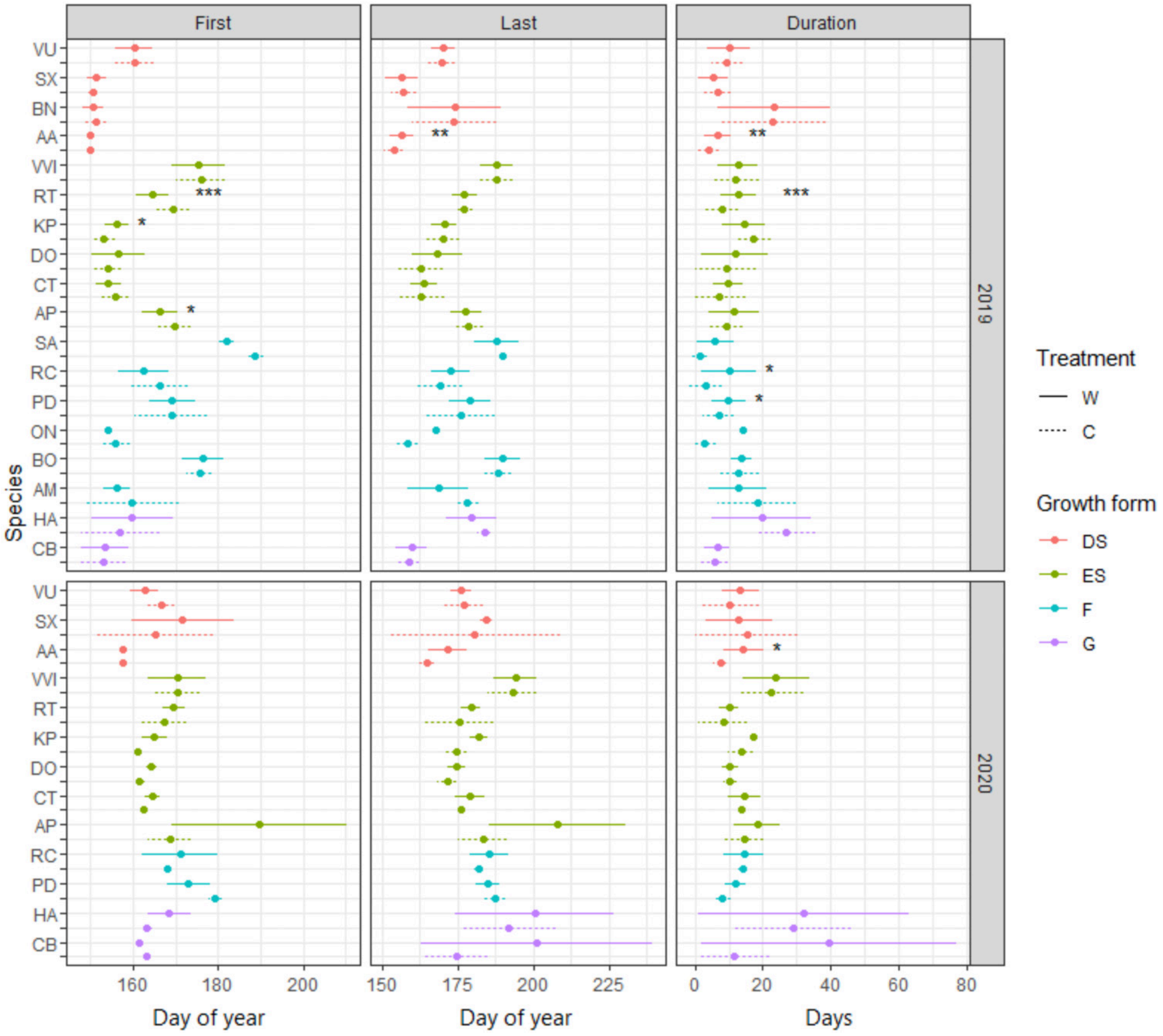
To determine if fruit set differed significantly by bag treatment (bagged versus open) and plot treatment (1 y and 26 y versus control), we fit generalized linear mixed models using a quasi-Poisson distribution (for *R. tomentosum*, *D. octopetala*, and *B. officinalis*), with site as a random effect for *R. tomentosum* and community type as a random effect for *B. officinalis.* No random effect was added for *D. octopetala* because all individuals were from the same site (Toolik) and community type (dry heath). We considered the number of fruits as the dependent variable, bag treatment and plot treatment as independent variables, and the number of flowers as an offset variable for *R. tomentosum* and *B. officinalis*. We did not use the number of flowers as a control variable for *D. octopetala* because each bag covers only one flower in this species, in contrast to the other three species that may have more than one flower per bag. We first checked for interaction effects between plot and bag treatments and then analyzed the main effects in the absence of interactions. The analysis for *C. tetragona* was done differently because the flowers sampled from control plots yielded no fruits, and those sampled from warmed plots yielded a fruit set of only three values (0, 0.5, and 1). Therefore, we first used a Mann–Whitney test to assess differences in bag treatment within warmed plots, and then to assess differences in plot treatment.

Nectar

We tested whether nectar quantity and quality differed by plot treatment through two generalized linear models with a gamma family, considering nectar volume and Brix (% sucrose) as dependent variables and plot treatment as an independent variable with three levels (control, 1 year warming, and 26 year warming).

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Fig. 1. Means (and SDs) for the first day, last day, and duration of anthesis for individual species in 2019 and 2020, considering sites and community types combined. Sample sizes can be found in Tables S4 and S5. *p*-values for Exact Wilcoxon–Mann–Whitney tests assess the difference between control and warmed plots for each variable: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. W = warmed plots (combining all warmed plots regardless of warming duration); C = control plots; DS = deciduous shrubs; ES = evergreen shrubs; F = forbs; G = graminoids. AA = *Arctous alpina*; AM = *Antennaria monocephala*; AP = *Andromeda polifolia*; BN = *Betula nana*; BO = *Bistorta officinalis*; CB = *Carex bigelowii;* CT = *Cassiope tetragona*; DO = *Dryas octopetala*; HA = *Hierochloe alpina*; KP = *Kalmia procumbens*; ON = *Oxytropis nigrescens*; RC = *Rubus chamaemorus*; RT = *Rhododendron tomentosum*; SA = *Saussurea angustifolia*; VU = *Vaccinium uliginosum*; VVI = *Vaccinium vitis-idaea*. To satisfy sample size requirements, we grouped a few species together: PD = *Pedicularis capitata*, *P. lanata*, and *P. lapponica*; SX = *Salix pulchra*, *S. phlebophylla*, and *S. reticulata*.



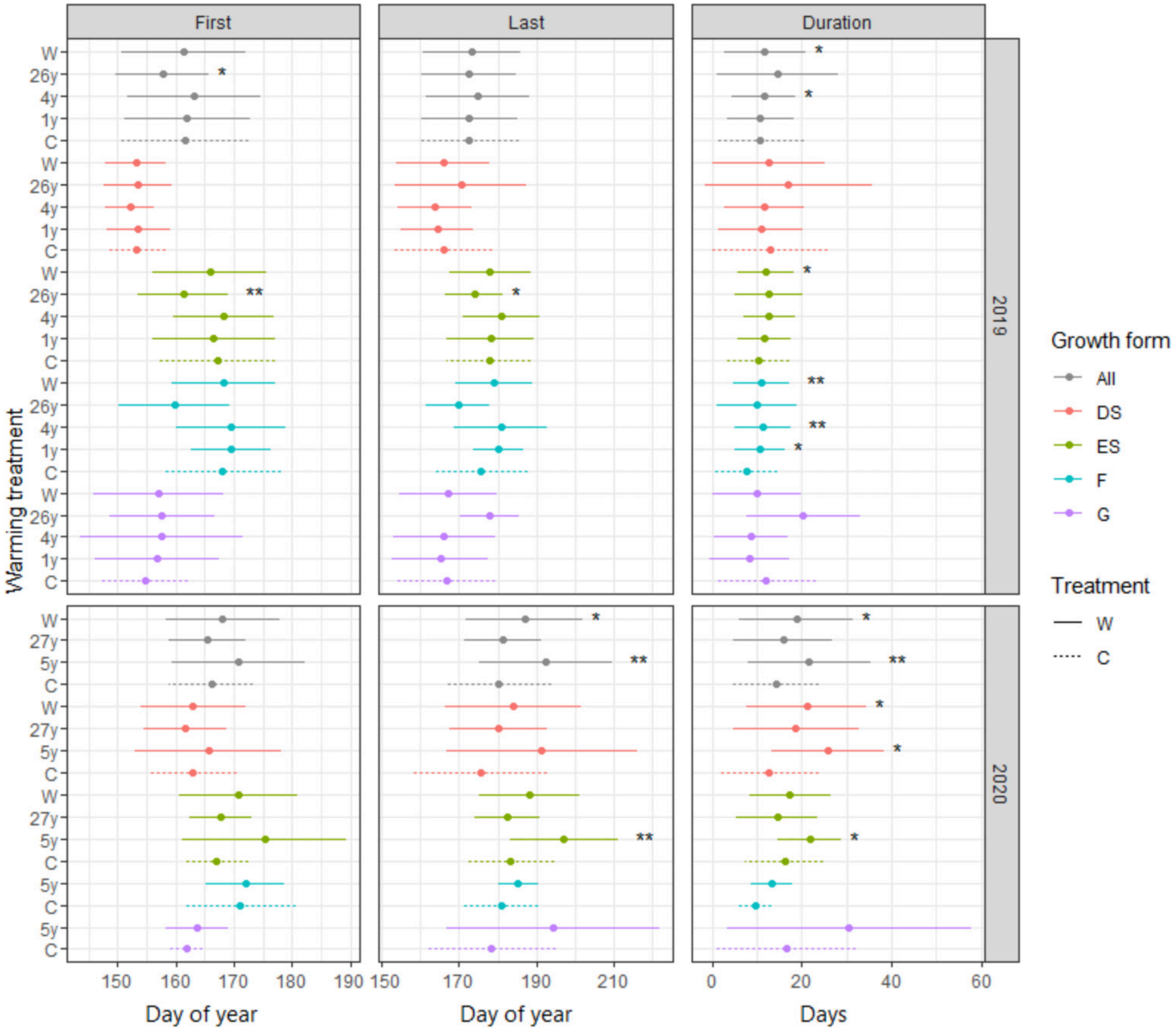
Results

Flowering phenology

Long-term warming advanced flowering onset in evergreen shrubs and forbs, although this difference was only significant in evergreen shrubs in 2019. This result also held when we excluded the species that had initiated flowering prior to the start of our data collection. Flowering onset occurred significantly earlier in warmed plots (considering all warmed plots combined) in 2019 in the evergreen shrub species *Andromeda polifolia* and *Rhododendron tomentosum*, but this response did not hold in 2020 (Fig. 1). Considering all species together, warming significantly delayed the mean last day of flowering in 2020 and increased the duration of flowering in both 2019 and 2020 (Fig. 2). Within growth form, warming increased the duration of flowering for forbs and evergreen shrubs in both years, although only significantly in 2019 (Fig. 2). In the evergreen shrub, *R. tomentosum,* and the forbs, *Rubus chamaemorus* and *Pedicularis* spp., flowering lasted longer in both 2019 and 2020 in warmed plots, although this increase

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Fig. 2. Means (and SDs) for the first day, last day, and duration of anthesis for growth forms in 2019 and 2020, considering sites and community types combined. W = all warmed plots combined; C = control plots. For warmed plots, the number of years undergone warming is indicated by 1 y, 4 y, and 26 y (2019), and 5 y and 27 y (2020). All = all species, DS = deciduous shrubs; ES = evergreen shrubs; F = forbs; G = graminoids. Sample sizes can be found in Tables S4 and S5. *p*-values for Exact Wilcoxon Mann–Whitney tests indicate significance between control and warmed plots for each variable: $^{*}p < 0.05$, $^{**}p < 0.01$. In 2020, graminoids and forbs only showed two treatments because forbs only flowered in one 27 y plot and graminoids did not flower in any 27 y plots.

