Article

TIMING OF FLOWERING AFFECTS POLLINATION OF *VIBURNUM EDULE* IN ALASKAN BOREAL FOREST

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Abstract—Flowering time in Alaskan boreal forest is advancing, and this may affect pollination rates of early-flowering species. *Viburnum edule* is one of the first understory plants to flower, when pollinator diversity and abundance are likely lower than later in the season. We evaluated the impact of flowering time on pollen deposition and composition of the pollinator community over two years (one in which plants flowered slightly earlier than average and one in which flowering time was close to average) using experimental arrays with branches that flowered either at the start or the peak of flowering for each year. Pollinator exclusion reduced fruit set by > 90%, but even plants freely pollinated by insects had fruit set rates of < 10%. Both within and across years, plants that flowered later had more insect visitors and higher proportions of stigmas visited (> 5 pollen grains per stigma); in the advanced year, plants that flowered later also had more pollen grains per stigma. Syrphid flies, solitary bees, and muscid flies constituted ~ 99% of visitors, with a higher proportion of syrphid flies for later-flowering plants within and across years. Despite evidence for potential pollen limitation, pollen loads for the earliest flowering plants were high (mean > 25 pollen grains per stigma). Fruit production in *V. edule* is likely limited by inefficient pollen transfer between genets, by resource availability, or both. Given the prevalence of syrphid and muscid flies as pollinators, we need a better understanding of what triggers emergence in these taxa to evaluate the potential for trophic mismatches in boreal forest.

Keywords—Climate change, flowering phenology, muscid fly, solitary bee, syrphid fly, trophic mismatch

INTRODUCTION

As the climate warms, plants are generally responding to warmer springs by flowering earlier, though the size of the shift differs by species (e.g., Parmesan & Yohe 2003; Caradonna et al. 2014; Mulder & Spellman 2019a). When the phenology of plants and their pollinators differ in their responses to climate change, there is the potential for trophic mismatches: differential shifts in timing of activity for two interacting species or trophic groups that lead to reduced overlap and lower fitness for one or both partner (e.g., Kudo & Ida 2013; Gillespie et al. 2016; McKinney et al. 2012; Prather et al. 2023). Such trophic mismatches are especially likely in high-altitude and high-latitude systems such as boreal forest, alpine tundra, and arctic tundra, where growth seasons are short and flowering periods even shorter. Yet while such phenotypic trophic mismatches have been studied in alpine habitats (e.g., Forrest & Thomson 2011; Iler et al. 2013; Prather et al. 2023) and arctic tundra (e.g., Gillespie et al. 2016; Schmidt et al. 2016), plant-pollinator relationships in the boreal forest have received little attention (Kevan et al. 1993; Díaz-Calafat et al. 2025).

The boreal forest is the largest biome on earth, covering approximately 35% of the North American continent (Brandt 2009), and it is warming more rapidly than lower latitudes, with temperature increases of 0.25 – 0.5 °C per decade since 1950 (Rantanen et al. 2022). In Interior Alaska (the region between the Alaska Range and the Brooks Range) all native tree species and many of the taller shrubs (*Alnus* and some *Salix* species) are wind-pollinated (Kevan et al. 1993); short understory shrubs and forbs are primary sources of nectar and pollen for insects. Shrubs flower earlier than forbs (Mulder & Spellman 2019a), providing nectar and pollen resources for early-emerging pollinators. Boreal plants have short flowering seasons with highly synchronous flowering within individuals and within populations (Molau 1993; Mulder & Spellman 2019b). Reinitiation of growth and development in spring, including flowering, is triggered by ground thaw (e.g., Wipf 2010; Parazoo et al. 2018; Mulder & Spellman 2019a), which in turn is affected by early season air temperatures and total snow depth at the end of the winter. The combination of extreme seasonality, short, synchronous flowering periods and rapid warming in spring (Rantanen et al. 2022) makes boreal forest understory plants potentially vulnerable to plant-pollinator mismatches.

Trophic mismatches have been studied in a range of systems, with inconsistent results (Kharouba & Wolkovich 2020, 2023). They are most likely to occur under conditions where the period of overlap is short and where one group is highly dependent on another (Kharouba & Wolkovich 2023). Boreal plant species that flower early in the season are most responsive to early snowmelt and ground thaw (e.g., CaraDonna et al. 2014; Mulder & Spellman 2019a), but they are also most likely to suffer from low pollinator availability, even though many are generalists (Armbruster & Guinn 1989; Kevan et al. 1993). Cold temperatures may reduce pollinator activity early in the season: flying insects such as solitary bees and syrphid flies are limited in foraging time and range by thermal constraints (Willmer 1983; Bishop & Armbruster 1999). The pool of potential pollinators increases over the course of the summer, as more species emerge (Armbruster & Guinn 1989). As a result, the potential for plant-pollinator mismatches is most likely to affect species that flower shortly after snowmelt and ground thaw. However, such mismatches would only occur if pollinators shift at a different rate than plants in response to changing spring conditions.

