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Title: Spring wildflower phenology and pollinator activity respond similarly to climatic variation in an eastern hardwood forest

Short title: Temporal overlap between bees and wildflowers

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Key words: Phenology, temporal overlap, ground-nesting bees, wildflowers, hardwood forest.

Authors' Contributions

J.F. and R.S. conceived the study and established the study plots. M.S. analysed the data, with input from J.F. M.S. and J.F. interpreted the results and wrote the manuscript. All authors contributed to data collection and to revising the manuscript.

Abstract

Climate warming could disrupt species interactions if organisms' phenologies respond to climate change at different rates. Phenologies of plants and insects can be sensitive to temperature and timing of snowmelt; however, many important pollinators including ground-nesting bees have been little studied in this context. Without knowledge of the environmental cues affecting phenologies of co-occurring species, we have little ability to predict how species assemblages, and species interactions, will be affected by climate change. Here, we studied a hardwood forest understory over six years, to determine how spring temperatures, snowmelt timing, and photoperiod influence the phenology of two spring wildflowers (*Anemone* spp. and *Trillium grandiflorum*), activity of ground-nesting bees, and their temporal overlap. Surface degree-day accumulation was a better predictor of phenology for *Anemone* spp. (plant) and *Nomada* (bees) than were day of year (a proxy for photoperiod) or snowmelt date, whereas *Trillium* flowering appeared most sensitive to photoperiodic cues. Activity periods of *Andrena* and *Lasioglossum* bees were equally well described by degree-day accumulation and day of year. No taxon's phenology was best predicted by snowmelt date. Despite these differences among taxa in their phenological responses, timing of bee activity and flowering responded similarly to variation in snowmelt date and early spring temperatures. Furthermore, temporal overlap between flowering and bee activity was similar over the years of this study and was unaffected by variability in snowmelt date or temperature. Nevertheless, the differences among some taxa in their phenological responses suggests that diverging temporal shifts are a possibility for the future.

Key words: Phenology, temporal overlap, ground-nesting bees, wildflowers, hardwood forest.

Introduction

Species-specific differences in responses to climate change could lead to modifications in community temporal structure (CaraDonna et al. 2014), changing the assemblages of concurrently active organisms (Forrest et al. 2010; Theobald et al. 2017) and potentially leading to the loss or creation of new interactions (Schweiger et al. 2010; McKinney et al. 2012; Burkle et al. 2013). Although it is now evident that interacting species can exhibit non-parallel shifts in phenology (Kharouba et al. 2018), the reasons for these shifts are typically unclear, because we usually do not know the specific environmental factors that control species' phenologies. This lack of knowledge makes it impossible to predict the occurrence or extent of future phenological changes. Nor is there a framework that would allow us to predict when co-occurring species should be expected to differ in their phenological responses (but see Rafferty et al. 2015 on mutualisms). For example, some evidence suggests that if interacting species overwinter in different habitats (McKinney et al. 2012), or in different parts of the globe (Saino et al. 2009; Mayor et al. 2017), they may be vulnerable to mismatch during the spring or summer; but even species overwintering in the same location can apparently be susceptible to mismatch (e.g., Kudo and Cooper 2019). Clearly, more studies of a broader array of species and ecosystems are needed if we are to arrive at a general understanding of when phenological disruptions are likely.

Climate change has already been associated with phenological disruptions across a range of interacting species, including plants and their herbivores, predators and prey, and plants and their insect pollinators (Parmesan 2006; Durant et al. 2007; Donnelly et al. 2011; Kharouba et al. 2018). In particular, the potential for climate change to interrupt temporal overlap between plants and pollinators has received considerable attention (Hegland et al. 2009; Petanidou et al. 2014; Forrest 2015). Some such disruptions have been shown to reduce plant fitness (Gezon et al. 2016;

Kudo and Cooper 2019). However, the possibility and extent of interaction disruption likely varies widely, depending on the biology of the species involved and how climate change is altering the environmental cues specific to each ecosystem.

The plants and insects of the eastern hardwood forests of North America experience a distinct set of environmental cues, characterized by long, cold winters, prior to which broad-leaved trees shed their leaves; a series of late winter freeze-thaw cycles; eventual snowmelt, tree leaf-out, and a significant risk of late spring frost (Augspurger 2009). These factors have shaped a series of seemingly well co-ordinated seasonal events in the life cycles of plants and insects. Most understory wildflowers emerge soon after snowmelt and finish flowering after canopy closure. Many of these species are dependent on insect pollinators, especially solitary bees and flies, for seed production (Motten 1986). Because the blooming of spring wildflowers occurs during a short phenological window, a mismatch between their flowering period and the activity of their pollinators may be especially likely (cf. McKinney et al. 2012). However, without knowledge of the environmental cues affecting the activity of these species, we have little ability to predict whether pollinators will continue to be well synchronized with flowering as the climate changes.