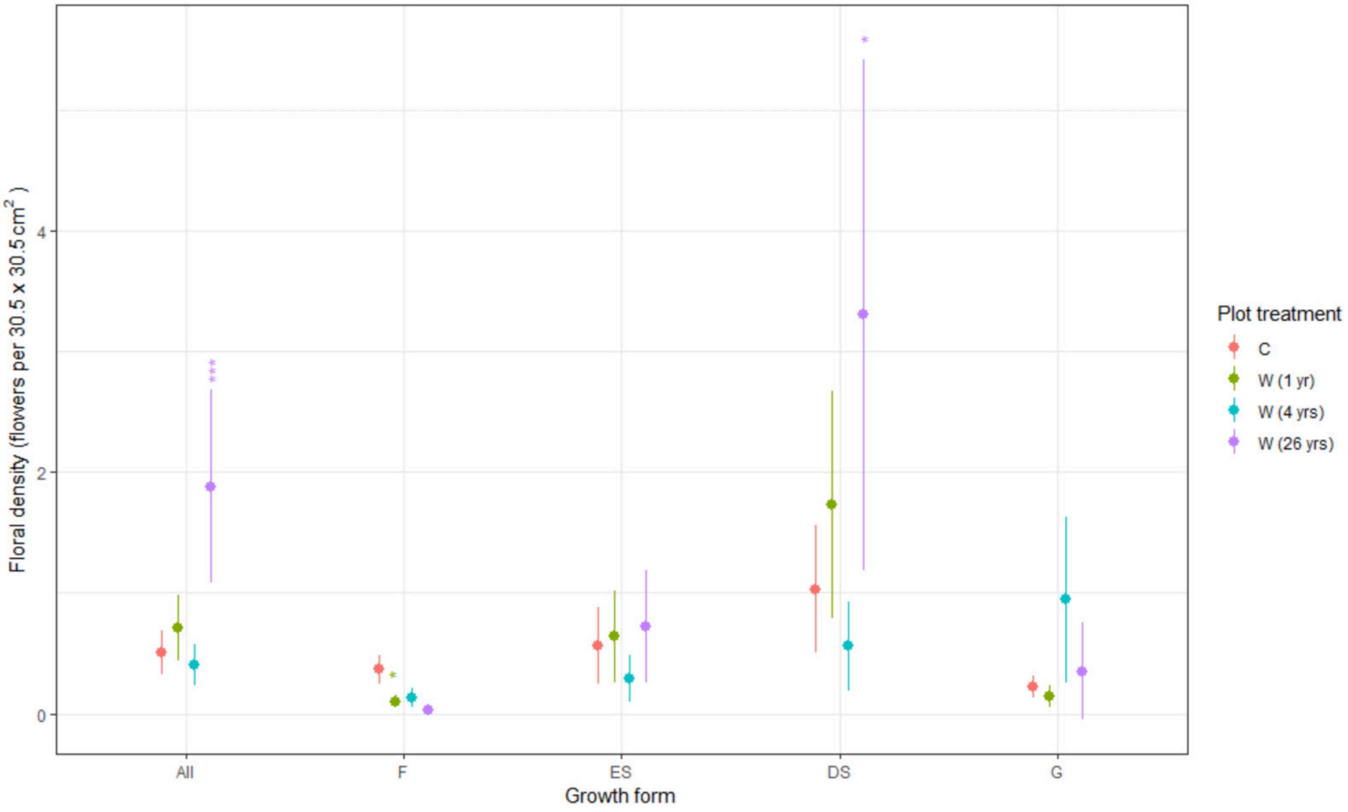


was statistically significant only in 2019 (Fig. 1). Warming also increased the duration of flowering in deciduous shrubs in both years, although it was significant only in 2020 (Fig. 2). This response was due to one species, *Arctous alpina*; flowering in *A. alpina* ended significantly later in the warmed plots compared to the control in 2019 and lasted significantly longer in both years (Fig. 1). The evergreen shrub, *C. tetragona*, showed no significant response to warming in either year (Fig. 1 and Tables S4 and S5).

Considering all growth forms together, GLMMs indicated that long-term warming significantly increased floral density (Fig. 3). Long-term warmed plots had significantly higher floral density ($M \pm SD = 1.57 \pm 1.86$ flowers per 930 cm^2 unit area) compared to control plots (0.58 ± 0.71) [$Z = 4.55$, $p < 0.001$]. For specific growth forms, we observed a more nuanced response. Long-term warmed deciduous and evergreen shrubs had higher floral density relative to the control, although only significant in deciduous shrubs (Fig. 3). In graminoids, 4 y and 26 y plots had higher floral density than control plots (non-significant). Forbs had lower floral density in each of the warming treatments (1 y, 4 y, and 26 y) compared to the control, but only 1 y was significant (Fig. 3). We also found significant differences in floral density for warmed plots compared to control plots by week and

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Fig. 3. Estimated marginal means and standard errors for floral density by growth form in 2019, considering sites and community types combined. All = all growth forms combined; F = forbs; ES = evergreen shrubs; DS = deciduous shrubs; G = graminoids. W (1 y), W (4 y), and W (26 y) denote plots that have been experimentally warmed for 1, 4, and 26 years, respectively. C = control plots. *p*-values for a GLMM (negative binomial) refer to the difference between warmed and control plots. $^{*}p < 0.05$, $^{***}p < 0.001$. Asterisks are placed directly above the corresponding warming treatment.



growth form. Notably, floral density was significantly higher in long-term warmed deciduous shrubs relative to the controls in weeks 2 through 6 (Fig. S3). This difference was due to *Betula nana;* between weeks 2 through 6, mean floral density in this species was at least six times higher in long-term warmed plots (range: 2.93–3.75) compared to control plots (range: 0.21–0.55). Although evergreen shrubs did not show a statistically significant response to warming as a group, mean floral density in *Kalmia procumbens* was approximately five times higher in long-term warmed plots in weeks 1 through 3 (range: 5.00–13.75) compared to control plots (range: 0.21–2.33).

In 2019, 26 y plots had a significantly lower number of species that bloomed ($M \pm \mathrm{SD} = 4.00 \pm 1.46$) compared to control plots (4.95 ± 1.72) [$t = -2.15$, $p < 0.05$]. This pattern was true for forbs, evergreen shrubs, and graminoids, although only significant for graminoids. Plots warmed for 4 years had a significantly higher number of forb species (1.69 ± 1.45) that bloomed compared to control plots (0.91 ± 0.94) [$t = 2.75$, $p < 0.01$]. No significant differences were found in 2020 between warmed plots (of any warming duration) and control plots. When assessing the number of species that bloomed on a weekly basis, the GLMMs indicated that in 2019, the number of forb species in bloom was significantly higher in 4 y plots relative to the control in weeks 3 through 7 (Fig. S4). We observed the same pattern in 2020, although only significant in week 5 (Fig. S5). The number of deciduous shrub species in bloom was consistently higher in long-term warmed plots in weeks 2 through 7, although only significant in week 5 of 2019 and week 3 of 2020 (Figs. S4 and S5). Peak flowering, as defined by the maximum number of species in anthesis, occurred during weeks 2 through 5 (5 June to 2 July) in 2019 and weeks 3 through 6 (12 June to 9 July) in 2020. In 2019, peak flowering in deciduous shrubs and graminoids occurred in weeks 2 and 3. In contrast, peak flowering in evergreen shrubs and forbs occurred between weeks 3 and 5 (Fig. S4). Although we found some variation in 2020, the patterns for growth form were similar to 2019: peak flowering in deciduous shrubs and graminoids occurred earlier than evergreen shrubs and forbs. In both years, we observed a clear decrease in the number of species in bloom after week 6 (Figs. S4 and S5).

Based on our phenological observations and sampling dates, seven species are considered early-flowering (29 May–18 June), seven species are mid-flowering (19 June–9 July), and two species are late-flowering (10 July–19 August) (Table 1). Some species overlap between seasonal periods and are considered early- to mid-season flowering species or mid- to

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Table 1. Species by seasonal category of flowering.

Early-flowering	Early- to mid-flowering	Mid-flowering	Mid- to late-flowering	Late-flowering
29 May–8 June	29 May–9 July	19 June–9 July	19 June–19 August	10 July–19 August
Antennaria monocephala (F)	*Betula nana* (DS)	*Andromeda polifolia* (ES)	*Bistorta officinalis* (F)	*Chamerion angustifolium* (F)
Arctous alpina (DS)	*Cassiope tetragona* (ES)	*Bupleurum americanum* (F)	*Rhododendron tomentosum* (ES)	*Chamerion latifolium* (F)
Carex bigelowii (G)	*Hierochloe alpina* (G)	*Pedicularis* spp. (F)		*Potentilla hyparctica* (F)
Dryas octopetala (ES)	*Rubus chamaemorus* (F)	*Poa arctica* (G)		
Eriophorum vaginatum (G)	*Salix* spp. (DS)	*Saussurea angustifolia* (F)		
Kalmia procumbens (ES)	*Vaccinium uliginosum* (DS)	*Stellaria borealis* (F)		
Luzula confusa (G)		*Vaccinium vitis-idaea* (ES)		
Oxytropis nigrescens (F)				
Petasites frigidus (F)				

Note: Species for which 90% of the range between the mean first day of flowering and the mean last day of flowering occurred within one seasonal category were assigned to early-, mid-, or late-flowering categories. If the mean first day of flowering and the mean last day of flowering extended over two categories, that species occupies two seasonal categories (early- to mid-, or mid- to late-flowering). DS = deciduous shrub; ES = evergreen shrub; F = forb; G = graminoid. To satisfy sample size requirements, we grouped a few species together: *Pedicularis* species = *P. capitata*, *P. lanata*, and *P. lapponica*; *Salix* species = *S. pulchra*, *S. phlebophylla*, and *S. reticulata*. The following species did not appear in control plots and are excluded from this table: *Arnica lessingii* (F) and *Bistorta vivipara* (F).

late-season flowering species (Table 1). *Bistorta officinalis* was one of the longest-flowering species at our sites, lasting 7 weeks in 2019 and 9 weeks in 2020 (Tables S4 and S5). When we assessed seasonal flowering by growth form, we found that all deciduous shrubs fell into the early- or early-to-mid-season categories. Graminoids qualified as early-season, with the exception of *Poa arctica*, which flowered during the mid-season. Forbs and evergreen shrubs flowered throughout the entire season (Table 1).

