Temporal synchrony between ground-nesting bees and spring ephemerals in an eastern hardwood forest ecosystem

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Abstract

Changes in phenology due to climate warming could disrupt temporal overlap between interacting organisms when previously synchronized species respond to climate change at different rates. Phenologies of plants and insects are known to be sensitive to temperature and/or timing of snowmelt, with warmer temperatures and earlier snowmelt generally advancing spring flowering and emergence; however, some groups of pollinators, such as solitary bees, have been little explored in this context. One striking aspect of eastern hardwood forests is the emergence of understory wildflowers each spring, most of which rely, at least to some extent, on wild native pollinators for seed set. Without an understanding of the environmental drivers of phenology of these species, we have little ability to predict whether pollinators will continue to be well synchronized with flowering as the climate changes. In this study, I determined how spring temperatures and timing of snowmelt influence the phenology of spring wildflowers, activity of bees, and their temporal overlap in Gatineau Park, Québec. From 2013 to 2018, I characterized bee activity phenology and flowering phenology of understory plants in multiple study plots, focusing on early-flowering *Anemone* spp. and later-flowering *Trillium grandiflorum*. The sampled bee community was dominated by *Andrena*, *Lasioglossum*, and *Nomada*, all of which have similar activity periods. Degree-day accumulation was a better predictor of *Anemone* and *Nomada* phenology than were day of year or snowmelt date, whereas *T. grandiflorum* appeared to be more sensitive to photoperiodic cues; since day of year was the variable that best described its phenology. Activity periods of *Andrena* and *Lasioglossum* were equally well described by degree-day accumulation and by day of year. No taxon's phenology was best predicted by snowmelt date. Despite these differences among taxa in the identities of the best predictors of phenology, bee activity and plant flowering phenologies responded at similar rates to interannual and among-site variation in snowmelt date and early spring temperature. Temporal overlap between flowering and

bee activity was similar over the years of this study and was affected neither by snowmelt date nor by temperature. These results suggest that interacting plant and bee taxa may respond to different environmental variables but still maintain their synchrony under the conditions recorded so far.

Résumé

Les changements phénologiques dus au réchauffement climatique pourraient perturber le chevauchement temporel entre des organismes en interaction lorsque des espèces préalablement synchronisées répondent au changement climatique à des taux différents. Les phénologies des plantes et des insectes sont reconnues pour leurs sensibilités à la température ou au moment de la fonte des neiges; les températures plus élevées et les fontes des neiges précoces avancent les périodes de floraison et d'émergence au printemps. Cependant, certaines lacunes persistent : notre compréhension des changements phénologiques chez certains groupes de pollinisateurs, tels que les abeilles solitaires, demeure limitée dans ce contexte. Particularité marquante des forêts de feuillus de l'Est, l'émergence de fleurs sauvages de sous-bois chaque printemps dépend pour la plupart, dans une certaine mesure, des pollinisateurs indigènes sauvages pour la production de graines. Sans une bonne compréhension des facteurs environnementaux qui modifient la phénologie de ces espèces, notre capacité à prédire la persistance (ou non) de la synchronisation pollinisateurs-fleurs demeure limitée dans le cadre des changements climatiques. Dans cette étude, j'ai déterminé la manière dont les températures printanières et le moment de la fonte des neiges influencent la phénologie des fleurs sauvages printanières, l'activité des abeilles et leur chevauchement temporel dans le parc de la Gatineau, au Québec. De 2013 à 2018, j'ai caractérisé la phénologie de l'activité des abeilles et celle de la floraison des plantes de sous-bois dans de nombreuses parcelles, en mettant l'accent sur *Anemone* spp. (floraison précoce) et *Trillium grandiflorum* (floraison tardive). La communauté d'abeilles étudiée était dominée par *Andrena*, *Lasioglossum* et *Nomada*, tous ayant des périodes d'activité semblables. L'accumulation de degrés-jours était un meilleur prédicteur que le jour de l'année ou la date de fonte des neiges pour les phénologies d'*Anemone* et de *Nomada.* Toutefois, *T. grandiflorum* semblait plus sensible aux signaux photopériodiques, car c'est la variable du jour de l'année qui décrivait le mieux sa

phénologie. Les périodes d'activité d'*Andrena* et de *Lasioglossum* étaient bien décrites tant par le nombre de degrés-jours accumulés que par le jour de l'année. La date de fonte des neiges n'était le meilleur prédicteur de la phénologie d'aucun taxon. Même si le meilleur prédicteur diffère pour les divers taxons décrits précédemment, les phénologies d'activité des abeilles comme celles de floraison des plantes répondaient similairement aux variations interannuelles et intersites des températures printanières précoces et de la date de fonte des neiges. Le chevauchement temporel entre les périodes de floraison et d'activité des abeilles a été similaire tout au long des années de cette étude et n'a été affecté ni par la date de fonte des neiges ni par la température. Ces résultats suggèrent que les taxons de plantes et d'abeilles en interaction peuvent réagir à différentes variables environnementales tout en conservant leur synchronisme sous les conditions observées jusqu'à présent.

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Introduction

Changes in phenology due to climate warming could disrupt temporal overlap between interacting organisms when previously synchronized species respond to climate change at different rates (Parmesan 2006). Phenological disruptions between interacting species due to rising temperatures have now been reported for many kinds of ecological relationships, including those between predators and prey and between herbivores and plants (Parmesan 2006; Durant et al. 2007; Donnelly et al. 2011; Cohen et al. 2018; Kharouba et al. 2018). Disruptions of mutualistic interactions, such as those between plants and pollinators, have been a subject of particular concern (Hegland et al. 2009; Rafferty and Ives 2011; Kudo 2014; Gezon et al. 2016).

Phenologies of both plants and insects are known to be sensitive to temperature (Fitter 2002; Gordo and Sanz 2006; Forrest and Thomson 2011), timing of snowmelt (Dunne et al. 2003; Høye et al. 2007; Høye and Forchhammer 2008; Gordo and Sanz 2010; Iler et al. 2013), and photoperiod (Tauber and Tauber 1976; Imaizumi and Kay 2006; Van Asch and Visser 2006), with warmer temperatures and early snowmelt typically advancing spring flowering and emergence from hibernation (Fitter 2002; Gordo and Sanz 2006; Bartomeus et al. 2011). However, not all species respond at the same rate to these environmental drivers: early-flowering plants and early-emerging insects tend to be more sensitive to environmental variation than plant and insect species that emerge later in the season (Fitter 2002; Sherry et al. 2007; Bartomeus et al. 2011; Wolkovich et al. 2013; Høye et al. 2014). Plant and insect species also vary in their sensitivity to photoperiod, from species with strong responses to changes in daylength, to species in which phenological events are not affected by photoperiodic conditions (Thomas and Vince-Prue 1997; Bale et al. 2002; Van Asch and Visser 2007). Furthermore, the effect of a particular photoperiod on the phenology of an organism can be altered by temperature, and vice versa (Thomas and Vince-Prue

1997; Bale et al. 2002; Saunders 2014; Nürnberger et al. 2018). If phenologies of plants and pollinators respond to different environmental variables (e.g., snowmelt date vs. temperature), or to the same variables but to a different extent, a phenological mismatch may occur as the climate changes.

A phenological mismatch between plants and their pollinators has been predicted in some studies (Memmott et al. 2007; McKinney et al. 2012); however, few studies have demonstrated temporal decoupling even in unusual warm years that might simulate climate change (Kudo and Ida 2013; Kudo 2014). The small number of documented examples of shifts in temporal overlap between plants and pollinators suggests either that plants and pollinators respond similarly to environmental drivers (Hegland et al. 2009; Bartomeus et al. 2011), or that interacting taxa respond differently but have still maintained synchrony within the climatic conditions recorded so far (Iler et al. 2013). Alternatively, the scarcity of documented examples of plant–pollinator mismatch may simply reflect the rarity of long-term monitoring studies, specifically programs designed to track changes in pollination and plant–pollinator interactions through time (Hegland et al. 2009; but see Thomson 2010).

Despite concerns about declining pollinator populations (Foley et al. 2005; Abrol 2012; Pyke et al. 2016) and the possible effects of climate change on their phenology (Memmott et al. 2007; Kudo 2014), there is little knowledge of the environmental factors that trigger pollinator emergence and activity, especially of groups such as solitary bees. Most attention has focused on eusocial bee taxa such as honey bees (*Apis mellifera;* Gordo and Sanz 2006) and bumble bees (*Bombus* spp.; Kudo and Ida 2013; Kudo 2014; Pyke et al. 2016), but the majority of the approximately 20,000 bee species worldwide are solitary (Michener 2000). Many wild plants and crops depend on insects for fruit production, and bees are considered the most important group of

pollinators due to their reliance on pollen and nectar throughout their life cycle (Michener 2000). Solitary bees are the main pollinators of wild plants in various environments (Willmer et al. 2017). Yet, in comparison with plants (e.g., Bradley et al. 1999; Fitter 2002; Menzel et al. 2006), we have limited knowledge of phenological responses of solitary bees to climate change (but see Bartomeus et al. 2011).