Common pollinators of boreal plants include bumblebees (*Bombus* spp.), solitary bees (e.g., *Andrena, Dialictus, Hylaeus, Megachile* spp.), syrphid flies (Syrphidae), and muscid flies (Muscidae) (Barrett & Helenurm 1987; Armbruster & Guinn 1989; Kevan et al. 1993). Research on potential mismatches in plant-pollinator interactions has focused primarily on bee pollination; these studies have shown that plants and bees use similar cues for flowering and emergence (timing of snow melt and degree days above a base temperature; Forrest & Thomson 2011; Ovaskainen et al. 2013). However, while some studies have shown that plants and bees exhibited similar phenological shifts in the last 40 - 50 years (Bartomeus et al. 2011; Ovaskainen et al. 2013), others have found larger shifts by plants than their pollinators (Forrest & Thomson 2011). Much less is known about the impact of climate change on the timing of emergence for other groups of pollinators such as syrphid flies and non-syrphid Diptera such as muscid flies (Muscidae) (Høye & Forchhammer 2008; Iler et al. 2013). The timing of snowmelt has been identified as an important factor for Muscidae in multiple systems (Høye & Forchhammer 2008; Iler et al. 2013) but one study conducted in alpine tundra found that although the date of snowmelt explained the date of first activity for insects, it did not explain the date of median activity, and it identified a range of additional environmental variables that helped explain the phenology of some species (Prather et al. 2023). In a high-arctic system, muscid flies increased their developmental rate immediately following snowmelt in warm years (Høye & Forchhammer 2008), again suggesting that changes in phenology go beyond a simple shift in start date. Very few studies of plant-pollinator interactions have been conducted in boreal forests (Kevan et al. 1993; Díaz-Calafat et al. 2025), and only one has evaluated shifts in the phenology of plants and insects (Ovaskainen et al. 2013). We are therefore a long way from making any predictions about potential phenological mismatches between plants and pollinators in this biome.

Viburnum edule (Michx.) Raf. (Adoxaceae, formerly Caprifoliaceae; common English names include highbush cranberry and squashberry; Koyukon Athabascan: donaaldloye) is abundant in the understory of deciduous and mixed deciduous – coniferous forest in Interior Alaska (Hollingsworth 2015) and across North American forest (Qian et al. 1998). *V. edule*'s exposed flowers provide insects with pollen but appear to produce little nectar (Kornhauser pers. obs.). We selected this species for evaluating potential mismatches with pollinators under future climate scenarios for three reasons. First, it flowers fairly early compared to most other insect-pollinated understory species in the same habitat (mean first flowering date 2013 – 2015: 3 June vs. 22 June average for 41 understory species; Mulder & Spellman, 2019b) and is therefore at greater risk of having open flowers at a time when few pollinators are active. Second, it shows larger interannual shifts in flowering time (~ 19 days) than co-flowering species such as *Mertensia paniculata*, *Rhododendron groenlandicum* and *Cornus canadensis* (all ~ 2 weeks), though similar to *Rosa acicularis* (3 weeks) (Mulder & Spellman 2019b). As a result, in a year with an advanced spring *V. edule* flowers prior to these species but in an average year their flowering times overlap (Mulder & Spellman 2019b), resulting in both an altered pollinator landscape and an altered landscape of potential competitors for pollinators. Third, it retains fruits throughout the fall and winter, making it an important food source for overwintering animals (Mulder et al. 2021).

We aimed to understand how variation in flowering time impacts plant-pollinator relationships for an early-flowering, generalist plant that shows large shifts in response to the timing of spring. In Fairbanks, Alaska, where this study was conducted, the start of the growing season has varied by about a month over the last century and has advanced at a rate of ~ 0.8 days per decade (Fig. S1). We completed a pollinator exclusion experiment to determine whether *V. edule* is capable of setting fruit in the absence of pollinators (self-compatibility has not been studied in this species). We experimentally manipulated the timing of flowering in two successive years, one in which spring was slightly earlier than average and one in which it was about average, and evaluated whether flowering time within year or between years impacted the number and composition of insect visitors and pollen deposition. Together, our experiments allow us to evaluate whether pollination of *V. edule* is sensitive to the time of flowering and whether this species is dependent on pollinators for fruit set. They do not test the potential for plant-pollinator mismatches under continued climate change directly, as shifts in pollinator timing were not evaluated, but they do indicate whether there is potential for loss of pollination services if pollinators show smaller shifts in timing than plants.

MATERIALS AND METHODS

STUDY SPECIES

Viburnum edule is a deciduous understory shrub (0.5 – 1.5 m tall) commonly found in the understory of forest dominated by *Betula neoalaskana* (Alaska birch) and *Picea glauca* (white spruce). Other common understory species in this forest type include the shrubs *Rosa acicularis* (prickly rose), *Alnus viridis* (alder), *Rhododendron groenlandicum* (Labrador tea), and *Ribes triste* (northern red currant); forbs such as *Mertensia paniculata* (northern bluebell), *Cornus canadensis* (dwarf dogwood), and *Linnaea borealis* (twinflower); and horsetails (*Equisetum arvense* and *E. sylvaticum*). *Viburnum edule* flowers occur in opposite pairs of compound corymbs that originate at the leaf axil, forming a semi-sphere of 15 – 40 flowers (Fig. 1A). Flowers are bisexual, with five short and spreading stamens and a short style with a single-rounded stigmatic surface. The five connate flower petals are 4 – 7 mm wide, flat, spreading, and white, cream, or light pink in color. The bright red drupes are 5 – 8 mm in diameter and contain a single seed. Anthesis is highly synchronous within inflorescences (usually within 24 hours) and among plants in a patch (within 1 – 2 days).

STUDY SITES

We selected three sites where *V. edule* was abundant. Two sites (A and B) were located in forest on the University of Alaska Fairbanks (UAF) campus in Fairbanks, Alaska, USA, approximately 300 m apart (Table. 1). A third site (C) was located about 2 km from the primary sites and used during the first year only. Trees at sites A and C were > 90% *B. neoalaskana* with some white spruce (*P. glauca*), while site B had similar proportions of these two species. Within each site we set up 5 experimental arrays of flowers in a circle with a circumference of approx. 250 m (Fig. 1B; see details below). The sites had some co-flowering species that were expected to be visited by similar pollinators in the area (within 50 m of the arrays) but with very few flowers within the experimental array circle. Potential co-flowering plants included