Floral visitor observations

In 2019, we recorded a total of 375 floral visits. We recorded only 60 total visits in 2020. A later start date for data collection in 2020 could possibly explain the lower number of visits recorded. For example, the early flowering species, *Arctous alpina,* received 33 visits in 2019 and no visits in 2020 (Table S6). Floral visitor observations did not begin until DOY 168 in 2020, 11 days after the first flowering recorded in this species (Table S5). Despite the difference in total visits between years, a clear pattern emerged: the majority of visits occurred in control plots and not in warmed plots (2019: 94% vs. 6%; 2020: 75% vs. 22%). In 2019, the mean number of visits per 5 min observation was significantly higher in the control plots ($M \pm SD = 1.58 \pm 2.87$) compared to the warmed plots (0.17 ± 0.62) ($Z = 6.62$, $p < 0.001$) (Table S6). This pattern held true in 2020, though it was not significant. The GLMMs indicated that the weekly patterns for the number of visits per observation were not significantly different between control and warmed plots (1, 4, and 26 y) in 2019 and 2020. Forbs and evergreen shrubs received more visits than deciduous shrubs and graminoids (Table S6). Graminoids received no visits (Table S6). In both 2019 and 2020, Diptera accounted for the majority of total recorded visits (2019: 56%; 2020: 75%), followed by Hymenoptera (2019: 46%; 2020: 18%) (Table S6). Lepidoptera and Coleoptera accounted for only a small minority of total visits (2019: 2%; 2020: 7%).

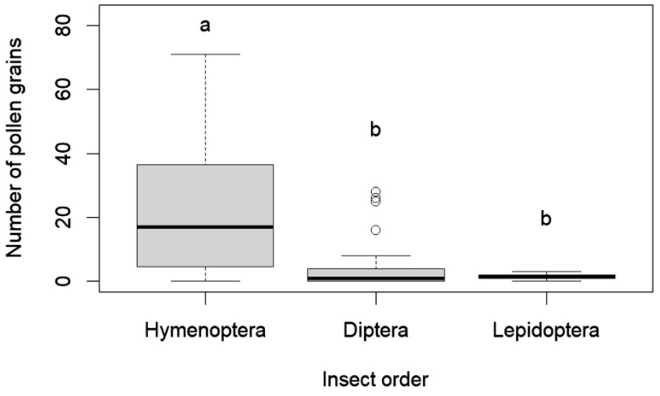
We found three distinct peaks of insect activity in 2019: early-season (weeks 1 and 2), mid-season (weeks 5 and 6), and late-season (weeks 8 and 9) (Table S7). In 2020, we observed only two distinct peaks: early- to mid-season (week 3) and mid- to late-season (weeks 6–8) (Table S8). The majority (88%) of these plant species were visited by both Dipterans and Hymenopterans, although not in equal proportions. For example, flies accounted for the majority of visits on *B. officinalis* and *R. tomentosum* (Table S6). Bees accounted for the majority of visits on *Chamerion angustifolium*, *Saussurea angustifolia*, *Vaccinium vitis-idaea*, and *Pedicularis* species (*P. kanei* and *P. lapponica*). Only a few plant species stand out as specialists: *A. alpina* was visited almost exclusively by bumblebees (97% of visits), while *D. octopetala* was visited almost exclusively by flies (95% of visits). *Stellaria* spp. and *P. hyparctica* were visited exclusively by flies (100% of visits) (Table S6).

Dipterans and Hymenopterans comprised 80% of the insects collected. The most abundant Dipteran families, from highest to lowest abundance, were Muscidae, Faniidae, and Culicidae (Table S9). An overwhelming majority of Hymenopterans were in the family Apidae, specifically bumblebees: *Bombus lapponicus sylvicola*, *B. jonellus*, *B. cryptarum*, *B. kirbiellus*, and *B. occidentalis*. Although only a minority ($n = 11$) of the insects we collected were Lepidopterans, the two most dominant families were Gracillariidae and Nymphalidae (Table S9). We also collected three beetles in the family Coccinellidae, specifically *Hippodamia arctica*. Although Order Hymenoptera taxonomically includes more than bees, we associate this order with bees based on our insect collection and visitor observations.

From a qualitative standpoint, Hymenopterans showed more active foraging behavior than Dipterans or Lepidopterans. Bumblebees made contact with the androecia and gynoecia, and a single individual landed up to eleven times in a single plot within a five-minute observation period. Collectively, flies were responsible for more visits than bees. However, a single individual only made up to three consecutive visits to a plot within a five-minute observation period. In contrast to bumble bees, flies basked on the flowers of *D. octopetala*, *R. tomentosum*, and *B. officinalis* for up to 5 min. Butterflies, *Boloria chariclea* and *B. improba*, contributed only a few visits and

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Fig. 4. Box plot showing the median number of pollen grains by insect order collected in 2019. Data are from all warmed and control plots combined. Coleopterans were not included in the analysis because of the insufficient sample size. Different letters indicate significance between Hymenoptera ($n = 19$) and Diptera ($n = 41$) at $\alpha = 0.001$, and Hymenoptera and Lepidoptera ($n = 10$) at $\alpha = 0.01$, using a Mann–Whitney *U* test.



stayed on an inflorescence of *B. officinalis* between 15 s and 5 min.

Pollen analyses

Three insect specimens were damaged, so pollen grains were counted for 73 insects. We found a clear pattern in the quantity of pollen attached to insects. The median number of pollen grains found in Hymenopterans was significantly higher than in Dipterans ($U = 150$, $p < 0.001$) or Lepidopterans ($U = 148.5$, $p = 0.01$). Pollen loads did not differ significantly between Dipterans and Lepidopterans ($U = 185.5$, $p > 0.05$) (Fig. 4).

Pollen-limitation experiments

All four species examined produced fruit in the pollen-limitation treatment (bagged), indicating they are all self-compatible. Excluding visitors reduced fruit set in all species except for *D. octopetala*, although the results were only significant for *B. officinalis* ($t = 2.65$, $p < 0.05$) (Fig. 5). Warming significantly decreased fruit set in *B. officinalis* ($Z = -1.97$, $p < 0.05$), while warming significantly increased fruit set in *R. tomentosum* ($Z = 4.60$, $p < 0.001$), *D. octopetala* ($t = 2.18$, $p < 0.05$), and *C. tetragona* ($Z = 2.72$, $p < 0.01$) (Fig. 5).

Nectar

Nectar volume (μL) in *V. uliginosum* was significantly higher in the warmed plots compared to control plots ($M \pm SD$: control $= 4.43 \pm 2.57$); 26 y $= 6.64 \pm 3.22$; 1 y $= 6.63 \pm 3.45$). This was true for both the 26 y warmed plots ($t = -4.04$, $p < 0.001$) and the 1 y warmed plots ($t = -4.01$, $p < 0.001$). However, % sucrose did not differ significantly between the warmed plots and control ($M \pm SD$: control $= 21.28 \pm 12.21$; 26 y $= 19.53 \pm 12.51$; 1 y $= 16.3 \pm 9.80$) ($t = 1.98$, $p > 0.05$). Although this species produces nectar, it received no floral visits (Tables S7 and S8).

Discussion

We tested four main research questions to address flowering phenology, floral visitor activity, pollen limitation, and nectar production. First, we found that long-term warming advanced flowering onset in evergreen shrubs and forbs. Flowering duration increased in warmed plots for evergreen shrubs, deciduous shrubs, and forbs. Considering all growth forms, long-term warming increased floral density. This increase was driven primarily by deciduous and evergreen shrubs. Second, floral visitation was lower in warmed plots. We also found more evidence for generalist plant–pollinator interactions than specialists. Although flies accounted for more floral visits, bees transported more pollen. Third, insect exclusion and warming decreased reproductive success in only one species: *B. officinalis*. Finally, warming increased nectar volume in *V. uliginosum* but did not affect nectar quality. These results advance our understanding of plant reproductive responses to warming in tundra systems.

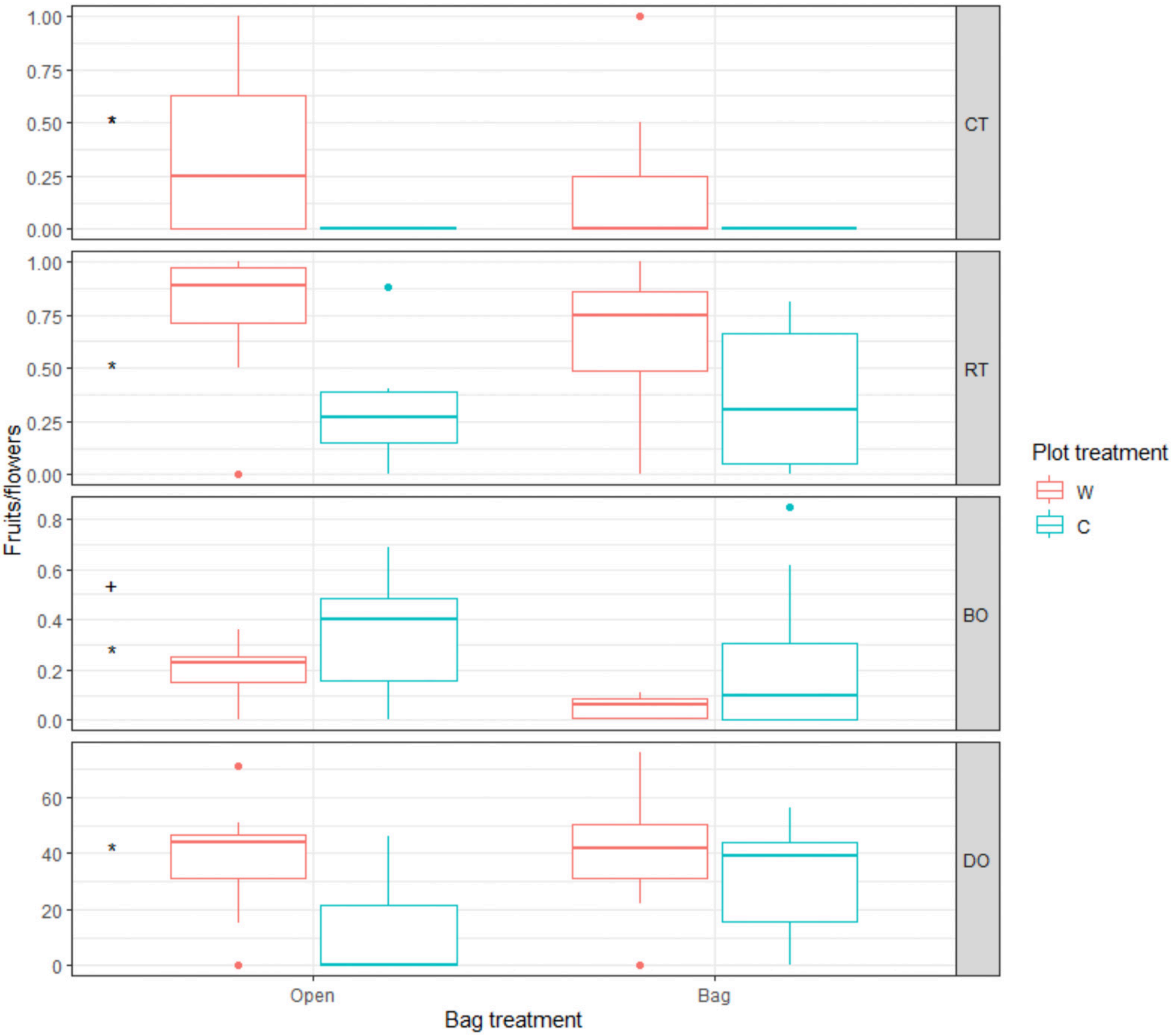
Flowering phenology, duration, and density

Warming has been shown to affect reproductive phenophases in a variety of ways (Collins et al. 2021). Heterogeneous and species-specific responses to warming are well documented, particularly for reproductive variables (Henry and Molau 1997; Arft et al. 1999; Klady et al. 2011; Collins et al. 2021). In our study, long-term warming advanced flowering onset in 2019, but not in 2020. This response was likely due to a few evergreen species (*A. polifolia* and *R. tomentosum*) flowering significantly earlier in the warmed plots in 2019. We also found that flowering lasted longer in forbs and evergreen shrubs. Chen et al. (2020) found increased flower duration in some but not all species in response to passive warming on the Tibetan Plateau. Other studies have highlighted the strong responses of forbs and evergreen shrubs to warming (Henry and Molau 1997; Arft et al. 1999; Dunne et al. 2003; Smith et al. 2012). Given that forbs and evergreen shrubs offer important floral rewards to floral visitors, changes in flowering duration in these growth forms could have important implications for pollinators and plant reproductive success. Differential effects between the 2 years in our study have two possible explanations. First, later snowmelt and a cooler mean July temperature in 2020 may have delayed flowering onset. Although onset was still advanced in the long-term warmed plots relative to the controls in 2020, this difference was not large enough to be statistically significant. The date of snowmelt has been shown to strongly affect flowering onset (Totland and Alatalo 2002; Bjorkman et al. 2015). Second, we only used the 5 y and 27 y warmed plots in 2020, which led to a reduced sample size (number of plots) and, therefore, a lower power to detect significant differences. Because a few species had initiated flowering prior to the start of our data collection, results about the onset and duration of flowering should be confirmed in future studies.