In the eastern hardwood forests of North America, understory wildflowers emerge soon after snowmelt and finish flowering before canopy closure, and many of them depend on insect pollinators for seed production (Motten 1986). Because the flowering of spring wildflowers occurs intensively during a short phenological window, a temporal mismatch between their flowering period and the activity of their pollinators may be especially likely (cf. McKinney et al. 2012). However, without an understanding of the environmental cues affecting activity of these species, we have little ability to predict whether pollinators will continue to be well synchronized with flowering as the climate changes.

In this study, I characterized bee activity and flowering phenology of two spring wildflower taxa for six years in Gatineau Park, Canada, to evaluate how environmental factors (photoperiod, temperature, and timing of snowmelt) influence the phenology and temporal synchrony of native spring wildflowers and wild bees. First, I identified the environmental predictor that best describes the phenology of each taxon; second, I investigated the phenological correspondence between flowers and bees, analysing how plant and insect phenologies covary and whether they respond to climate variation at different rates. Finally, I evaluated the effect of climatic variation on the temporal overlap between flowers and bees.

Methodology

Data collection

Study plots and climate. This study was conducted in the eastern hardwood forest of Gatineau Park, Quebec, Canada (N 45°27'01" W 75°46'58", 160 m elevation). In spring 2013, ten 5 × 5 m sampling plots were established near snowshoe trail 66 (Appendix 1). Each plot was at least 100 m distant from all others and from any forest edge. HOBO pendant data-loggers (Onset Corp., Bourne, MA; UA-002-64) were attached to the ground in the centre of each plot with wire mesh to record temperature at hourly intervals. To place the temperature data from these plots in the context of longer-term climate variation, I also obtained daily mean temperature data from Environment Canada weather station Ottawa CDA, ON, ~11 km south of our study area (http://climate.weather.gc.ca).

Each spring from 2013 to 2018, plots were sampled to characterize phenology of bees and the flowering of understory plants. Flower sampling occurred once every 1–7 days from early April until flowers began to senesce in early June. Bee sampling occurred once every 5–8 days from early April until late May, when no more bees were caught (Appendix 2). Five "bee bowls", white plastic bowls containing water and a drop of detergent (e.g., Droege et al. 2010), were set up along one randomly selected edge of each plot and left in place for approximately 24 hours before collection.

Study organisms

Plant taxa. Anemone spp. and *Trillium grandiflorum* were the most abundant insect-pollinated plant taxa in the sampling plots (Appendix 3): the former was present in five of the ten study plots and the latter in all plots. *Anemone* spp. (*A. americana* and *A. acutiloba*, Ranunculaceae; the two species were lumped together because flowering precedes leaf production, and without leaves they

are difficult to differentiate) and *Trillium grandiflorum* (Melanthiaceae) are perennial, rhizomatous herbaceous plants that occur in the understory of deciduous forests throughout eastern North America (Motten 1986; Case and Case 1997). *Anemone* species are clonal plants in which ramets produce 3–7 flowers that have 5–6 white or purple sepals with numerous stamens and pistils (Bernhardt 1976). *Trillium grandiflorum* are non-clonal, and reproductive plants consist of a single stem arising from a tuber-like rhizome, a whorl of three leaves, and a single terminal hermaphroditic flower with three white petals (Case and Case 1997). *Anemone* flowers produce no nectar; thus, pollen is the only reward for flower visitors (Motten 1982), which are mainly solitary bees (*Andrena* spp.; Bernhardt 1976). *Trillium grandiflorum* flowers are pollinated by insects, primarily bumble bees queens (*Bombus* spp.) attracted to the nectar and pollen (Irwin 2000).

Bee taxa. The bee community sampled by the bee bowls was dominated by three taxa: *Andrena*, *Lasioglossum*, and *Nomada* spp. (Appendix 4). Although bumble bee queens were active in the study area during the sampling periods, the bee bowls were ineffective in capturing them (Appendix 4), so bumble bees were not included in analysis. In eastern Canada there are approximately 75 species of *Andrena*, 71 *Lasioglossum* spp., and 37 *Nomada* spp. (Packer et al. 2007), and in my dataset there were at least five morphospecies of *Andrena*, six of *Lasioglossum*, and four of *Nomada*, but I did not attempt to distinguish these for analysis. Most North American *Andrena* and *Lasioglossum* species are ground-nesting bees (Michener 2000; Wilson and Messinger Carril 2016). *Andrena* spp. are among the first bees to emerge and fly in the spring (Wilson and Messinger Carril 2016); most are solitary and build individual nests in the ground, sometimes in large aggregations. The genus *Lasioglossum* includes species with diverse social behaviours, from solitary or communal to primitively eusocial (Wilson and Messinger Carril

2016). Solitary *Andrena* and *Lasioglossum* species have one generation per year and hibernate as adults in the same brood cells where they completed larval development. The brood cells are at the end of underground burrows, where mother bees store masses of pollen and nectar, on which eggs are laid (Michener 2000). In the social *Lasioglossum* species, fertilized females emerge in early spring from their overwintering burrows and build new individual burrows. They have multiple generations per year, where the first brood consists exclusively of females that help in the collection of pollen and nectar, as well as in the expansion of the burrow for the second generation. From the second-generation eggs, males and females emerge and mate (Wille and Orozco 1970; Breed 1975; Michener 2000). *Nomada* spp. are common cleptoparasites (brood parasites) of *Andrena* and, to a lesser extent, *Lasioglossum*. *Nomada* larvae destroy the host's eggs before feeding on the pollen-and-nectar masses left for the host's larvae (Michener 2000). Although *Nomada* bees do not collect pollen, they visit flowers for nectar.

Data analysis

First, I conducted an individual-level analysis (described below) to select which environmental predictor (day of year, a proxy for photoperiod; snowmelt day; or temperature) best describes the phenology of each taxon. Subsequently, I conducted a "plot-level" analysis using only the predictor (either snowmelt day or temperature) identified in the individual-level analysis for each taxon to test whether phenology responds significantly to these climate variables. Day of year was excluded from the plot-level analysis because it did not vary among plots or years. I selected only one environmental factor to avoid the problem of multicollinearity, due to snowmelt day and temperature being highly correlated ($r_{58} = -0.79$). I nevertheless explored whether plot-level models with the other predictor or incorporating both predictors had a better fit according to Akaike's information criterion (AIC).

For each sampling occasion in each year, I calculated the accumulated days since snowmelt and the accumulated degree-days until the observation event (e.g., the collection date of each insect specimen), using hourly temperature data specific to each plot (from data-loggers, described previously). The timing of snowmelt was estimated from the same temperature data as the first day after 1 January with daily ranges >5°C for at least three consecutive days. I calculated degree-days since 1 March using a range of base temperatures (0–15°C in 1°C increments). March 1 was selected as the starting date, as March is the month when temperatures at ground level begin to exceed freezing at the study sites. For all the following analyses, females and males were combined for each bee taxon, and 2013 was excluded from the bee analyses due to the low number of insects collected (Table 1).

Individual-level analyses of flower and bee phenology. To determine which environmental predictor best describes the phenology of each taxon, across plots and years, generalized linear mixed models were fitted, with binomial error and logit link, to the cumulative proportion of activity or flowering that had occurred by each observation date, using the lme4 package (Bates et al. 2018) in R (R Core Team 2018). I used degree-days above a particular base temperature, days since snowmelt, or day of sampling as the predictor variable of interest; year and plot (as random factors) were also included in the models. The base temperature that best describes the phenology of each plant or pollinator taxon was selected based on the best-fit model according to AIC.

Plot-level analyses of flower and bee phenology. The per-plot floral abundance of each focal species on each sampling occasion was used to extract the following population-level flowering variables: a) first flowering (the first day of the season on which a flower of that species was observed); b) last flowering (the last day on which a flower was observed); c) flowering duration

(days between first and last flowering day); and d) peak flowering (day of year with the highest total number of flowers within a plot).

For each focal bee taxon, the number of individuals collected per bee bowl in each year was counted to extract activity phenological variables. Because bee collection was less frequent than flower surveys, I used monotone linear interpolations to estimate the numbers of bees active on each day from snowmelt to May 30 (e.g., Appendix 5). From the interpolated daily values, the days on which 10% and 90% of the total number of collected individuals (for each bee taxon) were estimated to have occurred were selected as, respectively, the a) first and b) last interpolated days of pollinator activity. I also recorded c) activity period (days between the first and last interpolated days) and d) peak abundance for individual taxa (day of year with the highest total number of individuals collected).