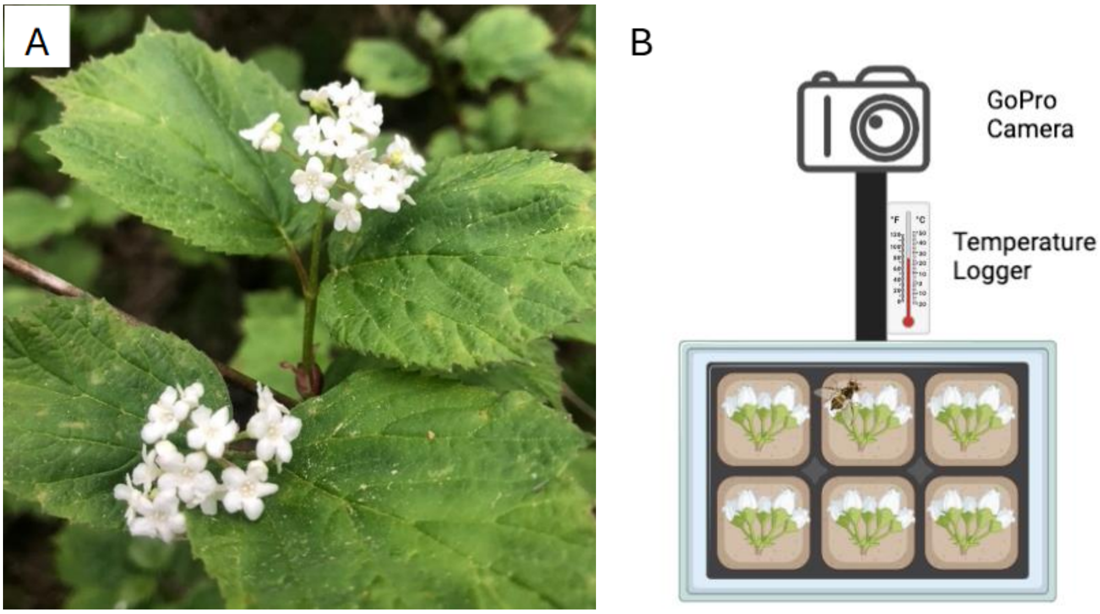

Figure 1. Experimental set-up. A) *Viburnum edule* inflorescences. B) schematic representation of an experimental array.

Rosa acicularis, *Mertensia paniculata*, *Geocaulon lividum*, and *Calypso bulbosa* (fairy slipper orchid).

POLLINATOR EXCLUSION EXPERIMENTS

The breeding system of *V. edule* has not been studied. To evaluate whether this species can set fruit in the absence of pollinators we conducted a pollinator exclusion experiment during the spring of 2020. We chose 16 plants that were adjacent to the sites (within 70 m): 6 at site A, 5 at site B, and 5 at site C. We selected one pair of inflorescences and randomly assigned one of the pair to receive a pollinator exclusion treatment, leaving the other as a control. This exclusion treatment involved placing a small mesh bag over the inflorescence, while the control inflorescence was left open. The inflorescences, which had 17 ± 4 flowers, were labelled and bagged in early May, while still in bud, then left until mid-August, at which point we counted unripe fruits and unfertilized flower remains. Based on extensive previous experience with this species every fruit contains one seed, and we therefore consider the production of a fruit evidence of successful fertilization. Flowering phenology of these plants was similar to that of the "peak flowering time" experimental plants in 2020 described below.

FLOWERING PHENOLOGY EXPERIMENTAL SETUP

The experiment had a 2 x 2 full factorial design with two years with different flowering times relative to long-term averages (advanced vs. average) and two flowering times of experiment arrays within each year (early vs. peak flowering). Peak flowering in the Fairbanks area in Year 1 (first week of June, 2020, the "advanced year") was slightly earlier than average while peak flowering in Year 2 (second week of June, 2021, the "average year") was close to the average compared to phenology data collected by Mulder & Spellman (2019b) (flowering range for very early year: May 23 – 26; average year: June 6 – 10; very late year: June 11 – 23; Mulder & Spellman 2019b). Thus, there was a 12-day range in day of the year (DOY) from the earliest to the latest date, and the peak flowering period in Year 1 coincided with the early flowering period in Year 2 (Table 2). In Year 1 the experiment was conducted at three sites (A, B, and C), with five arrays per site. This was logistically challenging, so in Year 2 we reduced this to two sites (A and B) and three arrays per site.

Table 1. Site information.

Site name	Latitude	Longitude	Elevation (m)	Canopy cover (% closed)
A	64.859	-147.856	180	76.5 ± 0.05
B	64.857	-147.858	180	72.5 ± 0.12
C	64.896	-147.814	210	73.8 ± 0.11

Table 2. Weather data by 3-day experimental bout. Data are means ± SD for minimum and maximum temperatures at each array. Precipitation is based on data from the Fairbanks International Airport. DOY = day of year.

Year	Within-year	Dates (DOY)	sites	Mean ± SD Temp (° C)	Temp. range (° C)	Total precipitation (mm)
advanced (2020)	early	28 – 30 May (149 – 151)	ABC	16.7 ± 0.65	6.1 – 29.3	0
			AB	16.9 ± 0.67	5.9 – 27.1	0
	peak	3 – 5 June (155 – 157)	ABC	13.6 ± 0.17	6.1 – 26.1	0.8
			AB	13.6 ± 0.19	6.1 – 24.0	0.8
average (2021)	early	1 – 3 June (152 – 154)	AB	17.8 ± 0.23	11.2 –26.0	0.5
	peak	7 – 9 June (158 – 160)	AB	14.1 ± 0.15	5.8 – 25.8	1.5

Early and late experimental flowering periods (“bouts”) within each year were 3 days long, with 3 days in between bouts (Table 2). Experimental bouts were timed to avoid rain. Because we were using plants that varied naturally in the time of flowering, the start of the early bouts was based on the first flowering *V. edule* plants we could find in the Fairbanks area, usually located in highly exposed areas with a southern aspect. We were limited to two bouts per year because all individuals in the Fairbanks area completed flowering during this period.