Flowering lasted longer in the early-flowering, prostrate deciduous shrub, *Arctous alpina*. Longer flowering duration in *A. alpina* has implications for early-season pollinators, as this early-flowering shrub is a critical nectar source for queen

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Fig. 5. Median fruit set by pollination and plot treatments in 2019. Pollination treatment refers to bagged or open/control. Plot treatment refers to warmed (W) or control (C) plots. The 203 observations were collected from 25 control plots and 29 warmed plots from all warming treatment durations in both sites and community types ($n_{26} = 13$, $n_4 = 6$, and $n_1 = 10$; subscripts refer to years of warming treatment). Fruit set is the proportion of fruit to flowers in CT (*Cassiope tetragona*), BO (*Bistorta officinalis*), and RT (*Rhododendron tomentosum*). Fruit set is the number of achenes per flower head in DO (*Dryas octopetala*), as DO produces only one terminal flower head per shoot. Note the different Y-axis scales for DO. The symbols * and + indicate significant main effects within the plot and bag treatments, respectively. $p < 0.05$ for *B. officinalis* and *D. octopetala*, and $p < 0.001$ for *R. tomentosum*. The interactions between the plot and bag treatment were not statistically significant.



bumble bees emerging from hibernation (Kudo 2014). A strong relationship has been reported between the duration of flowering and flower abundance (Dorji et al. 2020); a later end date can extend flowering duration and increase flower abundance over the course of the flowering season. This has implications for insect visitors as flower abundance and the number of floral visits are strongly correlated (Stang et al. 2006; Gillespie et al. 2016; Richman et al. 2020). Considering all species together, we found that floral density was significantly higher in the long-term warmed plots compared to the control. Klady et al. (2011) reported a similar trend: long-term warming of 12 years by OTCs significantly increased reproductive effort, defined as flower biomass. However, we found more nuanced responses from individual growth forms. Our results align with those of Frei and Henry (2022), who reported higher flower density with long-term warming, although these responses were species-specific. In our study, floral density in forbs was lowest in the long-term warmed plots compared to the control, though this difference was not statistically significant. A larger sample size in future

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

research could increase our ability to detect an effect. In the sub-alpine, Saavedra et al. (2003) also found that warming decreased the abundance of flowers in the forb, *Delphinium nuttallianum*. Forbs represent critical nectar and pollen resources for insects.

In contrast, when assessing floral density on a week-by-week basis, we found that the deciduous shrub, *Betula nana*, and the evergreen shrub, *Kalmia procumbens*, had consistently higher floral density in long-term warmed plots relative to control plots. Although *B. nana* is anemophilous (de Groot et al. 1997), *K. procumbens* offers an important early-season nectar resource for queen bumblebees (Kudo 2014). Thus, while long-term warming may increase floral density at the community level, only increases in growth forms such as evergreen shrubs that provide floral rewards will benefit nectar feeders and pollen foragers. On the other hand, decreased forb floral density could neutralize any benefit offered by evergreen shrubs.

In addition to flower abundance, the diversity of floral rewards is also critical to the pollinator community. We found fewer species in bloom in the long-term warming treatment compared to the control. Other studies have reported decreases in vascular plant species richness (Chapin et al. 1995; Hollister et al. 2005) and diversity (Molau and Alatalo 1998; Walker et al. 2006; Harris et al. 2021). While we focus on pollination and, therefore, the number of species in bloom as opposed to overall plant diversity, the patterns are similar: there is a general trend toward decreased diversity in warmed plots. Increased shrub cover (Wahren et al. 2005; Tape et al. 2006; Elmendorf et al. 2012*a*; Myers-Smith et al. 2015) and canopy height (Hollister et al. 2005; Elmendorf et al. 2012*b*; Bjorkman et al. 2018) are well-documented consequences of warming and can negatively impact plant species diversity and floral rewards. Increased canopy height has a shading effect, which can reduce reproductive output (Tolvanen 1995; Totland and Eide 1999; May et al. 2022). Sustained warming may also lead to soil drying, which has been shown to drive deciduous shrub expansion in wet meadow plant communities (Scharn et al. 2022). Evergreen shrubs and forbs provide important nectar rewards for insects, as opposed to graminoids and erect, deciduous shrubs. Thus, fewer species of flowering plants will result in a decreased diversity of floral rewards for pollinators.

Nectar

The nectar energy reward available to pollinators is determined by both volume and concentration (Pacini and Nicolson 2007). We found nectar production in *V. uliginosum* increased significantly in both the long-term and short-term warmed plots. Our results differ from other studies that found nectar volume decreased in response to artificial warming (Mu et al. 2015; Descamps et al. 2018; Descamps et al. 2021). In contrast to nectar quantity, we found no significant difference in nectar concentration between the warmed and control plots, in agreement with Carroll et al. (2001) and Mu et al. (2015) (but see Descamps et al. 2021 and McCombs et al. 2022). Nectar concentration may be less responsive to abiotic stress than volume, as concentration may be the result of selection by pollinators for concentrations that maximize feeding rate and energetic intake (Carroll et al. 2001; Erhardt et al. 2005; Descamps et al. 2018). We interpret our results with caution, given that they are from a single growing season. The studies to which we compare our results varied in the methods and duration of experimental warming and did not take place in the Arctic. Only a few studies have quantified nectar in tundra plants (Hocking 1968; Erhardt et al. 2005).

Plant–pollinator interactions

We recorded considerably fewer floral visits in 2020 compared to 2019; this difference has three possible explanations. First, the deciduous shrub, *Arctous alpina*, accounted for a high number of visits in 2019, but was not observed in 2020. A later start date for floral visitor data collection could possibly explain the lack of visits recorded on *A. alpina* in 2020. Second, some species, such as *B. officinalis*, which accounted for a high number of visits in 2019, bloomed in fewer plots in 2020. Third, floral visitor observations were conducted by EDC staff in 2020 and not the authors of this study, perhaps introducing an observer error. Despite this difference, the majority of floral visitor observations in 2019 and 2020 yielded zero visits. This result matches other studies in the Arctic that recorded low visitation rates, in general (Totland and Eide 1999; Robinson and Henry 2018; Gillespie and Cooper 2021).

Of the insect visits we recorded, significantly fewer visits occurred in the warmed plots compared to the control plots in both years. Previous studies have acknowledged that OTCs may impede visitation (Bocher 1996; Jones et al. 1997; Marion et al. 1997; Molau 1997) and herbivory (Richardson et al. 2000). In an early ITEX study, Jones (1995) reported reduced pollinator visits in OTCs in one year, but not the following year. In a subalpine study using OTCs, Adamson and Iler (2021) found clear evidence of a barrier effect, reporting a reduction in visitation by 92% in *Delphinium nuttallianum* and 85% in *Potentilla pulcherrima*. The OTC shape, vertical height, and size of the top opening may explain contrasting results in visitation rates throughout the literature. The walls of the OTC are perceived as a barrier to the insects, particularly if the OTC is small, as in the case of a cone chamber compared to a hexagon chamber (Marion et al. 1997). However, Robinson and Henry (2018) used larger, hexagonal OTCs and reported no difference in visitation rates between OTCs and controls. Our OTCs have an opening of 0.6 m (compared to 1.5 m), potentially explaining why we found evidence for a barrier effect. Future studies could involve the removal of some OTCs before conducting visitor observations to detect a possible barrier effect.

It is also possible that the plant responses within the OTC affect the visitation patterns. OTCs consistently warm the plants, not the mobile insects, and do not directly manipulate the phenology of pollinators (Forrest 2015). Warming has been shown to decrease the diversity of flowering species (Wahren et al. 2005; Harris et al. 2021) and increase canopy cover and shading by deciduous shrubs (Myers-Smith et al. 2011; Elmendorf et al. 2012*a*). These factors could contribute to reduced floral rewards in warmed plots. According to

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

optimal foraging theory (Macarthur and Pianka 1966), lower quality patches will receive fewer visitors. Thus, bottom-up effects could drive pollination network structure; in an ambient warming study, Robinson et al. (2018) found that the flower community was a stronger predictor of plant–pollinator network complexity than the insect community. Høye et al. (2013) hypothesize that the observed decline in insect visitors in the High Arctic is related to a shorter flowering season and decreased floral resource availability.

Other studies from the High Arctic have reported the majority of interactions coming from a small group of generalists (Olesen et al. 2008; Klein et al. 2008; Gillespie and Cooper 2021; Cirtwill et al. 2023). Generalist networks can act as buffers to rapid environmental change and are likely an important compensatory feature for species poor networks, such as in the Arctic (Bascompte and Jordano 2007; Gillespie and Cooper 2021). Within this generalist framework, we identified only a few plant species that attracted exclusively (or near exclusively) one insect order: bumblebees dominated visits on *Arctous alpina*, while flies dominated on *D. octopetala*, *Stellaria* spp., and *Potentilla hyparctica.* True specialists are uncommon in Arctic networks (Olesen and Jordano 2002). We recognize that our methods do not adequately capture the network structure because we did not sample all the interactions present, nor do our observations account for the surrounding landscape, which may potentially mitigate the effects of phenological mismatch (Gillespie et al. 2016; Jordano 2016). However, very few studies have provided compelling evidence for phenological mismatches between plants and pollinators (Iler et al. 2013; Ovaskainen et al. 2013; Forrest 2015; Gillespie and Cooper 2021; but see Thomson 2010 and Kudo and Ida 2013). Here, we document baseline patterns in floral visitation at our sites with the future goal of creating static and dynamic networks (Jordano 1987; Olesen and Jordano 2002; Gillespie and Cooper 2021), which are necessary to detect potential plant–pollinator asynchrony. Future studies will require systematic sampling at a larger spatiotemporal scale to test warming effects on plant–pollinator synchrony.