To analyze dependence of plot-level phenology on environmental variables, I calculated a single plot- and year-specific temperature metric for each focal plant and bee taxon (in addition to the plot- and year-specific snowmelt date, described above). To do this, I summed degree-days above 0°C (using plot- and year-specific temperature data) from March 1 until the mean day of the year for each phenological response (mean across plots and years). Then, to test the phenology response of each plant and bee taxon to the environmental variables, I ran linear mixed models using the lmerTest package (Kuznetsova et al. 2018). The phenology variable (first date, last date, period, or peak date) was the response; the environmental predictor identified in the individual-level analysis (temperature or snowmelt) was the fixed explanatory variable; plot and year were random factors. For each of the five taxa (two plants and three bees), a single linear mixed model was tested for each of the four phenological response variables, for a total of 20 models.

Second, to compare the magnitudes of phenology response to environmental variation among taxa (for first, last, and peak phenological events), I ran a second set of linear mixed models. Here, taxon (two plant and three bee categories), an environmental variable (snowmelt day or degree-days accumulated above 0°C from March 1 to April 30), and the interaction between taxon and the environmental variable were the fixed explanatory variables; year and plot were included as random factors. I summed degree-days between March and April because this is the period in which heat units start to accumulate, and because most of the phenological events happen in late April to May. Snowmelt date and temperature were tested in two separate models. A significant interaction term would indicate that the relationship between phenology and a given environmental variable differs among taxa.

Temporal overlap between flower and bee phenology. To evaluate how taxon-specific responses to environmental variation affect synchrony between bees and plants, I quantified pairwise proportional overlap using Schoener's index (Schoener 1970) between the flowering phenology of an individual plant taxon and the activity phenology of the three most abundant bee taxa (combined). This index considers the proportion of the total flowering and bee activity that occurred on each sampling occasion within the flowering period. This index ranges from 0 (no overlap between the two phenological curves) to 1 (the two phenological curves overlap perfectly). For each year and plot, I calculated an individual Schoener's index (SI) for each plant species, then I tested for a relationship between SI and the environmental factors (snowmelt date and temperature) using a binomial generalized linear mixed model with SI as a response variable, snowmelt date and degree-days accumulated from 1 March to 30 April as predictor variables, and year and plot as random factors.

All analyses were conducted in R v 3.4.2 (R Core Team 2018). For each model, assumptions and the influence of outliers were checked using LMERConvenienceFunctions package (Tremblay and Ransijn 2015). Removing outliers did not change the significance of any variables; so, outliers were retained.

Results

Climatic variation and flowering and insect phenology

April degree-days above 0°C (year $F_{5,45}$ = 26.39, P < 0.001) and snowmelt date (year $F_{5,45}$ = 50.78, P < 0.001) in our plots varied significantly among years (Table 1). Across years, the highest recorded mean temperature in April (5.8 ± 4.5°C) and the earliest snowmelt (April 10) were both recorded in 2017. Conversely, mean April temperature was lowest (3.3 ± 4.7°C) and snowmelt was latest (April 20) in 2018.

Regional temperatures from the Ottawa CDA weather station (daily mean temperatures from 20 March to 20 June) were strongly correlated with daily spring temperatures recorded in our study plots over the same time (Pearson r = 0.93, N = 93 days × 6 years). Based on the regional data, the variation in mean spring temperature in the last six years (10.2–10.8°C) encompasses only a portion of the temperature variation over the past 23 years (9.1–13.6°C). However, neither spring temperature (linear regression of mean spring temperature vs. year, R^2 = 0.00, N = 23 years, P = 0.951) nor annual temperature (R^2 = 0.03, N = 23 years, P = 0.435) has changed significantly since 1995 (Appendix 6).

The earliest-blooming spring ephemeral in the study plots was *Anemone* spp., flowering from mid-April, just a week after snowmelt, to early May (Fig. 1). Peak flowering occurred in late April, and the flowering period was on average 15.3 (± 3.9) days. The *T. grandiflorum* flowering period was 20.5 (± 4.5) days, from early to late May, with a peak in mid-May (Fig. 1). The three

bee taxa, *Andrena*, *Lasioglossum*, and *Nomada* spp., have similar activity phenology (Fig. 1). These bees were active for approximately three weeks, from mid-April to early May, with a peak in late April.

Table 1. Mean (SD) temperatures recorded by HOBO data-loggers and snowmelt dates across all plots.

Year	Day of year of snowmelt	April degree-days > 0°C	April mean temperature (°C)	April temperature range (°C)
2013	103.9 (3.8)	165.5 (27.6)	5.3 (7.3)	−3.7 to 43.8
2014	103.0 (1.5)	143.3 (30.0)	4.6 (5.2)	−3.3 to 35.3
2015	101.0 (3.3)	178.3 (25.3)	5.6 (5.9)	−0.01 to 29.5
2016	105.1 (1.0)	167.0 (34.3)	4.5 (4.5)	−3.1 to 22.9
2017	100.2 (1.4)	188.4 (19.5)	5.8 (4.5)	0.01 to 25.8
2018	110.2 (1.3)	107.1 (23.7)	3.3 (4.7)	−3.6 to 31.8

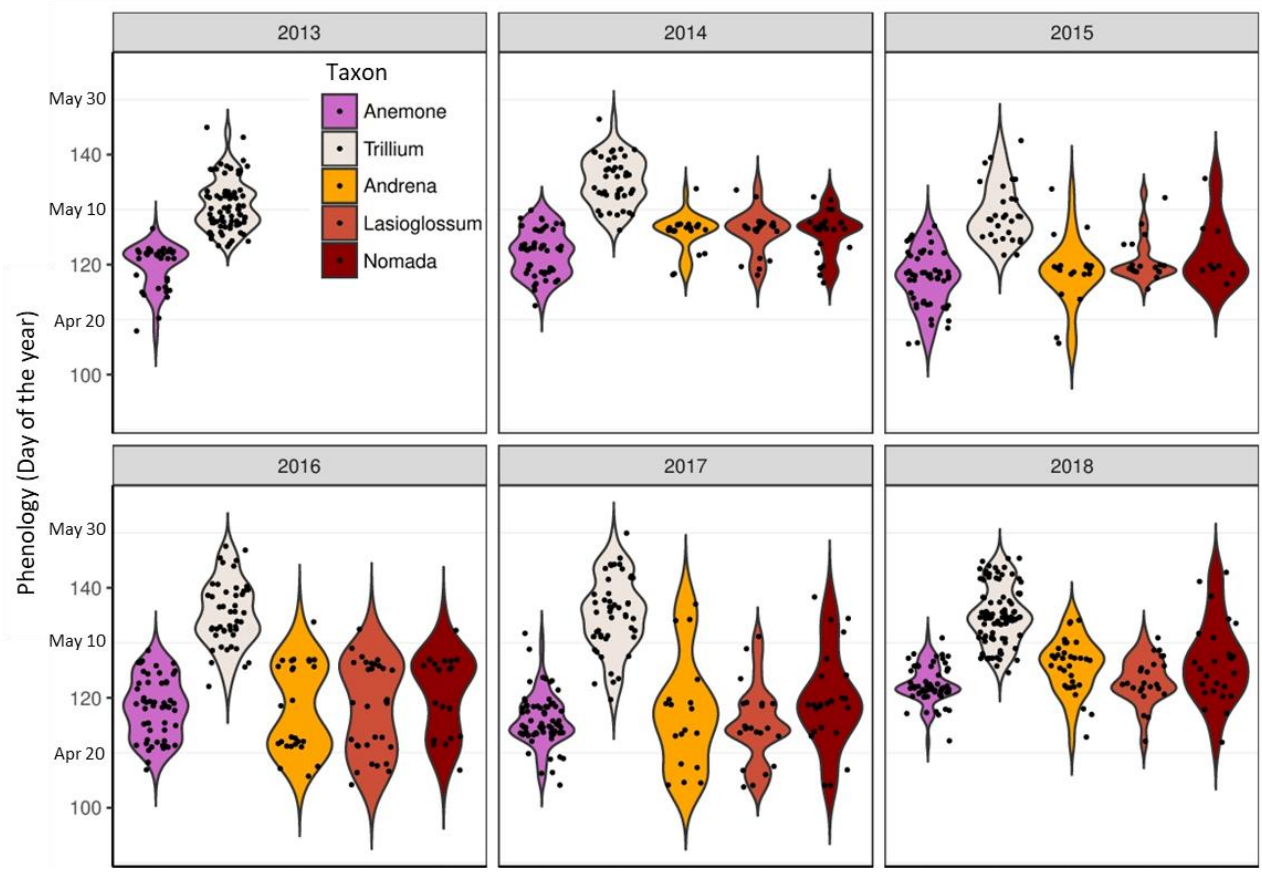

Fig. 1. Flowering and activity phenology of two plant and three bee taxa in Gatineau Park. Data collected in ten plots over six years (2013 bees are excluded due to low numbers collected). Different taxa are represented by different colours. The length of each "violin" represents the flowering or activity period, and the width corresponds to the abundance of each taxon during the season (summed across plots), the widest point being the flowering or activity peak over all plots. For *Anemone* spp. and the three bee taxa, dots represent 10% of the flowers open or bees collected on a sampling occasion (e.g. if there were 50 flowers on a given day, there are 5 dots for that date); *T. grandiflorum* dots represent 5% of the flowers open on a sampling occasion. Dots are jittered to minimize overlap.