For the early flowering bouts, branches with *V. edule* inflorescences were collected on a sunny south-facing slope approx. 500 m from site C while peak-flowering branches were collected from a shaded area with a west-facing slope within 500 m of site C. Each branch had 2 – 6 inflorescences. Most of the buds opened within a day of clipping; any buds that had opened prior to being placed in arrays were removed. The branches of inflorescences were kept in flower tubes (small plastic vials of water) which were refilled daily throughout the experiment.

At each of the three sites we placed five arrays in a circle, approximately 50 meters apart. Each array (Fig. 1B) consisted of a rectangular tray that held 6 cone-shaped containers (diameter = 4 cm diameter, height = 12 cm). Each container held one *V. edule* branch with at least 2 inflorescences, each with 15 to 40 flowers. Branches were selected so that the total number of flowers per array was approximately constant. The inflorescences were held in the containers at ≈ 50 cm above the ground. We used only arrays for which all inflorescences looked healthy at the end of the bout; this reduced our sample size (number of arrays) for the early bout in Year 1 to 4 in site A and to 2 in site B. To prevent non-experimental plants from influencing the pollinators’ behaviour we removed inflorescences from any non-experimental flowering *V. edule* plants within 25 m of experimental plants.

Each array had a GoPro camera (GoPro Hero 7 Black, GoPro Inc.) and a temperature logger (Onset, HOBO Pendant Temperature/Light 64K Data Logger) mounted 1 m above the ground on a fence post (Fig. 1B). The GoPro cameras were outfitted with external battery packs and 128 GB microSD cards and were used to monitor insect visitors at the arrays for 3 consecutive days (a bout) in each experimental week. Although we recorded at least 4 hours of video per day starting at approx. 10:00, we only analysed video taken for a two-hour block in late morning (~ 10:30 – 12:30), when floral visitors were most active (K. Kornhauser pers. obs.) and there was no precipitation. Evening observations using netting collection along transects confirmed low activity of floral visitors after 18:00 (K. Kornhauser unpubl. data.). We recorded videos at a resolution of 1080 p at 30 frames / second and temperature at 30-min intervals. Since canopy cover can affect total flower abundance and pollinator activity in this system (Spellman et al. 2015), canopy cover data were collected at each array using a concave crown densiometer (Forestry Suppliers, Canada) at a height of 1.5 meters in each cardinal direction; the resulting 4 values were averaged (Table 1).

FLOWER VISITORS

We identified the flower visitors to each array and inflorescence in all videos. Flies were identified as syrphid flies (Syrphidae) or muscid flies (Muscidae) but not classified further. Bees were classified as bumblebees (*Bombus* spp.) or solitary bee species (primarily family Halictidae or Andrenidae) but were not classified to lower taxonomic levels as they were not distinguishable from video recordings. Beetles (Coleoptera) and aphids (Aphidoidae) were also observed visiting *V. edule* flowers. Only insects that were observed landing on flowers or touching flower parts of *V. edule* were included in counts of visitors.

POLLEN LOADS

At the end of the three-day experimental bout all stigmas were removed from the flowers and placed in a petri dish with a base of agar for transport and storage. We mounted up to 15 healthy-looking stigmas from each branch (one or two inflorescences) onto microscope slides with a basic fuchsin gel stain (Kearns & Inouye 1993) within 36 hours of collection. Pollen grains were counted under a compound light microscope at 400 × magnification. Heterospecific pollen grains were found on < 1% of stigmas and were not identified or included in the total pollen count.

DATA ANALYSIS

All analyses were performed in R (Version 4.4.0, 2024).

Pollinator exclusion

To determine whether pollinator exclusion altered the number of fruits per inflorescence we performed a paired t-test. Since number of flowers was not constant across all inflorescences, we also calculated the proportion of flowers that produced fruits, but since pollination of flowers within an inflorescence are not likely to be independent events (that is, the inflorescence, not the flower, was the experimental unit) we did not conduct a statistical analysis.

Pollination experiments approach

To determine whether the timing of flowering within the year (early vs. peak) or between years (advanced vs. average) affected pollination, we evaluated differences between bouts in pollinator visitation and pollen deposition. The experimental unit was the array of 6 branches (N = 26 in year 1, N = 12 in year 2); inflorescences within an array were not considered independent of one another as their proximity increased the likelihood that a visitor attracted to one inflorescence would be attracted to others in the array. Because site C was only included in Year 1, we ran all models twice: the full dataset is the most powerful way to detect differences between early and peak flowering time within year, while the dataset without site C is more appropriate for interpreting between-year effects.

Number of visitors

To determine whether flowering time explained the number of insect visitors observed, we ran a maximum-likelihood based mixed effects linear model using the "lmer" function in the R package *lme4* (Bates et al. 2015) and a Gaussian distribution. This model used the total number of visitors per array across the 6 hours of video per bout as the response variable. Explanatory variables were the year (advanced vs. average), within-year flowering time (early vs. peak), and their interaction. Canopy cover was included in the model as a covariate and site identity as a random variable. To determine whether fixed effects significantly contributed to the model we compared full models to simplified models using chi-square values from maximum likelihood tests.

Pollinator community composition

We tested whether the pollinator community composition differed between early and late flowering bouts or between the two years using analysis of similarity (ANOSIM, "ano" function in the R package *vegan*, Oksanen et al. 2024) with the Bray-Curtis metric. The categories of pollinators were solitary bees, syrphid flies, and muscid flies; all other groups, including bumblebees, occurred too rarely for inclusion (see Results). We used absolute abundance and relative abundance (# of visitors of each group to an array / total # visitors to the array, including other species) and evaluated the differences between early and peak flowering bouts within year (all sites), advanced versus average year (only sites A and B) and all four bouts (only sites A and B).