Phenologies of both plants and insects are known to be sensitive to temperature (Fitter and 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 2007), with warmer temperatures and early snowmelt typically advancing spring flowering and emergence of bees (Fitter and Fitter 2002; Gordo and Sanz 2006; Bartomeus et al. 2011). Chilling requirements can also modify the phenological responses of plants and insects to temperature. For example, longer winters can enhance responsiveness to spring warmth (Bosch and Kemp 2003, 2004; Cook et al. 2012). However, species can respond to these environmental cues at different rates: for example, early-flowering plants and early-emerging insects tend to be more sensitive to environmental variation than species with later phenologies (Fitter and Fitter 2002; Sherry et al. 2007; Bartomeus et al. 2011; Wolkovich et al. 2013; Høye et al. 2014). Plant and insect species also vary enormously in their sensitivity to photoperiod (Thomas and Vince-Prue 1997; Bale et al. 2002; Van Asch and Visser 2007). Furthermore, the effect of photoperiod on phenology can be altered by temperature, and vice versa (Thomas and Vince-Prue 1997; Bale et al. 2002; Körner and Basler 2010; Saunders 2014). If phenologies of plants and pollinators respond to different environmental cues (e.g., snowmelt date vs. temperature), or to the same cues but at different rates, their temporal overlap and subsequent interactions may be affected as the climate changes.

Despite concerns about declining pollinator populations (Foley et al. 2005; Abrol 2012; Pyke et al. 2016; Soroye et al. 2020) and the possible effects of climate change on their phenology (Memmott et al. 2007; Kudo 2014), we know little about the environmental factors that trigger pollinator emergence and activity, especially for relatively under-studied groups such as solitary bees. Most research has focused on eusocial bee taxa such as honey bees (*Apis mellifera;* Gordo & Sanz, 2006) and bumble bees (*Bombus* spp.; Kudo and Ida 2013; Kudo 2014; Pyke et al. 2016; Kudo and Cooper 2019). However, most of the ~20,000 bee species worldwide are solitary (Michener, 2000), and many wild plants and crops depend on these insects for fruit production (Michener 2000; Garibaldi et al. 2013). Indeed, solitary bees are the main pollinators of many wild plants (Willmer et al. 2017). Yet, in comparison with plants (e.g., Bradley et al. 1999; Fitter and Fitter 2002; Menzel et al. 2006), we know little about phenological responses of solitary bees to climate change (but see Bartomeus et al. 2011).

The goals of this six-year study were to (1) identify the environmental cues or drivers of the phenology of wild bee activity and flowering of native spring wildflower taxa in a hardwood forest understory habitat, (2) to test whether phenologies of bees and wildflowers differ in their responses to these drivers, and (3) to evaluate how climatic variables (i.e., temperature and timing of snowmelt) influence the temporal overlap between bee activity and flowering. We did not directly investigate the interaction between these bee and wildflower taxa. Instead, we use these organisms as exemplars to help determine whether co-occurring (and potentially interacting) species that occupy the same habitat year-round are likely to respond similarly to future climatic changes.

Methodology

Data collection

Study plots. This study was conducted in Gatineau Park, Québec, 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 (Table S1). Each plot was located at least 100 m 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 hourly surface temperature. Every spring from 2013 to 2018, plots were sampled to characterize phenology of bees and the flowering of understory plants. The number of open flowers in each plot was counted once every 1–7 days from early April until early June (when most spring ephemerals have entered seasonal senescence). Bee sampling occurred once every 5–8 days from early April until late May, or the point when no more bees were caught in the traps (Table S2). Five “bee bowls”, white plastic bowls containing water and a drop of dish detergent (e.g., Droege et al. 2010), were set up on the ground along one randomly selected edge of each plot and left in place for ~24 hours before collection.