Individual-level analyses of flower and bee phenology

Logistic regressions described well the relationships between cumulative proportion of flowering or activity and accumulated degree-days, days since snowmelt, and day of year (Fig. 2, 3). The cumulative proportion of flowering for *Anemone* spp. was best described by a degree-day-based model; however, accumulation of days (i.e., day of year) was by far the best descriptor of the cumulative proportion of flowering for *T. grandiflorum* (Fig. 2; Table 2). For *Nomada* spp., degree-day-based models had lower AIC values than models using days since snowmelt or day of year (Table 2). For *Andrena* and *Lasioglossum*, cumulative proportion of activity was best described by day of year or accumulated degree-days (models differ by <2 AIC units; Fig. 3; Table 2). The best degree-day models for *Anemone* spp., *T. grandiflorum*, *Nomada*, and *Lasioglossum* spp. had a base temperature of 0°C, while for *Andrena* spp. the best-fit base temperature was 1°C (Table 2). The individual-taxon models show that different taxa require different numbers of accumulated heat units for their phenological events (Fig. 2, 3).

Table 2. Summary of AIC values for generalized linear mixed models of the cumulative proportion of flowering or activity that had occurred by each observation date with degree-days accumulated (DDA) above a particular base temperature, days since snowmelt (snow), or day of year as the predictor variable of interest; year and plot (as random factors) were also included in the models. Bold numbers indicate the best-fit model(s) for each taxon. Three base temperatures are presented for comparison purposes.

Taxon	**Snow**	**DDA > 0°C**	**DDA > 1°C**	**DDA > 5°C**	**Day of year**
Anemone spp.	123.5	**87.2**	96.2	112.8	105.3
T. grandiflorum	191.9	172.9	175.3	213.6	**117.6**
Andrena spp.	140.7	131.4	**124.8**	137.7	**126.6**
Lasioglossum spp.	127.6	**113.3**	114.9	118.2	**113.5**
Nomada spp.	120.9	**111.6**	114.8	128.4	117.1

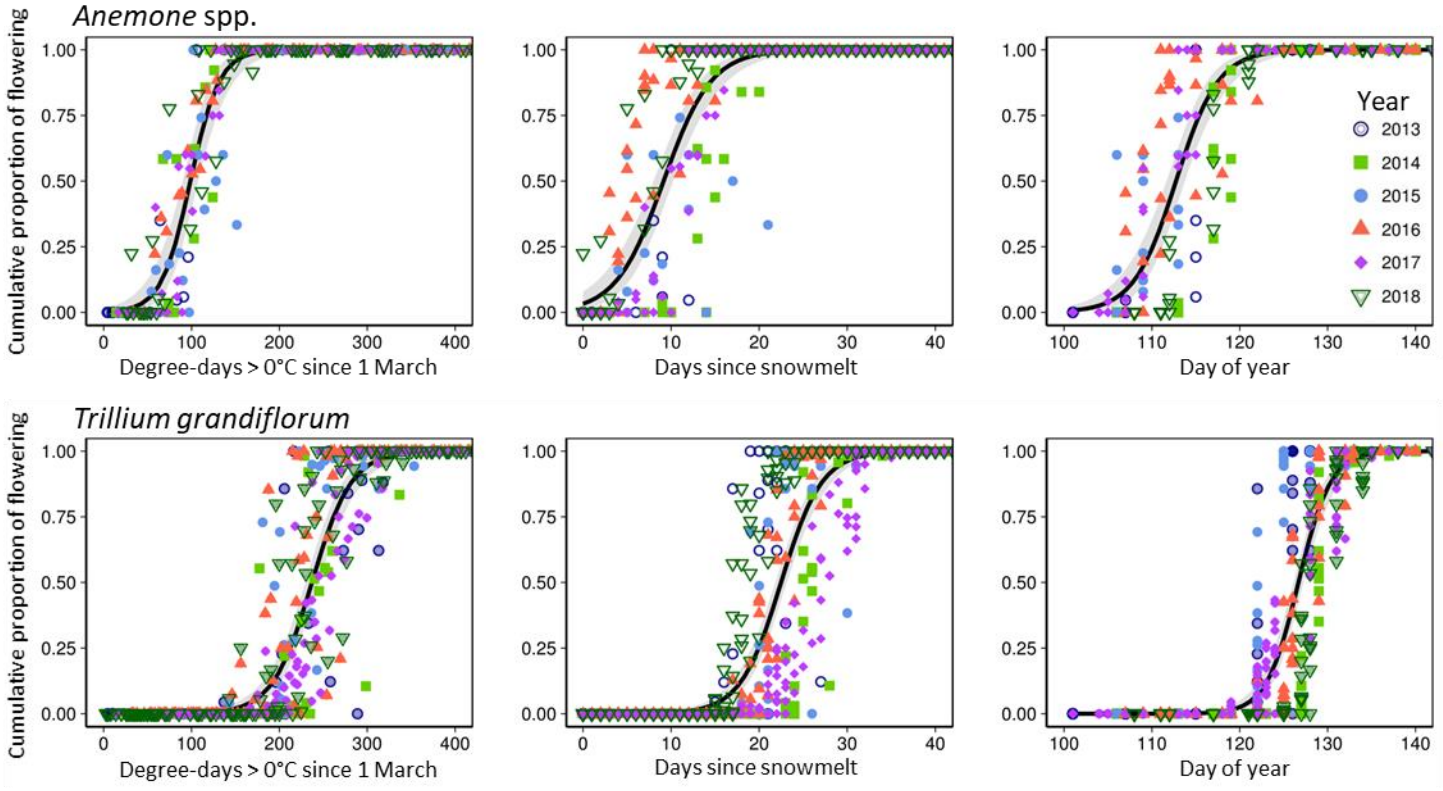

Fig. 2. Flowering phenology of two plant taxa at Gatineau Park. The cumulative proportion of flowering having occurred in a given plot on each sampling date is plotted against the number of degree-days (left), days since snowmelt (middle), and days since Jan. 1 (e.g. "Day of year 121 = May 1) (right) accumulated up to that date. Different years are indicated by the symbols. A base temperature of 0°C was selected because it provided the best fit to the data. The curve shows the best-fit logistic regression for each species across all plots and years; 95% CI are represented by the shaded areas.