We considered three main factors to determine if floral visitors were effective pollinators: foraging rate, collection efficiency, and vector pollen load (Inouye et al. 1994; Watts et al. 2011). Based on the first factor, foraging rate or visitation frequency, we conclude that Dipterans, specifically in the Muscidae, Fanniidae, and Syrphidae families, are the most important floral visitors at our sites, as they account for the most visits. These findings align with other Arctic studies (Kevan 1972; Elberling and Olesen 1999; Tiusanen et al. 2016; Robinson and Henry 2018; Urbanowicz et al. 2018). Flies are particularly important in Arctic and alpine tundra as Hymenopteran diversity decreases with latitude and altitude (Kearns 1992; Inouye et al. 2015; Raguso 2020). Other studies point to muscid and syrphid flies as the most common visitors on *D. octopetala* (Tiusanen et al. 2016), *Bistorta* spp. (Momose and Inoue 1993; Chen and Zang 2010), and *R. tomentosum* (Dlusskiĭ et al. 2005). In addition, variation in floral morphology influences the type of visitor. We found that bees had higher visitation rates on urn-shaped flowers such as in *A. alpina* and *Vaccinium vitis-idaea*, supporting the conclusion by Kevan (1972) that bees are important pollinators of the Ericaceae in the Arctic. We found flies more frequently visited flowers with “landing pads”, such as *D. octopetala*, *Potentilla* sp., and *Stellaria* sp. Woodcock et al. (2014) points out that the Dipteran preference for “open” flowers is likely explained by flies’ limited ability to manipulate flowers compared to Hymenopterans. However, we hesitate to assign importance to one insect type over another or subscribe to pollinator syndromes. Heterogeneity in plant morphology, as well as heterogeneity in insect morphology and behavior, impacts plant–pollinator structure (Gonzalez et al. 2010).

With respect to collection efficiency, we found that bumblebees had the most deliberate foraging behavior, probing flowers for nectar and actively collecting pollen. Our observations of bumblebees on *A. alpina*, *Chamerion angustifolium*, and *V. vitis-idaea* align with previous studies (Galen and Plowright 1985; Davis et al. 2003; Husband and Sabara 2004; Kennedy et al. 2006; Stephens 2012; Kudo 2014). In contrast to bumblebees, flies on *D. octopetala*, *R. tomentosum*, and *P. hyparctica* showed a mixture of foraging behavior and stationary basking. Dipterans visit flowers for reasons other than pollen/nectar, including to gain warmth, calories, and protection, as well as to mate (Hocking and Sharplin 1965; Kevan 1975; Kjellberg et al. 1982; Woodcock et al. 2014). Dipterans have lower foraging rates than Hymenopterans because of their longer handling time (Inouye et al. 2015). All of these factors could affect the low likelihood that flies will contact the sexual parts of the flower.

Thirdly, the transport of pollen grains is critical for a floral visitor to constitute a pollinator. We found a wide range of pollen loads on insect specimens, suggesting that some individuals are incidental visitors compared to constant visitors (Borkent and Schlinger 2008). While our field observations indicate that Dipterans were the most abundant visitors, we found that Hymenopterans carried significantly higher pollen loads than Dipterans or Lepidopterans. Dipterans are opportunistic floral visitors with low pollen uptake ability compared to Hymenopterans (Willmer 2011). In a montane study, Kearns and Inouye (1994) found that bumblebees deposited more pollen grains per visit than muscid flies or small bees. However, flies are important pollinators, as their high floral visitation rates and abundance can make up for their low pollen transport (Larson et al. 2001; Orford et al. 2015). It is also worth mentioning that muscid flies have bristles to trap pollen (Skevington and Dang 2002). Thus, we conclude that bumblebees and flies, particularly muscid flies, are important pollinators in our sites: bees for their pollen transport capacity and flies for their abundant floral visitation.

Pollen-limitation and reproductive output

Self-incompatibility is rare in tundra species (Molau 1993). Accordingly, we found all four species (*C. tetragona*, *D. octopetala*, *R. tomentosum*, and *B. officinalis*) to be self-compatible. We would expect autogamy to be prevalent in Arctic plants due to the highly variable environment (Kevan 1972). Koch et al. (2020) also found that eight Arctic species depended on pollinators but were not pollen-limited. While all four species we tested are self-compatible, cross-pollination appears to be

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

most important for *B. officinalis*, which produced significantly fewer fruit under the insect-exclusion treatment. Goldstein and Zych (2016) refer to *B. officinalis* as a hub species, as it represents a core floral resource for the insect community. Our visitor observations corroborate this finding, as *B. officinalis* attracted both Hymenopterans and Dipterans. Thus, by interacting with both Hymenopterans and Dipterans, *B. officinalis* appears to be a generalist species and may serve as an important "connector" of the pollination network (Gonzalez et al. 2010). This species warrants further research given that it interacts with multiple types of floral visitors, appears to be pollen-limited, and flowers for over half of the growing season. In the future, a proper network analysis of our sites can determine how strongly *B. officinalis* contributes to the nestedness and resilience of the plant–pollinator community.

In addition to the important role *B. officinalis* plays in attracting floral visitors for a substantial period of the growing season, this was the only species in our study that responded negatively to the warming treatment. Little is known about the reproductive responses of *B. officinalis* to warming, although some studies suggest warming decreases fruit and seed production in other Arctic and alpine species. Zi et al. (2023) found strong evidence that simulated warming decreases fruit numbers in Arctic and alpine tundra but not in other ecosystems. Stenstrom et al. (1997) found reduced fruit-to-flower ratios and seed production in warmed plants of *Saxifraga oppositifolia*. Alatalo et al. (2021) reported decreased fruit production in forbs when exposed to incremental increases in experimental warming but not to sustained OTC warming. High temperatures decrease the duration of stigma receptivity, which could lead to reduced pollination and fertilization success (Zinn et al. 2010). Pollen limitation and warming are particularly interesting to study in *B. officinalis* given its tristylous polymorphism (Chen et al. 2018); little is known about the relationship between warming and heterostyly.

In contrast to *B. officinalis*, fruit set in the evergreen shrubs, *C. tetragona*, *R. tomentosum*, and *D. octopetala* increased significantly in response to warming. Our results for *D. octopetala* align with other Arctic and alpine studies for this genus (Wookey et al. 1993; Welker et al. 1997; Alatalo et al. 2021). One explanation may be that warming reduces the rate of flower abortion (Wookey et al. 1993). However, Robinson and Henry (2018) found that seed number and seed mass of *D. integrifolia* did not change in response to OTC warming or hand-pollination, suggesting that warming and pollination are not strong drivers of seed production in *D. integrifolia*. In contrast to our findings, Suzuki and Kudo (2000) found warming by OTCs in the alpine tundra to have no effect on fruit production in *R. tomentosum*. Reproductive responses to warming may be site-specific and driven by local environmental conditions (Welker et al. 1997). Variable responses to warming may also be a result of different warming methods and the degree of warming (Zi et al. 2023). Based on our results, we conclude that warming has the potential to increase reproductive output in the evergreen shrub species at our sites, but these responses will likely vary with site and year (Collins et al. 2021).

Cassiope tetragona showed no evidence of pollen limitation. Our findings are supported by other studies showing this species is highly self-compatible (Kevan 1972; Molau 1993). In our study, *C. tetragona* produced low fruit set, in general, relative to the other species. Havström et al. (1993) also reported recruitment from seed to be rare, emphasizing the importance of vegetative propagation in this evergreen shrub. In the High Arctic, *C. tetragona* has been shown to make a trade-off between reproductive and vegetative allocation among years (Johnstone and Henry 1997). In addition, this species attracts few floral visitors and apparently relies little on outcrossing for reproductive success. Similar to our findings, Bergman et al. (1996) and Gillespie et al. (2016) found visitation on *C. tetragona* to be uncommon. A self-compatible breeding system may be advantageous for this species in the context of climate warming.

Conclusions

Warming affects the reproductive output of tundra plant species in asymmetric ways. Phenological results varied among growth forms and years, highlighting the complex and nuanced responses of the flowering community. Long-term warming advanced flowering onset in evergreen shrubs and forbs, and warming, in general, increased flowering duration in deciduous shrubs, evergreen shrubs, and forbs. Long-term warming increased floral density, driven primarily by deciduous and evergreen shrubs. All warming treatments decreased floral density in forbs. Phenological shifts may have important consequences for floral resource availability and pollinator fitness. Dipterans accounted for more visits than Hymenopterans, although Hymenopterans had higher pollen loads. Insect exclusion and warming significantly decreased fruit set in *B. officinalis,* suggesting that this species is pollen-limited and may not increase reproductive output in a warmer climate. In contrast, warming significantly increased fruit set in *D. octopetala* and *R. tomentosum*. OTCs appear to produce a barrier effect on pollinators at our sites; this effect may be related to the size of the OTCs. Thus, adequately testing the effects of warming on pollination will require new studies, such as the removal of OTCs or another warming method in the future. Finally, analyzing plant–pollinator interactions and floral rewards in various plant community types of the Arctic tundra will be critical to accurately predicting landscape-level changes in pollinator and plant reproductive responses to warming.

Acknowledgements

We are grateful to J. Feigelson, H. Henderson, A. Jennings, M. Luzincourt, and Z. Klingner for their dedication in the field and the lab. Data collection during the 2020 pandemic was made possible by A. Young and the staff of Toolik Field Station Environmental Data Center. Finally, we greatly appreciate the knowledge and work of B. Drummond, who identified all insect specimens.

Article information

History dates

Received: 20 July 2022
Accepted: 6 March 2024

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Accepted manuscript online: 22 March 2024
Version of record online: 28 June 2024

Notes

This paper is part of a Special Issue entitled "Impacts of climate change on tundra ecosystems: Three decades of results from the International Tundra Experiment (ITEX)".

Copyright

© 2024 The Author(s). This work is licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Data availability

Data are available through https://rpubs.com/fsancier/warming and from the corresponding author, RSK, upon reasonable request.

Author information

Author ORCIDs

Roxaneh S. Khorsand https://orcid.org/0000-0003-0607-0029
Flavia Sancier-Barbosa https://orcid.org/0000-0003-3097-0123
Jeremy L. May https://orcid.org/0000-0002-5622-9002
Toke T. Høye https://orcid.org/0000-0001-5387-3284
Steven F. Oberbauer https://orcid.org/0000-0001-5404-1658

Author contributions

Conceptualization: RSK, FSB, JLM, SFO
Data curation: RSK, FSB, JLM
Formal analysis: RSK, FSB
Funding acquisition: RSK, SFO
Investigation: RSK
Methodology: RSK, FSB, JLM, TTH, SFO
Project administration: RSK
Resources: RSK, SFO
Software: FSB
Supervision: RSK, SFO
Visualization: RSK, FSB
Writing – original draft: RSK, FSB
Writing – review & editing: RSK, FSB, JLM

Competing interests

The authors declare there are no competing interests.

Funding information

Funding was provided by the National Science Foundation (Award No. 1836898) and various entities of Colorado College, including the Department of Organismal Biology and Ecology, Natural Sciences Executive Council, and the Dean's Office. The Hevey Family Fund for Research Students at Colorado College also provided critical funding for this project.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/as-2022-0034.