Pollen deposition

To determine whether pollen deposition was affected by the flowering time within a year or by year we used two measures of pollen deposition: the proportion of stigmas that had evidence of pollinator visits ("pollinated stigmas") and the mean number of pollen grains per stigma. "Pollinated stigmas" were identified using a threshold of 5 pollen grains to indicate a flower had been visited by an insect. We used 5 rather than 1 pollen grain as our threshold to prevent accidental transfer of a few pollen grains during processing to be interpreted as "visitation", but we repeated the analyses using thresholds of 1 and 10 pollen grains to evaluate how our definition affected the results. We calculated the mean proportion per inflorescence and then the mean proportion per array. For pollen grains per stigma we first calculated the mean number per stigma for each inflorescence and then the mean per inflorescence for each array. We again ran mixed linear models (Gaussian distribution) with mean pollen grains per stigma or the proportion of pollinated stigmas as the response variables, year, within-year flowering time, and their interaction as explanatory variables, canopy cover as a covariate, and site identity as a random variable.

RESULTS

FRUIT SET UNDER POLLINATOR EXCLUSION

Viburnum edule flowers produced very few fruits when exposed to insects, and even fewer when insects were excluded. Inflorescences accessible to pollinators produced 2.1 ± 1.4 (mean ± SD) fruits per inflorescence, while bagged inflorescences produced 0.13 ± 0.35 fruits per inflorescence ($t_{(1, 15)} = 4.94$, $P < 0.0001$). Results were similar at the individual flower level, with 12 ± 9% of exposed flowers producing a fruit compared to 1 ± 3% of flowers on inflorescences where pollinators were excluded. Overall, 87.5% of open inflorescences and 12.5% of bagged inflorescences produced at least one fruit.

FLOWER VISITORS

Across all sites and time periods, there were a mean of 8.3 insect visitors per inflorescence over the 6-hour observation period (1.4 insects hour^{-1}). Insects usually visited multiple flowers within an inflorescence, spending up to one minute on a single inflorescence before moving on to another inflorescence within the array or to another array. The number of visitors was explained by within-year flowering time (early vs. peak) and the year of flowering (Fig. 2A, Table 3). On average visitors were about twice as abundant during peak flowering as during early flowering, and twice as abundant in the average year (Year 2) as in the advanced year (Year 1) (Fig. 3A). When only sites A and B were included, there was a significant interaction between within-year flowering time and year: the difference between early and peak flowering was much greater in the advanced year than in the average year (≈ 8.5 – fold vs. ≈ 1.5 – fold; Fig. 3A).

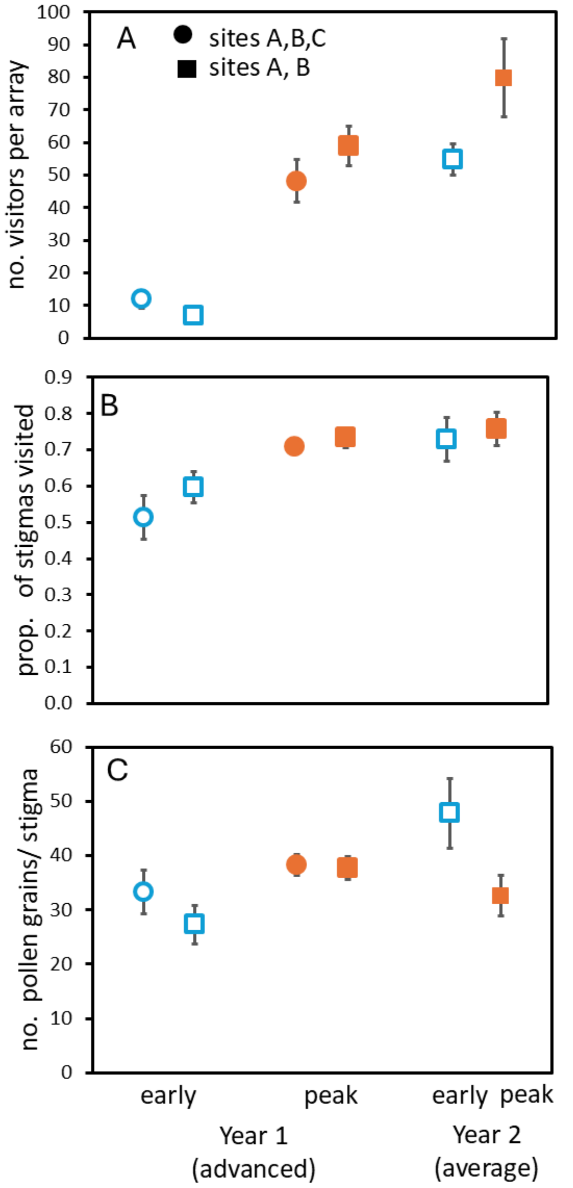

Figure 2. Pollination results by year (advanced or average with respect to long-term averages) and flowering period (early or peak within the year). Open blue symbols are data for early flowering and closed orange symbols are data for peak flowering. See Table 2 for flowering dates. Arrays were the experimental units; sample sizes from left to right for all panels: 11, 6, 15, 10, 6, 6. Panel A) Mean number of visitors per array during the 6-hour period of observation; B) Mean proportion of flowers visited (threshold = 5 pollen grains); C) mean number of pollen grains per stigma.

Table 3. Effect of timing of flowering on number of visitors per array, proportion of stigmas pollinated (using a threshold of 5 pollen grains), and mean number of pollen grains per stigma.