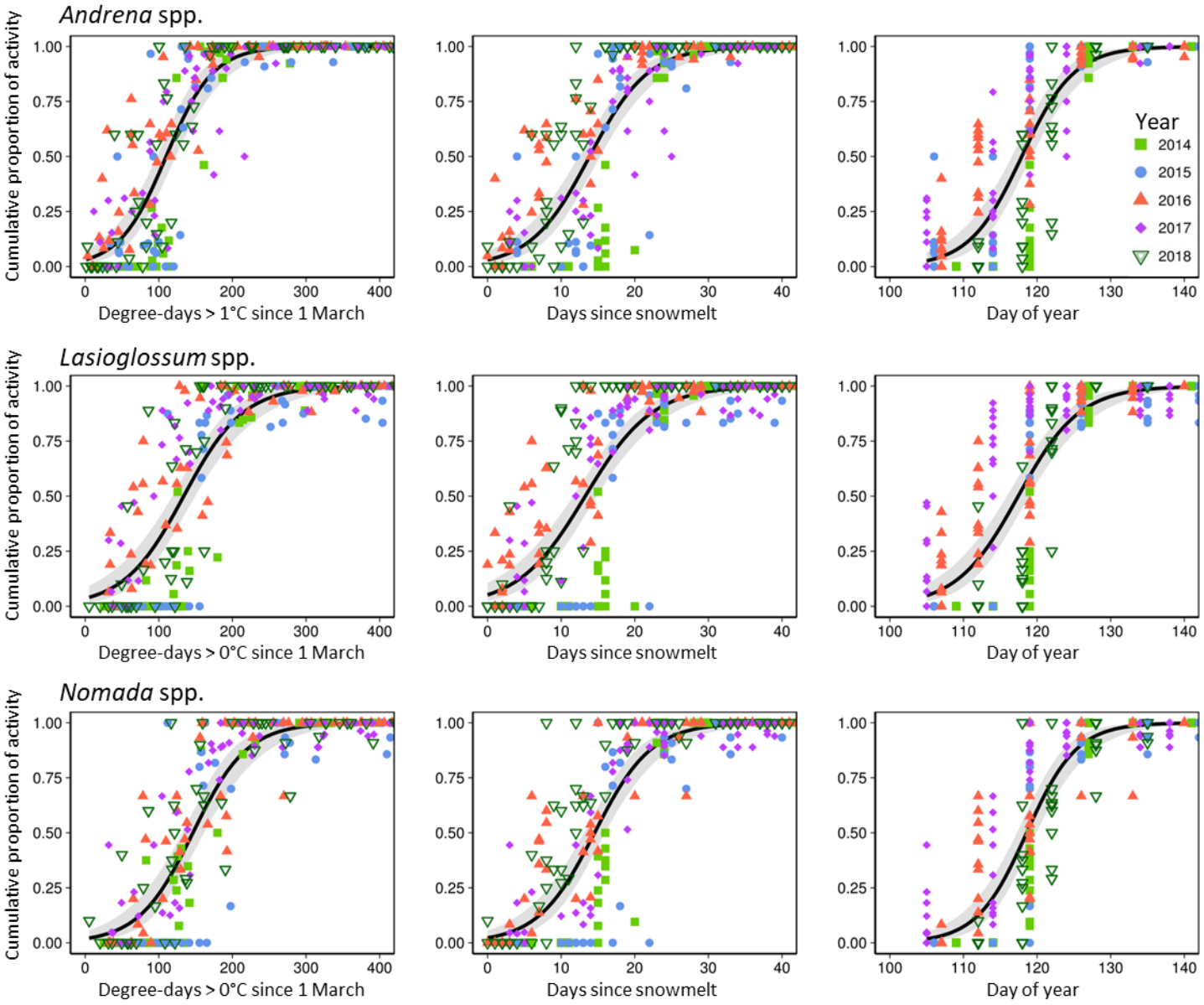
Andrena spp.
Lasioglossum spp.
Nomada spp.
Cumulative proportion of activity
1.00
0.75
0.50
0.25
0.00
0
100
200
300
400
Degree-days > 1°C since 1 March
Degree-days > 0°C since 1 March
10
20
30
40
Days since snowmelt
110
120
130
140
Day of year
Year
2014
2015
2016
2017
2018

Fig. 3. Phenology of activity of three bee taxa at Gatineau Park. The cumulative proportion of activity having occurred in a given plot on each sampling date is plotted against the number of degree-days (left), days since snowmelt (middle) and days since Jan. 1 (right) accumulated up to that date. Different years are indicated by the symbols. Each taxon has a particular base temperature based on the best-fit model across all the years. The curve shows the best-fit logistic regression for each species across all plots over all years; 95% CI are represented by the shaded areas.

Plot-level analyses of flower and bee phenology

Plot-level flowering phenology of *Anemone* spp. was strongly associated with temperature (Table 3). First, peak, and last flowering day were negatively correlated with accumulated degree-days (from 1 March until mean date of the phenological event), with flowering starting and ending earlier in warmer springs. For *T. grandiflorum*, peak flowering day was negatively correlated with temperature, but first and last flowering days were not sensitive to temperature (Table 3). Flowering period was not predicted by temperature in either species. Models including only degree-day accumulation accounted for most of the variation in *Anemone* spp. flowering phenology but not that of *T. grandiflorum* (Appendix 7).

Lasioglossum spp. and *Nomada* spp. peak activity days were associated with temperature, with greater accumulation of heat units accelerating peak activity (Table 3), but first and last dates and activity period were not. No aspect of *Andrena* phenology was predicted by temperature (Table 3). Linear mixed models including accumulation of degree-days were generally better than models containing snowmelt date or both environmental variables (Appendix 7), but accumulation of degree-days failed to predict most of the variation in bee phenology (Table 3).

Table 3. Response of flowering and bee activity phenology to degree-day accumulation (DDA, from March 1 until the mean date of each phenological response). Year and plot were included in models as random factors. Marginal R^2 (R^2m; variance explained by fixed factors only) and conditional R^2 (R^2c; variance explained by both fixed and random factors) provide an indication of the goodness-of-fit of each model (Nakagawa et al. 2017). Bold numbers indicate a significant response.

Phenology	Estimate ± SE	*df*	*t*	*P*	R^2m	R^2c
***Anemone* spp.**						
First flowering	−0.08±0.01	24	−5.72	**< 0.0001**	0.56	0.75
Peak flowering	−0.07±0.01	24	−7.18	**< 0.0001**	0.67	0.67
Last flowering	−0.06±0.02	24	−3.84	**0.0009**	0.39	0.57
Flowering period	0.01±0.02	24	0.51	0.612	0.01	0.33
T. grandiflorum						
First flowering	0.00±0.01	54	0.65	0.516	0.00	0.86
Peak flowering	−0.01±0.01	54	−2.03	**0.047**	0.05	0.58
Last flowering	−0.01±0.01	54	−1.27	0.20	0.02	0.58
Flowering period	−0.01±0.01	54	−0.65	0.519	0.01	0.65
***Andrena* spp.**						
First bee	−0.01±0.03	45	−0.21	0.836	0.001	0.74
Peak bee	0.00±0.03	45	−0.02	0.986	0.001	0.47
Last bee	−0.01±0.02	45	−0.55	0.586	0.007	0.07
Activity period	0.02±0.03	45	0.69	0.492	0.01	0.30
***Lasioglossum* spp.**						
First bee	0.00±0.01	41	−0.07	0.945	0.001	0.97
Peak bee	−0.06±0.03	41	−2.15	**0.045**	0.07	0.63
Last bee	−0.01±0.03	41	−0.23	0.822	0.001	0.45
Activity period	0.01±0.04	41	0.33	0.745	0.007	0.54
***Nomada* spp.**						
First bee	−0.02±0.02	41	−0.94	0.354	0.007	0.81
Peak bee	−0.06±0.02	41	−2.93	**0.007**	0.20	0.37
Last bee	−0.03±0.01	41	−2.03	0.064	0.09	0.10
Activity period	0.00±0.02	41	0.09	0.923	0.001	0.66

Variation in phenology response across taxa

The phenologies of the five taxa showed similar responses to snowmelt date and degree-day accumulation from 1 March to April 30 (i.e., no taxon by environmental predictor interactions, Fig. 4, Table 4). Specifically, first and peak days were positively correlated with snowmelt date and negatively correlated with temperature in all taxa (Fig. 4). Last flowering or activity day was positively correlated with snowmelt date and negatively correlated with temperature only for *Anemone* spp. and *Nomada* spp. (Fig 4).

Table 4. Effects of snowmelt date (Snow) and temperature (DDA; degree-day accumulation above 0°C from 1 March to 30 April) on flowering and bee activity phenology. Results from linear mixed models with taxon as a categorical variable with five levels (two plant and three bee categories); plot and year were included as random factors.