References

Adamson, C.P., and Iler, A.M. 2021. Open-top warming chambers reduce animal pollination of two subalpine herbs. Journal of Pollination Ecology **29**: 231–239. doi:10.26786/1920-7603(2021)638.

Alarcón, R. 2010. Congruence between visitation and pollen-transport networks in a California plant–pollinator community. Oikos, **119**: 35–44. doi:10.1111/j.1600-0706.2009.17694.x.

Alatalo, J.M., Jägerbrand, A.K., Dai, J., Mollazehi, M.D., Abdel-Salam, A.S.G, Pandey, R., and Molau, U. 2021. Effects of ambient climate and three warming treatments on fruit production in an alpine, subarctic meadow community. American Journal of Botany, **108**(3): 411–422. doi:10.1002/ajb2.1631. PMID: 33792046.

Arft, A.M., Walker, M.D., Gurevitch, J.E.T.A., Alatalo, J.M., Bret-Harte, M.S., Dale, M., et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. Ecological Monographs, **69**(4): 491–511.

Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., et al. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology, **85**(9): 2408–2421. doi:10.1890/03-8024.

Bascompte, J., and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. Annual Review of Ecology, Evolution, and Systematics, **38**: 567–593. doi:10.1146/annurev.ecolsys.38.091206.095818.

Bell, K.L., and Bliss, L.C. 1980. Plant reproduction in an arctic environment. Arctic and Alpine Research, **12**: 1–10. doi:10.2307/1550585.

Bennett, J.M., Steets, J.A., Burns, J.H., Durka, W., Vamosi, J.C., Arceo-Gómez, G., Burd, M., et al. 2018. GloPL, a global data base on pollen limitation of plant reproduction. Scientific Data, **5**(1): 1–9. doi:10.1038/sdata.2018.249. PMID: 30482902.

Bergman, P., Molau, U., and Holmgren, B. 1996. Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. Arctic and Alpine Research, **28**(2): 196–202. doi:10.2307/1551760.

Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., Vellend, M., and Henry, G.H. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. Global Change Biology, **21**(12): 4651–4661. doi:10.1111/gcb.13051. PMID: 26216538.

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S.A., et al. 2018. Plant functional trait change across a warming tundra biome. Nature, **562**: 57–62. doi:10.1038/s41586-018-0563-7. PMID: 30258229.

Bocher, J. 1996. Further insect studies. In The ITEX manual. 2nd ed. *Edited by* U. Molau and P. Mølgaard. Danish Polar Center, Copenhagen, Denmark. pp. 37–38.

Borghi, M., Perez de Souza, L., Yoshida, T., and Fernie, A.R. 2019. Flowers and climate change: a metabolic perspective. New Phytologist, **224**(4): 1425–1441. doi:10.1111/nph.16031. PMID: 31257600.

Borkent, C.J., and Schlinger, E.I. 2008. Pollen loads and pollen diversity on bodies of *Eulonchus tristis* (Diptera: Acroceridae): implications for pollination and flower visitation. The Canadian Entomologist, **140**(2): 257–264. doi:10.4039/n07-061.

Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.J.W., et al. 2019. Key indicators of Arctic climate change: 1971–2017. Environmental Research Letters, **14**(4): 045010. doi:10.1088/1748-9326/aafc1b.

Carroll, A.B., Pallardy, S.G., and Galen, C. 2001. Drought stress, plant water status, and floral trait expression in fireweed, *epilobium angustifolium* (Onagraceae). American Journal of Botany, **88**(3): 438–446. doi:10.2307/2657108. PMID: 11250821.

Chapin, F.S., Bret-Harte, S.M., Hobbie, S.E., and Zhong, H. 1996. Plant functional types as predictors of transient responses of Arctic vegetation to global change. Journal of Vegetation Science, **7**: 347–358. doi:10.2307/3236278.

Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., and Laundre, J.A. 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology, **76**(3): 694–711. doi:10.2307/1939337.

Chen, M.L., and Zhang, X.P. 2010. Distyly in *Polygonum jucundum* Meisn. (Polygonaceae). Plant Systematics and Evolution **288**: 139–148. doi:10.1007/s00606-010-0318-x.

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Chen, J., Luo, Y., Chen, Y., Felton, A.J., Hopping, K.A., Wang, R.W., et al. 2020. Plants with lengthened phenophases increase their dominance under warming in an alpine plant community. Science of the Total Environment, **728**: 138891. doi:10.1016/j.scitotenv.2020.138891. PMID: 32361364.

Chen, M.L., Wang, X.Y., and Funke, A.L. 2018. Floral polymorphism in *Polygonum bistorta* l. Bangladesh Journal of Plant Taxonomy, **25**(1): 1–11. doi:10.3329/bjpt.v25i1.37174.

Cirtwill, A.R., Kaartinen, R., Rasmussen, C., Redr, D., Wirta, H., Olesen, J.M., et al. 2023. Stable pollination service in a generalist high Arctic community despite the warming climate. Ecological Monographs **93**: e1551. doi:10.1002/ecm.1551.

Collins, C.G., Elmendorf, S.C., Hollister, R.D., Henry, G.H., Clark, K., Bjorkman, A.D., et al. 2021. Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. Nature Communications, **12**(1): 1–12. doi:10.1038/s41467-021-23841-2.PMID: 33397941.

Davis, A.N., Holloway, P.S., and Kruse, J.J. 2003. Insect visitors and potential pollinators of lingonberries, *Vaccinium vitis-idaea* subsp. *Minus*, in sub-Arctic Alaska. Acta Horticulturae, **62**: 433–438. doi:10.17660/ActaHortic.2003.626.60.

De Groot, W.J., Thomas, P.A., and Wein, R.W. 1997. *Betula nana* L. and *Betula glandulosa* Michx. The Journal of Ecology, **85**(2): 241–264. doi:10.2307/2960655.

Descamps, C., Boubnan, N., Jacquemart, A.L., and Quinet, M. 2021. Growing and flowering in a changing climate: effects of higher temperatures and drought stress on the bee-pollinated species *impatiens glandulifera* Royle. Plants, **10**: 988. doi:10.3390/plants10050988. PMID: 34063542.

Descamps, C., Quinet, M., Baijot, A., and Jacquemart, A.L. 2018. Temperature and water stress affect plant–pollinator interactions in *Borago officinalis* (Boraginaceae). Ecology and Evolution, **8**(6): 3443–3456. doi:10.1002/ece3.3914. PMID: 29607037.

Dlusskiĭ, G.M., Glazunova, K.P., and Perfileva, K.S. 2005. Mechanisms that limit pollinator range in Ericaceae. Zhurnal Obshchei Biologii, **66**(3): 224–238.

Dorji, T., Kelly, A.H., Fandong, M., Shiping, W., Jianga, L., and Kleine, J.A. 2020. Impacts of climate change on flowering phenology and production in alpineplants: The importance of end of flowering. Agriculture, Ecosystems and Environment **291**: 106795. doi:10.1016/j.agee.2019.106795.

Dunne, J.A., Harte, J., and Taylor, K.J. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. Ecological Monographs, **73**(1): 69–86. doi:10.1890/0012-9615(2003)073%5b0069:SMFPRT%5d2.0.CO;2.

Elberling, H., and Olesen, J.M. 1999. The structure of a high latitude plant–flower visitor system: the dominance of flies. Ecography, **22**(3): 314–323. doi:10.1111/j.1600-0587.1999.tb00507.x.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T.V., et al. 2012a. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters, **15**: 164–175. doi:10.1111/j.1461-0248.2011.01716.x.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., et al. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change, **2**: 453–457. doi:10.1038/nclimate1465.

Erhardt, A., Rusterholz, H.P., and Stöcklin, J. 2005. Elevated carbon dioxide increases nectar productionin Epilobium angustifolium L. Oecologia **146**: 311–317. doi:10.1007/s00442-005-0182-5.

Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis, E.J., Steltzer, H., and Wallenstein, M.D. 2014. Predicted responses of Arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology, **20**(10): 3256–3269. doi:10.1111/gcb.12568.

Forrest, J.R. 2015. Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? Oikos, **124**(1): 4–13. doi:10.1111/oik.01386.

Frei, E.R., and Henry, G.H.R. 2022. Long-term effects of snowmelt timing and climate warming on phenology, growth, and reproductive effort of Arctic tundra plant species. Arctic Science, **8**: 700–721. doi:10.1139/as-2021-0028.

Fulkerson, J.R., Whittall, J.B., and Carlson, M.L. 2012. Reproductive ecology and severe pollen limitation in the polychromic tundra plant, *Parrya nudicaulis* (Brassicaceae). PLoS One, **7**(3): e32790. doi:10.1371/journal.pone.0032790.

Galen, C., and Plowright, R.C. 1985. Contrasting movement patterns of nectar-collecting and pollen-collecting bumble bees (*Bombus terricola)* on fireweed (*Chamaerion angustifolium)* inflorescences. Ecological Entomology, **10**(1): 9–17. doi:10.1111/j.1365-2311.1985.tb00530.x.

Gillespie, M.A., Alfredsson, M., Barrio, I.C., Bowden, J.J., Convey, P., Culler, L.E., et al. 2020. Status and trends of terrestrial arthropod abundance and diversity in the North Atlantic region of the Arctic. Ambio, **49**(3): 718–731. doi:10.1007/s13280-019-01162-5.

Gillespie, M.A.K., and Cooper, E.J. 2021. The seasonal dynamics of a High Arctic plant—visitor network: temporal observations and responses to delayed snow melt. Arctic Science, 1–18.

Gillespie, M.A.K., Baggesen, N., and Cooper, E.J. 2016. High Arctic flowering phenology and plant–pollinator interactions in response to delayed snow melt and simulated warming. Environmental Research Letters, **11**: 115006. doi:10.1088/1748-9326/11/11/115006.

Goldstein, J., and Zych, M. 2016. What if we lose a hub? Experimental testing of pollination network resilience to removal of keystone floral resources. Arthropod-Plant Interactions, **10**(3): 263–271. doi:10.1007/s11829-016-9431-2.

González, A.M.M., Dalsgaard, B., and Olesen, J.M. 2010. Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity, **7**(1): 36–43. doi:10.1016/j.ecocom.2009.03.008.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature, **250**: 26–31. doi:10.1038/250026a0.

Harris, J.A., Hollister, R.D., Botting, T.F., Tweedie, C.E., Betway, K.R., May, J.L., et al. 2022. Understanding the climate impacts on decadal vegetation change in northern Alaska. Arctic Science, **8**(3): 878–898. doi:10.1139/as-2020-0050.

Havström, M., Callaghan, T.V., and Jonasson, S. 1993. Differential growth responses of *Cassiope tetragona*, an Arctic dwarf-shrub, to environmental perturbations among three contrasting high-and subArctic sites. Oikos, **66**: 389–402. doi:10.2307/3544933.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., and Totland, Ø. 2009. How does climate warming affect plant–pollinator interactions? Ecology Letters, **12**(2): 184–195. doi:10.1111/j.1461-0248.2008.01269.x.

Henry, G., Hollister, R., Jónsdóttir, I.S., Klanderlud, K., Molau, U., Oberbauer, S.F., et al. 2013. The International Tundra Experiment: an Arctic monitoring network. Available from https://Arcticobservingsummit.org/aos-2013-white-papers.

Henry, G., Hollister, R.D., Klanderud, K., Björk, R.G., Bjorkman, A.D., Elphinstone, C., et al. 2022. The International Tundra Experiment (ITEX): 30 years of research on Tundra ecosystems. Arctic Science, **8**: 550–571. doi:10.1139/as-2022-0041.