Sites	Response variable	Within Year (early vs. peak)		Between Year (advanced vs. average)		Interaction	
		$\chi 2$	*P*	$\chi 2$	*P*	$\chi 2$	*P*
A, B and C	no. visitors	22.09	**<0.0001**	20.53	**<0.0001**	0.80	0.371
	pollinated stigmas	10.4	**0.0013**	5.08	**0.024**	3.81	0.051
	no. pollen grains / stigma	0.18	0.670	1.17	0.280	7.88	**0.005**
A and B only	no. visitors	26.4	**<0.0001**	19.02	**<0.0001**	5.57	**0.018**
	pollinated stigmas	5.54	**0.019**	4.46	**0.035**	2.34	0.126
	no. pollen grains / stigma	0.06	0.81	2.44	0.12	12.0	**0.0005**

Syrphid flies were the most frequent visitors (77% of total), followed by solitary bees (12%) and muscid flies (11%) (Fig. 3). Bumblebees were rarely observed (4 instances out of 1663 visitors) and beetles, aphids and wasps were observed even less frequently (2, 2, and 1 times resp.); together, these groups represented ~ 0.5 % of visitors. As expected given the large differences in total pollinator numbers, there were significant differences in pollinator community composition between early and peak flowering bouts, and between all four bouts (Fig. 3A, Table 4). Relative abundance of the three frequently observed taxonomic groups also differed between the four flowering bouts (Fig. 3B, Table 4). While visitors in all three groups increased over the season, for plants that flowered later syrphid flies increased more than solitary bees and muscid flies; the proportion of syrphid flies for the latest flowering plants (peak flowering in the average year) doubled compared to the earliest flowering plants (early flowering in the advanced year) while the proportion of solitary bees was reduced by about 80% and that of muscid flies by about 70% (Fig. 3). Composition was most dissimilar between the earliest flowering bout and all other bouts (Fig. 3), resulting in a much greater dissimilarity index when considering all four bouts than when considering only differences between or within years (Table 4).

POLLEN LOADS

The proportion of stigmas at each array with ≥ 5 pollen grains (pollinated stigmas) was generally high (> 50% for all bouts; Fig 2B). Both within-year flowering time and year explained variation, with 16% higher values for peak flowering compared to early flowering (all sites comparison) and 12%

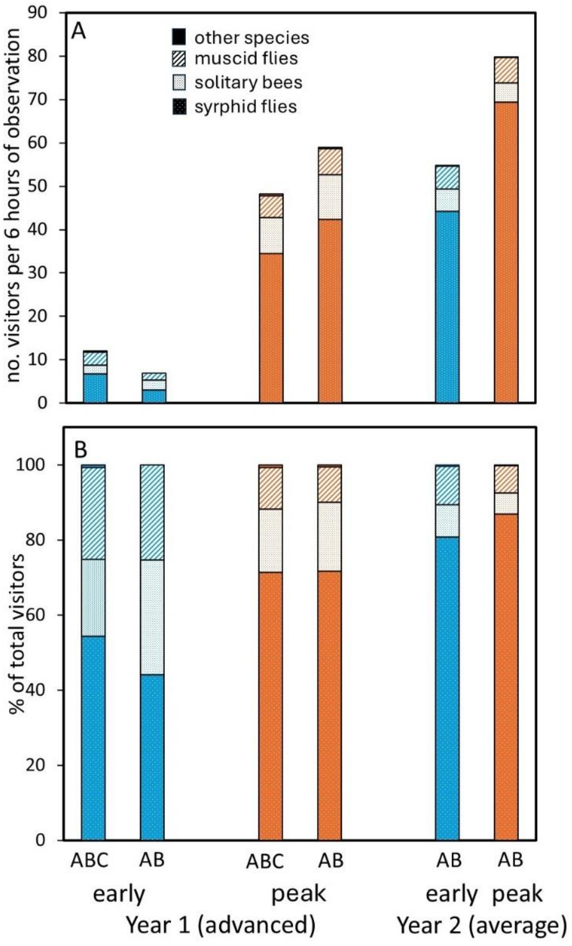

Figure 3. Insect groups visiting flowers per 3-day experimental bout based on 6 hours of observations per array. Bumble bees, aphids and beetles together represented < 0.5% of visitors and were combined into the "other species" category. A) absolute abundance (mean no. per array). B) relative abundance (% of total visitors in each array).

Table 4. ANOSIM results for pollinator communities. Results are based on absolute and relative abundance of syrphid flies, solitary bees, and muscid flies per array.

Variable	Comparison	Sites included	R	P
Absolute abundance	Early vs. late flowering within year	A, B, C	0.19	0.003
	Early vs. late flowering within year	A, B	0.23	0.004
	Year 1 vs. Year 2	A, B	0.11	0.051
	All four bouts	A, B	0.45	<0.001
Relative abundance	Early vs. late flowering within year	A, B, C	0.050	0.098
	Early vs. late flowering within year	A, B	0.093	0.069
	Year 1 vs. Year 2	A, B	0.189	0.009
	All four bouts	A, B	0.332	<0.001

(sites A and B only) higher values in the average year than in the advanced year. Results were similar when we used thresholds of 1 and 10 pollen grains (not reported). Mean number of pollen grains per stigma was explained by an interaction between year and within-year flowering time (Table 3, Fig 2C). In the advanced year, plants flowering at peak time had more pollen grains (15% more for all sites, 38% more for site A and B only) than plants that flowered early, while in the average year plants flowering at peak time had 32% fewer pollen grains (Fig. 2C). This shift was consistent, with lower values at peak flowering than early flowering for all six array locations.

RELATIONSHIP BETWEEN NUMBER OF VISITORS AND POLLEN LOADS

The proportion of stigmas per inflorescence with ≥ 5 pollen grains showed a statistically significant but weak relationship with the number of floral visitors observed ($R^2 = 0.07$, $t_{(198)} = 3.8$, $P < 0.001$), as might be expected given that data were based on 6 hours of observation, but pollination could take place over the entire 72-hour bout. Despite this limitation a clear pattern emerged: although there was high variability between arrays at the low end of the visitor number range, arrays that had many visitors had consistently high proportion of pollinated stigmas (Fig. 4). To evaluate the validity of this pattern, for each level of visitor number we determined the lowest value (minimum) and highest value (maximum) for the proportion of stigmas visited. We binned visitor numbers by two values (i.e., 0 – 1 visitor, 2 – 3 visitors, etc.) to prevent very low sample sizes. We then reran the linear regressions for proportion of stigmas visited vs. number of visitors using these minimum and maximum values. The minimum proportion of stigmas visited increased with the number of visitors while the maximum proportion did not (Fig. 4). This supports the notion that visitors were effectively pollinating plants (a high number of visitors was always associated with high proportions of stigmas with pollen but a low number of visitors was not) but that a lot of visits were occurring outside of our 6-hour observation window (some, but not all, arrays for which we observed few visitors had a high proportion of stigmas with pollen).