Predictor	**Sum Sq**	***df***	***F***	***P***
	First flowering or activity day			
Snow	27.551	1, 31	3.0	0.091
Taxon	44.078	4, 213	1.2	0.305
Snow × taxon	18.038	4, 213	0.5	0.737
DDA	36.652	1, 22	4.0	0.059
Taxon	164.71	4, 194	4.5	**0.002**
DDA × taxon	46.538	4, 194	1.3	0.287
	Peak flowering or activity day			
Snow	67.597	1, 46	4.3	**0.041**
Taxon	106.493	4, 216	1.7	0.156
Snow × taxon	63.881	4, 216	1.0	0.405
DDA	122.4	1, 186	8.0	**0.005**
Taxon	164.25	4, 195	2.7	**0.033**
DDA × taxon	102.27	4, 195	1.7	0.159
	Last flowering or activity day			
Snow	42.542	1, 45	2.8	0.100
Taxon	146.537	4, 222	2.4	**< 0.05**
Snow × taxon	91.686	4, 223	1.5	0.196
DDA	53.44	1, 95	3.5	0.066
Taxon	321.95	4, 201	5.2	**< 0.001**
DDA × taxon	97.34	4, 201	1.6	0.182

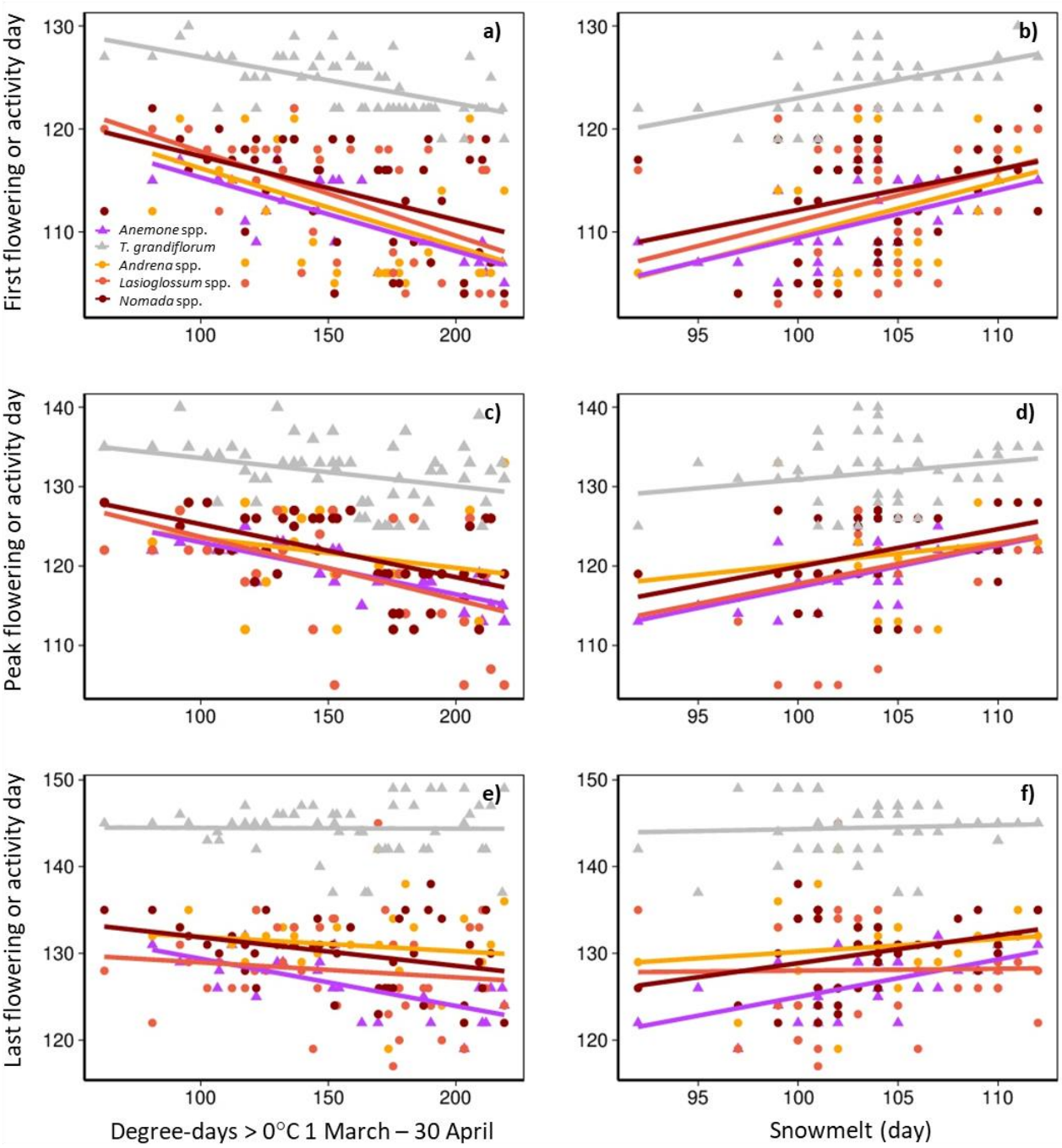

Fig. 4. Phenological responses of two plant and three bee taxa to temperature (accumulated degree-days; left) and snowmelt (day of year; right). First (a, b), peak (c, d) and last (e, f) flowering and activity dates are shown. Plant flowering phenology is represented by triangles and bee activity by circles; different taxa are shown in different colours. Regression lines are from simple linear regressions. Data collected from ten sampling plots over six years for plants and five years for bees. Slopes are not significantly different between taxa (Table 4).

Temporal overlap between flower and bee phenology

The three focal bee taxa combined (*Andrena*, *Nomada*, and *Lasioglossum* spp.) overlap to a greater extent with the flowering period of *Anemone* spp. than with that of *T. grandiflorum*, but temporal overlap (Schoener's index) between flowering and bee activity was similar over the years of my study (year $F_{4,16} = 0.7$, $P = 0.57$). Temporal overlap between the activity of bees and flowering ranged across plots and years from 0.40 to 0.87 for *Anemone* vs. 0.01 to 0.36 for *T. grandiflorum*. There was no relationship between environmental variables and overlap between either plant taxon and bees (Table 5).

Table 5. Effects of environmental variation on temporal overlap (Schoener's index) between bees and flowering plants. Results from generalized linear mixed models for SI, with snowmelt date (Snow) or temperature (DDA; degree-days accumulated from 1 March to 30 April) as fixed factors, and year and plot as random factors. Mean overlapping days and SI (standard deviation across ten plots and five years) are also reported.

Plant taxa	**Overlap**	**Predictor**	**Sum Sq**	***F***	***P***
Anemone	0.62 (0.32)	DDA	2.35	2.35	0.120
		Snow	1.01	1.01	0.314
T. grandiflorum	0.15 (0.08)	DDA	0.00	0.72	0.409
		Snow	0.00	3.65	0.128

Discussion

Flowering phenology has remained similar over the years of this study, but there was substantial variation in bee abundance and phenology among years. Generally, temperature (degree-day accumulation) was the best predictor of flowering and bee activity phenology, but temperature-sensitivity varied among taxa. *Anemone* spp. flowering phenology was strongly associated with temperature, but that of *T. grandiflorum* was best described by photoperiod. Bee phenology was more difficult to predict from climatic variables, but *Lasioglossum* and *Nomada* spp. peak activity dates were sensitive to temperature. Despite the interannual variation in environmental conditions and in species' sensitivities to environmental variables, temporal synchrony between bees and flowers remained similar over the years of this study and was affected neither by temperature nor by snowmelt date.

Drivers of flowering phenology

Flowering phenology of the two wildflower taxa was associated with different environmental factors. Phenology of early-flowering *Anemone* spp. was strongly associated with temperature, with springtime degree-days predicting the onset, peak, and end of flowering. *Trillium grandiflorum* phenology was better fitted by day of year than by temperature or snowmelt date, suggesting that photoperiod may be the main environmental trigger for its flowering phenology. Nevertheless, the accumulation of degree-days explained some of the variation in *T. grandiflorum* phenological variables: faster accumulation of degree-days was associated with earlier peak flowering. Flowering duration was unaffected by interannual variation in climatic conditions in either taxon; however, this was because of differing responses to temperature between the two taxa. The flowering period of *Anemone* spp. was unaffected by temperature because first and last flowering days responded similarly to variation in temperature, whereas the flowering period of *T.*

grandiflorum was unaffected because its first and last flowering days were both relatively insensitive to variation in temperature. In many temperate-region species, flowering time is influenced primarily by the length and intensity of warm spring temperatures (Fitter 2002; Chuine et al. 2010; Tooke and Battey 2010; Schwartz 2013; Guo et al. 2015). A species-specific daylength also promotes flowering in diverse herbaceous plants, but sensitivity to photoperiod is typically temperature-dependent (Capovilla et al. 2015), an interaction I did not investigate in this study. Phenology of early-flowering plants tends to be more sensitive to temperature variation than that of mid-season or late-flowering species (Menzel et al. 2006; Sherry et al. 2007; Wolkovich et al. 2012), and this was the pattern observed in my study site, with early-flowering *Anemone* spp. more responsive than later-flowering *T. grandiflorum* to the accumulation of degree-days in springtime.

Temperature and photoperiod are considered the primary drivers of phenological events in many short-lived herbs and trees in temperate forests (Diekmann 1996; Fitter 2002; Chuine et al. 2010; Kudo and Ida 2013), whereas snowmelt date is often found to be the strongest predictor of flowering phenology in alpine and artic environments (Inouye et al. 2002; Inouye 2008; Lambert et al. 2010; Cooper et al. 2011). Temperature and snowmelt date are almost always confounded in nature (as observed in this study), making it difficult to separate independent effects of the two variables. However, degree-day accumulation at ground level incorporates more information than days after snowmelt, since heat units start to accumulate only after snowmelt. For this reason, it is unsurprising that degree-day accumulation was a better predictor of phenology than snowmelt date for all taxa in this study. Conversely, in studies that find snowmelt date to be a better predictor of phenology than heat accumulation, temperature tends to have been measured at weather stations, above the snowpack and potentially some distance from the study plots (e.g. Inouye et al. 2002;

Iler et al. 2013)—in other words, in a microhabitat quite different from that occupied by the plants—whereas snowmelt is measured more locally.