Henry, G.H.R., and Molau, U. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). Global Change Biology, **3**(S1): 1–9. doi:10.1111/j.1365-2486.1997.gcb132.x.

Hocking, B. 1968. Insect–flower associations in the High Arctic with special reference to nectar. Oikos, **19**: 359–387. doi:10.2307/3565022.

Hocking, B., and Sharplin, C.D. 1965. Flower basking by Arctic insects. Nature, **206**: 215. doi:10.1038/206215b0.

Hoiss, B., Krauss, J., and Steffan-Dewenter, I. 2015. Interactive effects of elevation, species richness and extreme climatic events on plant–pollinator networks. Global Change Biology, **21**: 4086–4097. doi:10.1111/gcb.12968.

Hollister, R.D., Elphinstone, C.E., Henry, G.H.R., Bjorkman, A.D., Klanderud, K., Björk, R.G., et al. 2022. A review of open-top chamber (OTC) performance across the ITEX Network. Arctic Science, 1–14.

Hollister, R.D., Webber, P.J., and Tweedie, C. 2005. The response of Alaskan Arctic Tundra to experimental warming: differences between short- and long-term responses. Global Change Biology, **11**: 525–536. doi:10.1111/j.1365-2486.2005.00926.x.

Hothorn, T., Hornik, K., van de Wiel, M.A., and Zeileis, A. 2008. Implementing a class of permutation tests: the coin package. Journal of Statistical Software, **28**(8): 1–23. doi:10.18637/jss.v028.i08.

Høye, T.T. 2020. Arthropods and climate change–Arctic challenges and opportunities. Current Opinion in Insect Science, **41**: 40–45. doi:10.1016/j.cois.2020.06.002.

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Høye, T.T., Post, E., Meltofte, H., Schmidt, N.M., and Forchhammer, M.C. 2007. Rapid advancement of spring in the High Arctic. Current Biology, **17**(12): R449–R451. doi:10.1016/j.cub.2007.04.047.

Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K., and Forchhammer, M.C. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. Nature Climate Change, **3**(8): 759–763. doi:10.1038/nclimate1909.

Husband, B.C., and Sabara, H.A. 2004. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, *Chamerion angustifolium* (Onagraceae). New Phytologist, **161**(3): 703–713. doi:10.1046/j.1469-8137.2004.00998.x.

Iler, A.M., Høye, T.T., Inouye, D.W., and Schmidt, N.M. 2013. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? Philosophical Transactions of the Royal Society B, **368**: 20120489. doi:10.1098/rstb.2012.0489.

Inouye, D.W., Gill, D.E., Dudash, M.R., and Fenster, C.B. 1994. A model and lexicon for Pollen fate. American Journal of Botany, **81**(12): 1517–1530. doi:10.1002/j.1537-2197.1994.tb11462.x.

Inouye, D.W., Larson, B.M., Ssymank, A., and Kevan, P.G. 2015. Flies and flowers III: ecology of foraging and pollination. Journal of Pollination Ecology, **16**(16): 115–133. doi:10.26786/1920-7603(2015)15.

Johnstone, J.F., and Henry, G.H. 1997. Retrospective analysis of growth and reproduction in *Cassiope tetragona* and relations to climate in the Canadian High Arctic. Arctic and Alpine Research, **29**: 459–469. doi:10.2307/1551993.

Jones, M.H., 1995. Experimental investigations into effects of climate-change on high arctic plants PhD thesis.University of Alberta, Edmonton, Canada.

Jones, M.H., Bay, C., and Nordenhäll, U. 1997. Effects of experimental warming on Arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish SubArctic. Global Change Biology, **3**(Suppl. 1): 55–60. doi:10.1111/j.1365-2486.1997.gcb135.x.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. The American Naturalist, **129**: 657–677. doi:10.1086/284665.

Jordano, P. 2016. Sampling networks of ecological interactions. Functional Ecology, **30**(12): 1883–1893. doi:10.1111/1365-2435.12763.

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B., and Caflisch, A. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. Ecology Letters, **13**: 442–452. doi:10.1111/j.1461-0248.2009.01437.x.

Kearns, C.A. 1992. Anthophilous fly distribution across an elevation gradient. American Midland Naturalist, **127**(1): 172–182. doi:10.2307/2426332.

Kearns, C.A., and Inouye, D.W. 1993. Techniques for pollination biologists. University Press of Colorado, Niwot, CO.

Kearns, C.A., and Inouye, D.W. 1994. Fly pollination of *Linum lewisii* (Linaceae). American Journal of Botany, **81**(9): 1091–1095. doi:10.1002/j.1537-2197.1994.tb15602.x.

Kennedy, B.F., Sabara, H.A., Haydon, D., and Husband, B.C. 2006. Pollinator-mediated assortative mating in mixed ploidy populations of *Chamerion angustifolium* (Onagraceae). Oecologia, **150**(3): 398–408. doi:10.1007/s00442-006-0536-7.

Kevan, P.G. 1972. Insect pollination of high Arctic flowers. The Journal of Ecology, **60**: 831–847. doi:10.2307/2258569.

Kevan, P.G. 1975. Sun-tracking solar furnaces in high Arctic flowers: significance for pollination and insects. Science, **189**(4204): 723–726. doi:10.1126/science.189.4204.723.

Khorsand Rosa, R., Oberbauer, S.F., Starr, G., ParkerLa Puma, I., Pop, E., Ahlquist, L., and Baldwin, T. 2015. Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. Global Change Biology, **21**(12): 4520–4532. doi:10.1111/gcb.13040.

Kjellberg, B., Karlsson, S., and Kerstensson, I. 1982. Effects of heliotropic movements of flowers of *Dryas octopetala* L. on gynoecium temperature and seed development. Oecologia, **54**(1): 10–13. doi:10.1007/BF00541101.

Klady, R.A., Henry, G.H., and Lemay, V. 2011. Changes in high Arctic tundra plant reproduction in response to long-term experimental warming. Global Change Biology, **17**(4): 1611–1624. doi:10.1111/j.1365-2486.2010.02319.x.

Klein, D.R., Bruun, H.H., Lundgren, R., and Philipp, M. 2008. Climate change influences on species interrelationships and distributions in High-Arctic Greenland. Advances in Ecological Research, **40**: 81–100. doi:10.1016/S0065-2504(07)00004-9.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., and Holt, R.D. 2005. Trophic cascades across ecosystems. Nature, **437**(7060): 880–883. doi:10.1038/nature03962.

Koch, V., Zoller, L., Bennett, J.M., and Knight, T.M. 2020. Pollinator dependence but no pollen limitation for eight plants occurring north of the Arctic Circle. Ecology and Evolution **10**: 13664–13672. doi:10.1002/ece3.6884.

Kudo, G. 2014. Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. Ecological Research, **29**(4): 571–581. doi:10.1007/s11284-013-1108-z.

Kudo, G., and Cooper, E.J. 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B: Biological Sciences, **286**(1904): 20190573. doi:10.1098/rspb.2019.0573.

Kudo, G., and Ida, T.Y. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. Ecology, **94**(10): 2311–2320. doi:10.1890/12-2003.1.

Larson, B.M.H., Kevan, P.G., and Inouye, D.W. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. The Canadian Entomologist, **133**(4): 439–465. doi:10.4039/Ent133439-4.

Lundgren, R., and Olesen, J.M. 2005. The dense and highly connected world of Greenland's plants and their pollinators. Arctic, Antarctic, and Alpine Research, **37**: 514–520. doi:10.1657/1523-0430(2005)037%5b0514:TDAHCW%5d2.0.CO;2.

MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. The American Naturalist, **100**(916): 603–609. doi:10.1086/282454.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., et al. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology, **3**(S1): 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x.

May, J.L., Oberbauer, S.F., Unger, S.L., Simon, M.J., Betway, K.R., and Hollister, R.D. 2022. Shading decreases and delays NDVI and floweringof prostrate Arctic shrubs. Arctic Science **8**: 967–978. doi:10.1139/as-2020-0043.

McCombs, A., Debinski, D., Reinhardt, K., Germino, M.J., and Caragea, P. 2022. Warming temperatures affect meadow-wide nectar resources, with implications for plant–pollinator communities. Ecosphere, **13**: e4162. doi:10.1002/ecs2.4162.

Molau, U. 1993. Relationships between flowering phenology and life history strategies in tundra plants. Arctic and Alpine Research, **25**(4): 391–402. doi:10.2307/1551922.

Molau, U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. Global Change Biology, **3**(Suppl. 1): 97–107. doi:10.1111/j.1365-2486.1997.gcb138.x.

Molau, U., and Alatalo, J.M. 1998. Response of subarctic–alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. Ambio, **27**: 322–329.

Molau, U., and Mølgaard, P. 1996. ITEX Manual, Second Edition.

Molau, U., and Shaver, G.R. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. Global Change Biology, **3**(S1): 80–88. doi:10.1111/j.1365-2486.1997.gcb130.x.

Momose, K., and Inoue, T. 1993. Pollination and factors limiting fruit set of chasmogamous flowers of an amphicapric annual, *Polygonum thunbergii* (Polygonaceae). Population Ecology, **35**(1): 79–93. doi:10.1007/BF02515647.

Mu, J., Peng, Y., Xi, X., Wu, X., Li, G., Niklas, K.J., and Sun, S. 2015. Artificial asymmetric warming reduces nectar yield in a Tibetan alpine species of Asteraceae. Annals of Botany, **116**(6): 899–906. doi:10.1093/aob/mcv042.

Murray, D.F. 1997. Systematics of the ITEX species. Global Change Biology, **3**(Suppl. 1): 10–19. doi:10.1111/j.1365-2486.1997.gcb131.x.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S., Wilmking, M., Hallinger, M., Blok, D., et al. 2015. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change, **5**(9): 887–891. doi:10.1038/nclimate2697.

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters **6**: 045509. doi:10.1088/1748-9326/6/4/045509.

Ne'eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S.G., and Dafni, A. 2010. A framework for comparing pollinator performance: effectiveness and efficiency. Biological Reviews, **85**(3): 435–451. doi:10.1111/j.1469-185X.2009.00108.x.

Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., et al. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Philosophical Transactions of the Royal Society B: Biological Sciences, **368**(1624): 20120481. doi:10.1098/rstb.2012.0481.

Olesen, J.M., and Jordano, P. 2002. Geographic patterns in plant–pollinator mutualistic networks. Ecology, **83**(9): 2416–2424.

Olesen, J.M., Bascompte, J., Duponta, Y.L., and Jordano, P. 2006. The smallest of all worlds: Pollination networks. Journal of Theoretical Ecology **240**: 270–276. doi:10.1016/j.jtbi.2005.09.014.

Olesen, J.M., Bascompte, J., Elberling, H., and Jordano, P. 2008. Temporal dynamics in a pollination network. Ecology, **89**(6): 1573–1582. doi:10.1890/07-0451.1.

Orford, K.A., Vaughan, I.P., and Memmott, J. 2015. The forgotten flies: the importance of non-syrphid Diptera as pollinators. Proceedings of the Royal Society B: Biological Sciences, **282**(1805): 20142934. doi:10.1098/rspb.2014.2934.

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., et al. 2013. Community-level phenological response to climate change. Proceedings of the National Academy of Sciences, **110**(33): 13434–13439. doi:10.1073/pnas.1305533110.