CO-FLOWERING SPECIES

There were few co-flowering species during the early flowering bouts: *Calypso bulbosa* (Calypso orchid) was the only nearby species in flower and it was only found near site B (within 15 m of one of the arrays). During peak flowering bouts in both years other species began to flower, including *Rosa acicularis* (prickly rose), *Mertensia paniculata* (northern bluebells), *Geocaulon lividum* (pumpkinberry) and two *Taraxacum* (dandelion) species. Other than *R. acicularis* at site C in year 1 (advanced year), these flowering plants were not found within 25 m of the arrays but were present along trails and roads within a few hundred meters of the sites.

DISCUSSION

For *Viburnum edule*, timing of flowering affects pollination: across all four bouts plants that flowered later in the year had more visitors, higher proportions of stigmas visited, and a shift in the pollinator community toward a higher proportion

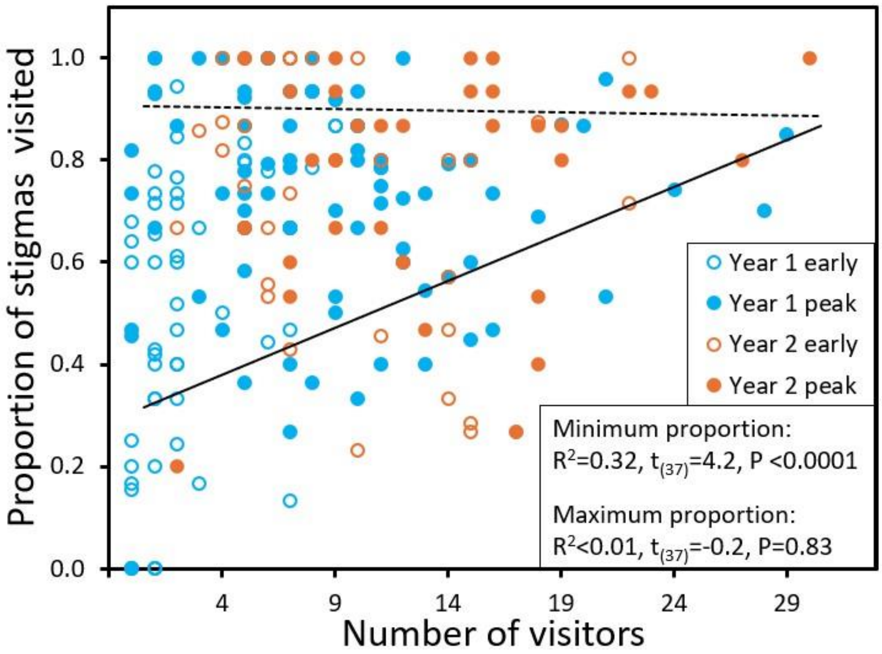

Figure 4: Proportion of stigmas visited (≥ 5 pollen grains) by the number of visitors observed during the 6 hours of observation for each array. Lines represent linear regressions for the minimum (solid line) or maximum (dashed line) proportion of stigmas visited by number of visitors observed, with categories for number of visitors binned by 2 values (0 – 1, 2 – 3, etc.).

of syrphid flies and a lower proportion of solitary bees and muscid flies. While differences between years in timing were small and changes in response variables could be affected by factors other than timing, the fact that the shifts between early and peak flowering were in the same direction for these variables in both years, and that values were similar for the two bouts that had some overlap in dates (Year 1 peak flowering and Year 2 early flowering), support the notion that day of the year is an important contributor to these differences. Notably, for all these response variables the biggest differences were between the very earliest bout (28 – 30 May) and the other three periods (June 3 – 9). That we detected large differences in pollinator activity and community composition between bouts only a maximum of 12 days apart demonstrates how rapidly changes occur in the short spring of boreal forest in Interior Alaska.

The pollinator exclusion experiments indicated that *V. edule* is highly dependent on pollinators for fruit production: eliminating pollinator access reduced the number of fruits per inflorescence by 94% and the number of fruits per flower by 92%. The small but non-zero number of fruits produced in the pollinator exclusion bags suggest that this species is self-compatible, but that herkogamy or dichogamy limits auto-pollination. However, other species of *Viburnum* are known to be self-incompatible (Nebot & Mateu 1990), so it is possible that these fruits are the result of contamination with outcrossed pollen, or apomixis; hand pollination experiments are needed to clarify this.

Even flowers accessible to pollinators produced on average only 2 fruits, representing 12% of the flowers per inflorescence. This result is surprising given the high pollen loads (39 mean grains per stigma and 66% with ≥ 5 grains per stigma) for the experimental plants flowering at the same time in the same location (site C) but that were exposed for less time. The strong relationship between minimum number of pollinators observed and proportion of stigmas with ≥ 5 pollen grains also demonstrated the effectiveness of pollinators in transporting pollen. However, observations of fruits on *V. edule* at site C in other years support consistently low rates of conversion of flowers to fruits. For example, on August 6, 2016, as fruits were ripening, there were only 2.7 ± 1.5 (range 1 – 6) fruits per inflorescence for 20 plants at site C (CPH Mulder, unpublished data), and during 5 years of observations clusters of > 10 fruits were rarely seen (CPH Mulder, pers. obs.). A study in Newfoundland, Canada, found similarly low flower to fruit conversion rates (≈ 9%; Fequet 2011). Our experimental arrays, which included at least 12 inflorescences in close proximity, mimicked the high end of inflorescence densities in nature (CPH

Mulder, pers. obs.) and therefore may have overestimated pollination rates of plants in non-experimental settings. In addition, given that flowers within an inflorescence were closely spaced and that most pollinators visited multiple flowers within an inflorescence, the majority of pollen grains in our experimental arrays may have been transferred within inflorescences. Our pollinator exclusion experiments did not allow us to distinguish between a lack of self-pollination and self-incompatibility, so even high pollen loads might result in low seed set if this species is self-incompatible. It appears likely that fruit production in *V. edule* is either limited by inefficient pollen transfer between genets, by resource availability, or both.