Drivers of bee activity phenology

The activity phenology of bees was difficult to predict, but individual-level and plot-level variation among years was generally better predicted by temperature than by snowmelt date. As in other studies (Bartomeus et al. 2011; Kudo 2014), bee phenological responses varied among taxa: *Lasioglossum* and *Nomada* seem to be more responsive to accumulated heat than are *Andrena* bees. For all three taxa, activity phenology was best described by degree-days calculated from a base temperature between 0 and 1°C, in contrast with previous studies showing that insects generally require higher base temperatures (4–18°C) for different phenological events (e.g., emergence of cavity-nesting bees and wasps from hibernation (Forrest and Thomson 2011); development of *Osmia lignaria* from pupa to adult (Kemp and Bosch 2005); larval eclosion of the winter moth *Operophtera brumata* (Kimberling and Miller 1988)).

It is intriguing that day of year was as good as temperature in describing the phenology of *Andrena* and *Lasioglossum* spp. It seems unlikely that insects overwintering in the ground use photoperiod per se as a cue to emerge from hibernation; however, thermoperiod (the daily schedule of temperature variation) can be an important cue influencing the termination of overwinter diapause in light-restricted insects (Miyazaki et al. 2011, 2016; Yocum et al. 2016; Bennett et al. 2018). It is possible that *Lasioglossum* and *Andrena* spp. emerge from hibernation in response to daily fluctuations of temperature or to the gradual soil warming after snowmelt. As with plants, bee activity phenology is likely governed by a combination of environmental factors rather than a single cue. Environmental and physiological factors that I did not consider here, such as precipitation, soil temperature, and body condition, may also play a role (Ellwood et al. 2012;

Olliff-Yang and Mesler 2018; Schenk et al. 2018b). In addition, the lack of a strong phenological response of bees to temperature could indicate that different bee species belonging to the same genus vary in their sensitivity to temperature, diluting the overall response (Bartomeus et al. 2011).

Finally, bee activity phenology may be influenced by temperature at a regional scale rather than a local scale. Bees are continuously searching for floral resources, and their activity is affected by current environmental conditions such as temperature, precipitation, and wind speed (Kevan and Baker 1983). Indeed, phenology models based on mean temperatures across plots better described bee activity phenology than did models based on plot-specific temperatures (higher marginal and conditional R^2 values; data not shown), but this was not the case for flowering phenology. Environmental conditions on the sampling day may also have affected the numbers of bees collected in the bee bowls; for example, *Andrena bicolor* (Herrera 1995) and honey bees (Vicens and Bosch 2000) are more active on warm and sunny days. I tried to minimize this problem by sampling on days without precipitation, with cloud-cover <50% and daytime air temperature >10°C. Nevertheless, fluctuation in the number of bees captured, due to environmental conditions on the day of sampling, could have influenced the ability of the models to predict the phenological response of bees to degree-day accumulation, which is relatively insensitive to sampling-day temperature.

Interactions between wildflowers and ground-nesting bees

Overall, my results suggest that bee activity and flowering phenology have responded in parallel to variation in climate over the last six years. First, both bees and plants responded at a similar rate to springtime degree-days and snowmelt date, despite the fact that, for some taxa, associations between these environmental variables and phenology were not significant. Second, similar best-fit base temperatures for flowering and bee phenology (0–1°C) suggest that small changes in

temperature will affect plants and bees at similar rates, not affecting their temporal overlap. Third, despite the observed interannual variation in temperature and snowmelt date, temporal synchrony between bees and plants remained similar over the course of this study and was unaffected by these environmental factors. Nonetheless, as the climate changes beyond the range of conditions observed so far, *T. grandiflorum* may experience a reduction in temporal overlap with solitary bees, since its phenology had a strong photoperiodic response, whereas solitary bees showed greater sensitivity to temperature.

In my study system, even if phenology of plants and solitary bees were to become uncoupled in future climate scenarios, this may not translate into severe fitness consequences for either of the interaction partners. Neither of the two plant taxa seems to be totally dependent on solitary bees for seed production. *Anemone* flowers are capable of autogamy (Motten 1982), and *T. grandiflorum*, although reliant on pollinators for seed production, is primarily pollinated by bumblebees (Irwin 2000). However, self-pollination reduces seed set relative to out-crossing in *Anemone* spp. (Bernhardt 1976). Also, solitary bees may play an increasingly important role in *T. grandiflorum* pollination in the future, as populations of some bumble bee species decline, and their ranges shrink in North America (Goulson et al. 2008; Cameron et al. 2011; Kerr et al. 2015). In the context of bumble bee declines, changes in overlap with solitary bees could impair reproduction in this species.

Bees typically started their activity at the same time as or shortly after the flowering of *Anemone* spp., the first flowering herbaceous plant in our study site. Occasionally, early *Lasioglossum* females and *Andrena* males started their activity as much as three days before the first *Anemone* flower, suggesting a possible mismatch from the bees' perspective. However, these bees have fat reserves that allow them to survive a few days without food resources (Michener

2000; Weissel et al. 2012). Nonetheless, climatic conditions beyond the range of values recorded so far could cause bee activity to precede floral resources by more than a few days, having negative impacts on bee lifespan, reproduction, and colony development (Kudo 2014; Schenk et al. 2018a).

Conclusions

Understanding the factors that shape the phenology of interacting species allows us to predict some of the possible consequences of climate change. In this study, I investigated how different environmental factors affect the phenology and temporal synchrony of two spring wildflowers and three ground-nesting bee taxa. My results suggest that, even though plants and bees have taxon-specific responses to different environmental factors, they respond at a similar rate to the interannual variation in climatic variables observed so far (cf. Bartomeus et al. 2011). I therefore expect them to maintain similar temporal overlap in the future. However, *T. grandiflorum* could experience a reduction in temporal overlap with solitary bees if springtime temperatures increase, since it was less sensitive than bees to temperature.

I was unable to determine with confidence the cues that drive bee phenology, since most variation in bee phenology was unexplained. Exploring more environmental factors such as precipitation, temperature on the days of sampling, or soil temperature, in addition to continuing long-term monitoring studies (Hegland et al. 2009; Ellwood et al. 2012; Cohen et al. 2018; Olliff-Yang and Mesler 2018), will be necessary to predict the future interactions between plants and pollinators. Future research should also focus on the ecological consequences of decreases in temporal synchrony between plants and pollinators. Finally, it is important to explore the environmental factors that drive phenology of flowering trees and of other pollinators such as bumble bees and flies in the hardwood forest, which may interact with my study species and which could be using environmental cues different than those used by spring wildflowers and solitary bees.

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Appendix 1

Study plot locations in Gatineau Park, QC.

Plot	Position	Altitude
Plot 1	N 45° 27′ 077″ W 75° 46′ 931″	132 m
Plot 2	N 45° 27′ 074″ W 75° 46′ 820″	177 m
Plot 3	N 45° 27′ 044″ W 75° 46′ 732″	162 m
Plot 4	N 45° 26′ 996″ W 75° 46′ 715″	171 m
Plot 5	N 45° 27′ 015″ W 75° 46′ 583″	197 m
Plot 6	N 45° 26′ 944″ W 75° 46′ 592″	-
Plot 7	N 45° 26′ 989″ W 75° 46′ 428″	164 m
Plot 8	N 45° 26′ 892″ W 75° 46′ 392″	144 m
Plot 9	N 45° 26′ 873″ W 75° 46′ 268″	157 m
Plot 10	N 45° 26′ 945″ W 75° 46′ 287″	133 m

Appendix 2

Total number of observations and interval (in days) between sampling occasions of flower plots and bee bowls in each year.

	Flower plots			**Bee bowls**		
Year	Total	Interval	Period	Total	Interval	Period
2013	10	6 – 8	Apr 11 to Jun 02	10	6 – 8	Apr 11 to May 25
2014	12	2 – 7	Apr 16 to Jun 09	7	5 – 9	Apr 19 to May 27
2015	14	3 – 5	Apr 16 to Jun 02	7	5 – 8	Apr 16 to May 30
2016	19	1 – 3	Apr 17 to May 30	7	5 – 6	Apr 17 to May 27
2017	20	1 – 3	Apr 15 to Jun 10	8	5 – 9	Apr 15 to Jun 01
2018	18	1 – 3	Apr 10 to May 30	6	5 – 9	Apr 22 to May 30

Appendix 3

Plant taxa present in the study plots, showing criteria used to select focal taxa (*Anemone* spp. and *Trillium grandiflorum*).