Pacini, E., and Nicolson, S.W. 2007. Introduction, chapter 1. In Nectaries and nectar. *Edited by* S.W. Nicolson, M. Nepi and E. Pacini. Springer.

Panchen, Z.A., Frei, E.R., and Henry, G.H.R. 2022. Increased Arctic climate extremes constrain expected higher plant reproductive success in a warmer climate. Arctic Science, **8**: 680–699. doi:10.1139/as-2020-0045.

Parker, F.D. 1981. Sunflower pollination: abundance, diversity, and seasonality of bees and their effect on seed yields. Journal of Apicultural Research, **20**: 49–61. doi:10.1080/00218839.1981.11100473.

Parkinson, L.V., and Mulder, C.P.H. 2020. Patterns of pollen and resource limitation of fruit production in *Vaccinium uliginosum* and *V. vitis-idaea* in Interior Alaska. PLoS One, **15**(8): e0224056. doi:10.1371/journal.pone.0224056.

Parmesan, C., and Hanley, M.E. 2015. Plants and climate change: complexities and surprises. Annals of Botany, **116**(6): 849–864. doi:10.1093/aob/mcv169.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science, **325**: 1355–1358. doi:10.1126/science.1173113.

Prevéy, J., Elmendorf, S., Bjorkman, A., Alatalo, J., Ashton, I., Assmann, J., et al. 2021. The tundra phenology database: more than two decades of tundra phenology responses to climate change. Arctic Science.

Prevéy, J., Rixen, C., Rüger, N., Høye, T.T., Bjorkman, A.D., Myers-Smith, I.H., et al. 2019. Warming shortens flowering seasons of tundra plant communities. Nature Ecology & Evolution, **3**: 45–52. doi:10.1038/s41559-018-0745-6.

R Core Team 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Raguso, R.A. 2020. Don't forget the flies: dipteran diversity and its consequences for floral ecology and evolution. Applied Entomology and Zoology, **55**(1): 1–7. doi:10.1007/s13355-020-00668-9.

Richardson, S.J., Hartley, S.E., and Press, M.C. 2000. Climate warming experiments: are tents a potential barrier to interpretation? Ecological Entomology, **25**: 367–370. doi:10.1046/j.1365-2311.2000.00263.x.

Richman, S.K., Levine, J.M., Stefan, L., and Johnson, C.A. 2020. Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness. Global Change Biology, **26**(5): 3052–3064. doi:10.1111/gcb.15041.

Robinson, S.V., Losapio, G., and Henry, G.H. 2018. Flower-power: Flower diversity is a stronger predictor of network structure than insect diversity in an Arctic plant–pollinator network. Ecological Complexity, **36**: 1–6. doi:10.1016/j.ecocom.2018.04.005.

Robinson, S.V.J., and Henry, G.H.R. 2018. High Arctic plants show independent responses to pollination and experimental warming. Botany, **96**: 385–396. doi:10.1139/cjb-2017-0200.

Saavedra, F., Inouye, D.W., Price, M.V., and Harte, J. 2003. Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. Global Change Biology, **9**(6): 885–894. doi:10.1046/j.1365-2486.2003.00635.x.

Scaven, V.L., and Rafferty, N.E. 2013. Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. Current Zoology, **59**(3): 418–426. doi:10.1093/czoolo/59.3.418.

Scharn, R., Brachmann, C.G., Patchett, A., Reese, H., Bjorkman, A.D., Alatalo, J.M., et al. 2022. Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden. Arctic Science, **8**(3): 858–877. doi:10.1139/as-2020-0042.

Schmidt, N.M., Mosbacher, J.B., Nielsen, P.S., Rasmussen, C., Høye, T.T., and Roslin, T. 2016. An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. Ecography, **39**(12): 1250–1252. doi:10.1111/ecog.02261.

Settele, J., Bishop, J., and Potts, S.G. 2016. Climate change impacts on pollination. Nature Plants, **2**(7): 1–3. doi:10.1038/nplants.2016.92.

Shulski, M., and Wendler, G. 2007. The climate of Alaska. University of Alaska Press, Fairbanks, AK.

Skevington, J.H., and Dang, P.T. 2002. Exploring the diversity of flies (Diptera). Biodiversity, **3**(4): 3–27. doi:10.1080/14888386.2002.9712613.

Smith, J.G., Sconiers, W., Spasojevic, M.J., Ashton, I.W., and Suding, K.N. 2012. Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. Arctic, Antarctic, and Alpine Research, **44**(1): 135–142. doi:10.1657/1938-4246-44.1.135.

Stang, M., Klinkhamer, P.G.L., and van der Meijden, E. 2006. Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. Oikos, **112**: 111–121. doi:10.1111/j.0030-1299.2006.14199.x.

Stenström, M., and Molau, U. 1992. Reproductive ecology of *Saxifraga oppositifolia*: phenology, mating system, and reproductive success. Arctic and Alpine Research, **24**(4): 337–343. doi:10.2307/1551289.

Stenström, M., Gugerli, F., and Henry, G.H.R. 1997. Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. Global Change Biology, **3**(S1): 44–54. doi:10.1111/j.1365-2486.1997.gcb144.x.

Stephens, D. 2012. Pollination ecology and the floral reward of *Vaccinium myrtilloides* and *V. vitis-idaea* (Ericaceae). Doctoral dissertation, University of Saskatchewan.

Suzuki, S., and Kudo, G. 2000. Responses of alpine shrubs to simulated environmental change during three years in the mid-latitude mountain, northern Japan. Ecography, **23**(5): 553–564. doi:10.1111/j.1600-0587.2000.tb00174.x.

Tape, K.E.N., Sturm, M., and Racine, C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology, **12**(4): 686–702. doi:10.1111/j.1365-2486.2006.01128.x.

Thomson, J.D. 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. Philosophical Transactions of the Royal Society B: Biological Sciences, **365**: 3187–3199. doi:10.1098/rstb.2010.0115.

Tiusanen, M., Hebert, P.D., Schmidt, N.M., and Roslin, T. 2016. One fly to rule them all—muscid flies are the key pollinators in the Arctic. Proceedings of the Royal Society B: Biological Sciences, **283**(1839): 20161271. doi:10.1098/rspb.2016.1271.

Tolvanen, A. 1995. Aboveground growth habits of two *Vaccinium* species in relation to habitat. Canadian Journal of Botany, **73**(3): 465–473. doi:10.1139/b95-047.

Totland, Ø., and Alatalo, J.M. 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. Oecologia, **133**: 168–175. doi:10.1007/s00442-002-1028-z.

Totland, Ø., and Eide, W. 1999. Environmentally-dependent pollen limitation on seed production in alpine *Ranunculus acris*. Écoscience, **6**: 173–179. doi:10.1080/11956860.1999.11682518.

Urbanowicz, C., Virginia, R.A., and Irwin, R.E. 2017. The response of pollen-transport networks to landscape-scale climate variation. Polar Biology, **40**(11): 2253–2263. doi:10.1007/s00300-017-2138-8.

Arctic Science Downloaded from cdnsciencepub.com by 71.206.86.215 on 04/22/25

Urbanowicz, C., Virginia, R.A., and Irwin, R.E. 2018. Pollen limitation and reproduction of three plant species across a temperature gradient in western Greenland. Arctic, Antarctic, and Alpine Research, **50**(1): S100022. doi:10.1080/15230430.2017.1414485.

Vasiliev, D., and Greenwood, S. 2021. The role of climate change in pollinator decline across the Northern Hemisphere is underestimated. Science of the Total Environment, **775**: 145788. doi:10.1016/j.scitotenv.2021.145788.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York. ISBN 0-387-95457-0.

Wahren, C.H., Walker, M.D., and Bret-Harte, M.S. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biology, **11**(4): 537–552. doi:10.1111/j.1365-2486.2005.00927.x.

Walker, D.A., Raynolds, M.K., Daniëls, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A., et al. 2005. The Circumpolar Arctic vegetation map. Journal of Vegetation Science, **16**(3): 267–282. doi:10.1111/j.1654-1103.2005.tb02365.x.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H., Ahlquist, L.E., Alatalo, J.M., et al. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences, **103**(5): 1342–1346. doi:10.1073/pnas.0503198103.

Walker, M.D., Webber, P.J., Arnold, D., and Ebert-May, E.H. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology, **75**: 393–408. doi:10.2307/1939543.

Waser, N.M., and Price, M.V. 2016. Drought, pollen and nectar availability, and pollination success. Ecology, **97**(6): 1400–1409. doi:10.1890/15-1423.1.

Watts, S., Ovalle, D.H., Herrera, M.M., and Ollerton, J. 2011. Pollinator effectiveness of native and non-native flower visitors to an apparently generalist Andean shrub, *Duranta mandonii* (Verbenaceae). Plant Species Biology, **27**(2): 147–158. doi:10.1111/j.1442-1984.2011.00337.x.

Webber, P.J., and Walker, M.D. 1991. The International Tundra Experiment (ITEX): resolution. Arctic and Alpine Research, **23**: 124. doi:10.2307/1551451.

Welker, J.M., Molau, U., Parsons, A.N., Robinson, C.H., and Wookey, P.A. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. Global Change Biology, **3**: 61–73. doi:10.1111/j.1365-2486.1997.gcb143.x.

Wendler, G., Gordon, T., and Stuefer, M. 2017. On the Precipitation and Precipitation Change in Alaska. Atmosphere **8**: 253. doi:10.3390/atmos8120253.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York. p. 2.

Wickham, H., Francois, R., Henry, L., Muller, K., and Vaughan, D. 2023. dplyr: a grammar of data manipulation. R package version 1.1.2.

Williams, J.W., and Batzli, G.O. 1982. Pollination and dispersion of five species of lousewort (*Pedicularis*) near Atkasook, Alaska, U.S.A. Arctic and Alpine Research, **14**: 59–73. doi:10.2307/1550816.

Willmer, P. 2011. Pollination and floral ecology. Princeton University Press, Princeton, NJ.

Woodcock, T.S., Larson, B.M., Kevan, P.G., Inouye, D.W., and Lunau, K. 2014. Flies and flowers II: floral attractants and rewards. Journal of Pollination Ecology, **12**: 63–94. doi:10.26786/1920-7603(2014)5.

Wookey, P.A., Parsons, A.N., Welker, J.M., Potter, J.A., Callaghan, T.V., Lee, J.A., and Press, M.C. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. Oikos, **67**: 490–502. doi:10.2307/3545361.

Wyatt, R., Broyles, S.B., and Derda, G.S. 1992. Environmental influences on nectar production in milkweeds (*Asclepias syriaca* and *A. exaltata*). American Journal of Botany, **79**(6): 636–642. doi:10.1002/j.1537-2197.1992.tb14605.x.

Zi, H., Jing, X., Liu, A., Fan, X., Chen, S.C., Wang, H., and He, J.S. 2023. Simulated climate warming decreases fruit number but increases seed mass. Global Change Biology, **29**: 841–855. doi:10.1111/gcb.16498.

Zimmerman, M. 1983. Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. Oikos, **41**: 57–63. doi:10.2307/3544346.

Zinn, K.E., Tunc-Ozdemir, M., and Harper, J.F. 2010. Temperature stress and plant sexual reproduction: uncovering the weakest links. Journal of Experimental Botany, **61**(7): 1959–1968. doi:10.1093/jxb/erq053.