Syrphid flies were the overwhelming majority of observed visitors to *V. edule*, followed by muscid flies and solitary bees (likely primarily in the Andrenidae and Halictidae); very few bumblebees were seen. *V. edule* provides very little, if any, nectar so it is not surprising that guilds of pollinators that primarily forage for nectar, such as butterflies, were not observed. Syrphid and muscid flies are important pollinators in high-latitude and high-altitude flowering plants, but while they have received attention in tundra environments (e.g., Kevan 1972; Elberling & Olesen 1999; Fulkerson et al. 2012; Tiusanen et al. 2016), their role in boreal forest is little studied (Kevan et al. 1993). Interior Alaska has at least 41 species of solitary bees, but they are less abundant than *Bombus* species in closed-canopy boreal forest, and their importance as boreal pollinators is not well understood (Armbruster & Guinn 1989). Solitary bees rival bumblebees (*Bombus*) and honeybees (*Apis*) in pollen transfer efficiency (Orford et al. 2015). Non-syrphid Diptera in general have received very little attention as pollinators, although they are just as efficient as syrphid flies in transferring pollen (but less efficient than solitary bees; Orford et al. 2015). Given the prevalence of muscid flies and solitary bees early in the season, greater attention to their role as pollinators in boreal forest is warranted.

The only variable that did not show an increase with day of the year was number of pollen grains per stigma, which dropped for the last flowering bout (Fig. 2C) in all array locations despite an increase in proportion of stigmas with > 5 pollen grains. This is unlikely to be the result of reduced pollen production, as flowers in all bouts were the same age. And although the proportion of solitary bees, the most efficient group of pollinators (Orford et al. 2015), decreased, all pollinators (including solitary bees) were more abundant than during the early flowering period (Fig. 3A). It is possible that there was a shift in the identities of pollinators within the broad taxonomic groups we chose, leading to more visitations but reduced pollen transfer.

The shift in the pollinator community composition toward syrphid flies as the season progressed may be driven by changes in the pollinator pool as species emerge from overwintering, changes in attraction or competition for pollinators by co-flowering plants (e.g., Waser 1983; Laverty 1992), or both. They are unlikely to result from weather-driven changes in pollinator activity, as air temperatures were similar between years and lower during peak flowering bouts than early flowering bouts in both years, and precipitation was minimal during all bouts. In general, syrphid flies are more sensitive than non-syrphid flies to ambient temperatures (Mizunaga & Kudo 2017), and less tolerant of low temperatures than muscid flies, as indicated by their reduced prevalence at high latitudes (Elberling & Oleson 1999). Armbruster & Guinn (1989) recorded 8 species of solitary bees that were in flight starting in May, before our first plants flowered, and noted that solitary bees had similar emergence dates across 8 years of observations. These observations are consistent with greater relative abundance of muscid flies and solitary bees early in the season, and greater relative abundance of syrphid flies later in the season.

STUDY LIMITATIONS

This study evaluated only two years of data, and it is possible that the differences between years were partially or wholly due to differences in pollinator populations driven by factors beyond variability in spring conditions. For example, pollinator populations may have been affected by conditions during the previous year. This limitation points to the importance of a better understanding of the natural history of common boreal pollinators so that further experiments can be focused on times during which or conditions under which pollinators are most likely to be affected by variation in environmental conditions. A second limitation is the lack of hand-pollination experiments, which would have allowed us to determine whether the low fruit set of *V. edule* is due primarily to pollen limitation (in which case hand pollination would result in much higher fruit set) or whether lack of resources to complete fruit production plays a significant role. We recommend performance of such experiments in the future.

ECOLOGICAL CONSEQUENCES

Current trends for temperature show shifts of about 0.8 days per decade in the start of the growing season (Fig. S1), or about 6 days by the end of the century. *Viburnum edule* individuals live for at least a decade (CPH Mulder, pers. obs.); given the high interannual variability in flowering date (Mulder et al. 2019b) and small change in the start of the growing season it is unlikely that a lack of pollinators will greatly reduce seed production over the course of most plants' lifetimes. However, in recent years flowering was a week earlier than the earliest flowering bout in this study (around 22 May in 2015; Mulder & Spellman 2019b); if low fruit set in general is driven primarily by pollen limitation, then fruit set is likely already very low in some years and likely to be even lower in future. Furthermore, *V. edule* represent an important source of fruits for boreal forest frugivores such as voles, foxes and migrating birds in winter and early spring, when overwintering fruits remain on the plant at a time when few other sources of food are available (e.g., West 1982; Wegge & Kastdalen 2008; Needham et al. 2014; Mulder et al. 2021). As a result, the consequences of low-fruit years due to low pollinator availability may be severe for frugivores. Our study shows that even small shifts in timing can greatly affect pollinator visitation rates; to better understand the ramifications for frugivores we need a more thorough understanding of the factors that trigger emergence the most important pollinators – solitary bees, syrphid flies, and non-syrphid flies – in boreal forest.

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AUTHOR CONTRIBUTION

Concept and design KK & CM, data collection KK, data analysis KK & CM, writing KK & CM, edits and approval for publication CM & KK.

DISCLOSURE STATEMENT

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data for this study are available via the Bonanza Creek Long Term Ecological Research data catalog (https://www.lter.uaf.edu/data/data-catalog) at http://dx.doi.org/10.6073/pasta/7ead24267b59c5b58b8edc4e98f7f781.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I: Change in start of the growing season (1930 – 2024) for Fairbanks, Alaska, USA

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