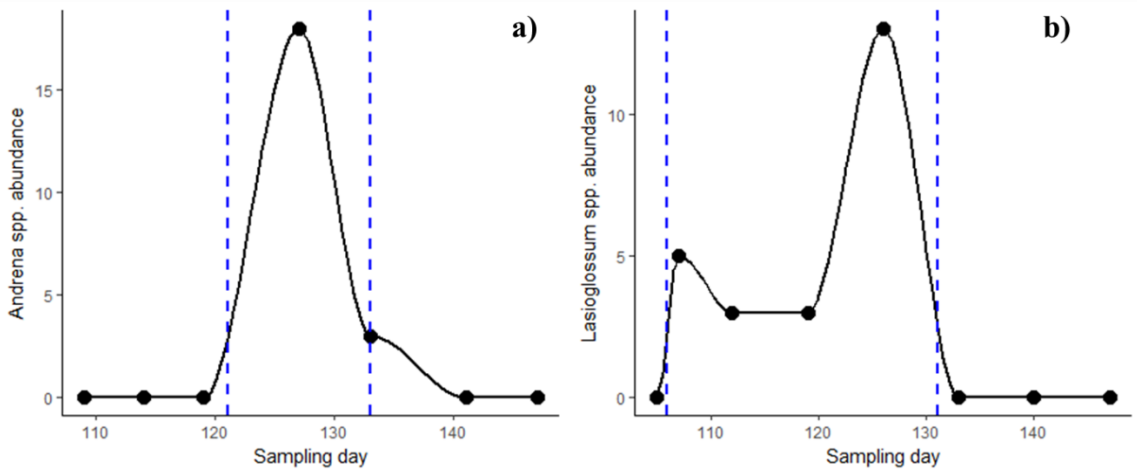
Species	Present 3 or more years	Present in >1 quadrat per year	Present on 3 or more sampling occasions	Insect-pollinated (reference)
Aquilegia canadensis				
Alliaria petiolata				
Dicentra cucullaria		×		
Erythronium americanum	×	×		
Galium spp.				
Anemone acutiloba & A. americana	×	×	×	Yes (Motten, 1986) (Bernhardt, 1976)
Maianthemum racemosum	×	×		Yes (Piper, 1989)
Mitella diphylla				
Polygonatum pubescens			×	
Rosa spp.				
Sanguinaria canadensis	×			
Saxifraga virginiensis		×		
Thalictrum dioicum	×	×	×	No (Kaplan and Mulcahy, 1971)
Trillium grandiflorum	×	×	×	Yes (Case and Case, 1997)

Appendix 4

Numbers of bees collected in Gatineau Park in each year, summed across plots. Relative abundance (percent of a particular bee taxon relative to the total number of bees collected in that year) is given in parentheses.

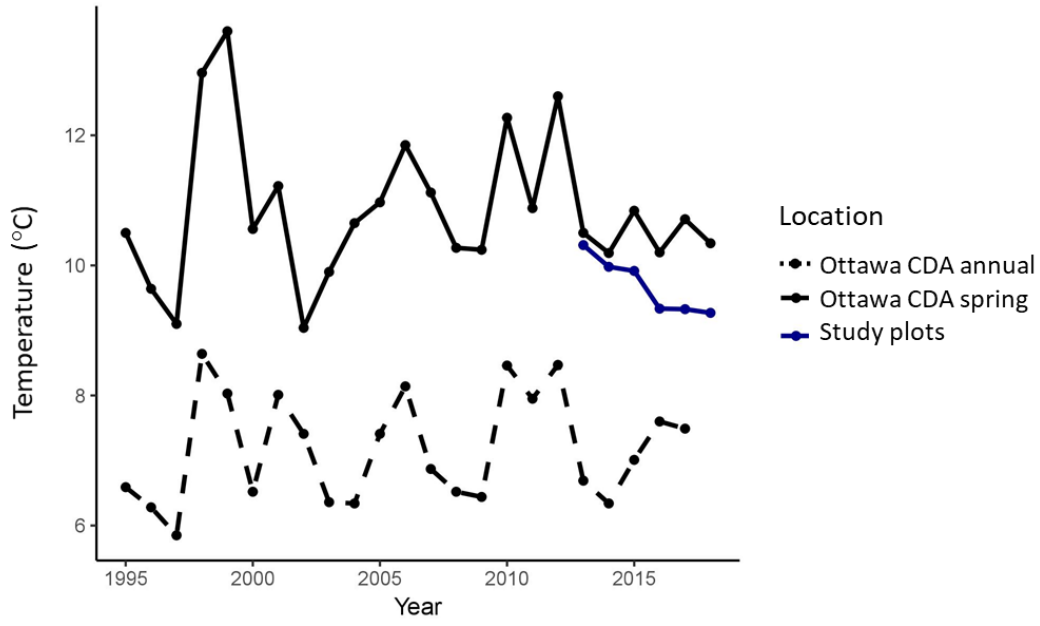
		Year					
Family	**Taxa**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
Andrenidae	*Andrena* spp.	20 (26.7)	253 (35.9)	169 (37)	271 (31.8)	137 (25)	117 (32.7)
Apidae	*Bombus* spp.	3 (4)	2 (0.3)	2 (0.4)	9 (1)	7 (1.3)	0 (0)
	Nomada spp.	15 (20)	179 (25.4)	84 (18.4)	192 (22.5)	195 (35.6)	109 (30.4)
	Ceratina spp.	3 (4)	6 (0.9)	11 (2.4)	54 (6.3)	6 (1.9)	8 (2.2)
Colletidae	*Colletes* spp.	-	6 (0.9)	1 (0.2)	12 (1.4)	11 (2)	3 (0.8)
Halictidae	*Lasioglossum* spp.	28 (37.4)	235 (33.4)	160 (35)	292 (34.3)	160 (29.2)	102 (28.5)
	Halictus spp.	-	-	8 (1.7)	30 (3.5)	17 (3.1)	4(1.1)
	Augochlora spp.	-	-	3 (0.6)	6 (0.7)	-	3 (0.8)
Megachilidae	*Osmia* spp.	6 (8)	23 (3.2)	22 (4.8)	35 (4.1)	15 (2.7)	11 (3)
	Total bees (100%)	**75**	**704**	**457**	**852**	**548**	**358**

Appendix 5



Examples of bee phenology, showing observed (points) and interpolated (lines) abundances. (a) *Andrena* spp. phenology in plot 9, 2014; (b) *Lasioglossum* spp. phenology in plot 8, 2016. Each point represents one insect sampling occasion; dashed lines indicate interpolated first and last activity days (i.e., days by which 10% and 90% of individuals, respectively, would have been observed).

Appendix 6



Interannual variation in temperature recorded by Ottawa CDA weather station and HOBO stations at the study site. The black lines represent mean annual temperature (dotted) and mean spring temperature (solid; March 20 – June 20) at the weather station. The blue solid line shows mean spring temperature at the study plots.

Appendix 7

Summary of AIC values for linear mixed models of the flowering and activity phenological events (first, peak, last, and period) in response to climatic variables: degree-day accumulation (DDA, from March 1 until the mean date of each phenological response) and snowmelt day (snow); year and plot were included as random factors. Bold numbers indicate the best-fit model. Models within 2 AIC units of one another are considered equally good,

Model	First ~	Peak ~	Last ~	Period ~
Anemone spp.				
DDA	**124.6**	**125.4**	**138.4**	**150.7**
snow	143.7	147.7	151.6	163.7
DDA + snow	128.1	**125.7**	**137.4**	153.6
T. grandiflorum				
DDA	246.5	310.7	288.6	326.2
snow	**241.0**	**308.3**	**283.8**	**320.1**
DDA + snow	250.3	314.5	293.8	329.2
Andrena spp.				
DDA	**250.3**	**267.9**	**241.2**	**300.5**
snow	263.6	288	270.8	319.7
DDA + snow	**252.1**	269.9	250.4	**302.1**
Lasioglossum spp.				
DDA	**156.8**	**224.2**	**237.7**	**242.9**
snow	172.8	249.2	253.2	260.4
DDA + snow	160.3	**225.8**	**239.3**	**244.2**
Nomada spp.				
DDA	**226.3**	**245.7**	**250.5**	**255.1**
snow	237.5	266.9	263.7	271.7
DDA + snow	228.6	247.9	**251.8**	257.6