Study organisms

Plant taxa. *Anemone* spp. (Ranunculaceae) and *Trillium grandiflorum* (Michx.) Salisb. (Melanthiaceae) were the most abundant insect-pollinated plants in the plots (Kaplan and Mulcahy 1971; Bernhardt 1976; Motten 1982, 1986; Piper 1989; Case and Case 1997; Table S3; Figure S1): the former was present in five plots and the latter in all 10. *Anemone americana* (DC.) H. Hara and *A. acutiloba* Laws. were treated as a single taxon (*Anemone* spp.) in this study because flowering precedes leaf production in these species, and without leaves they are difficult to differentiate. *Anemone* spp. and *T. grandiflorum* are perennial, rhizomatous herbaceous plants that occur in the understory of deciduous forests throughout eastern North America (Motten 1986; Case and Case 1997). *Anemone* spp. are clonal plants with ramets that produce 3–7 flowers, each with 5–6 white or purple sepals with numerous stamens and pistils (Bernhardt 1976). *Trillium grandiflorum* are non-clonal; 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 bee queens (*Bombus* spp., Irwin 2000), although solitary bees including *Andrena* also visit this species in our study region (Darling and Barrett 2011).

Bee taxa. The bee community sampled by the bee bowls was dominated by three genera: *Andrena*, *Lasioglossum*, and *Nomada* spp. (Table S4). All three genera were also observed visiting the two focal plant taxa. Although bumble bee queens were active in the study area during sampling, the bee bowls captured very few (Table S4), 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 our dataset there were at least five morphospecies of *Andrena*, six of *Lasioglossum*, and four of *Nomada*, but we did not distinguish among 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). *Nomada* spp. are common cleptoparasites (brood parasites) of *Andrena* and, to a lesser extent, *Lasioglossum*. Although *Nomada* bees do not collect pollen, they visit flowers for nectar.

Data analysis

First, we conducted a taxon-level analysis (described below) to select the environmental predictor (day of year, a proxy for photoperiod; snowmelt day; or surface temperature) that best described the phenology of each taxon. Subsequently, we conducted a plot-level analysis to test whether phenology of each taxon responds significantly to variation in snowmelt day or surface temperature. We also explored whether regional surface temperature (mean surface temperature across plots) and air temperature (recorded at Ottawa CDA weather station, 8.85 km from the sampling plots) were better phenological predictors in the plot-level analysis. Day of year was excluded from the plot-level analysis because it does not vary among plots or years. Finally, we tested whether plot-level models with one or both environmental predictors (temperature and snowmelt day) exhibited a better fit according to Akaike's information criterion (AIC).

For each sampling occasion in each year, we calculated the accumulated days since snowmelt and the accumulated degree-days until the observation event (e.g., collection date of each insect specimen), using hourly temperatures from the data-loggers at each plot. Snowmelt day was estimated from the temperature data as the first day after 1 January with daily ranges >5°C for ≥3 consecutive days (cf. Kudo and Cooper 2019). Snowmelt date estimated this way was corroborated by multiple visits to each plot before snowmelt, during which snow cover and depth were measured. We calculated surface degree-days from March 1 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 surface level begin to exceed freezing at the study sites. For all the following analyses, females and males were combined for each bee taxon; 2013 was excluded from the bee analyses due to the low number of insects collected (Table 1).

Taxon-level analyses of flower and bee phenology. To determine which environmental predictor best describes 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). We used surface 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. 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 four 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 bowl in each year was counted to extract phenological variables. Because bee collection was less frequent than flower surveys, we used monotone linear interpolations to estimate the numbers of bees active on each day from snowmelt to May 30 (e.g., Figure S2). 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. We 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 the dependence of plot-level phenology on environmental variables, we 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, we 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 phenological response of each plant and bee taxon to the environmental variables, we ran linear mixed models using the lmerTest package (Kuznetsova et al. 2018). The appropriate phenology variable (first date, last date, period, or peak date) was the response; the environmental predictor (surface, regional, air temperature or snowmelt) was the fixed explanatory variable; and plot and year were included as random factors. For each of the five focal taxa, a single linear mixed model was tested for each of the four phenological response variables.

Second, to compare the magnitude of the phenological response to environmental variation among taxa (for first, last, and peak phenological events), we ran a second set of linear mixed models. Here, taxon (two plant and three bee categories), an environmental variable (snowmelt day or surface 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. We summed surface 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 in our study 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, we quantified pairwise proportional overlap using Schoener's index (SI; 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. When expressed as a proportion (rather than as a percentage, as in Schoener 1970), it ranges from 0 (no overlap between the two phenological curves) to 1 (the curves overlap perfectly). For each year and plot, we calculated the SI between bees (the three bee taxa combined) and each plant taxon separately. We then tested for a relationship between each SI and each environmental factor (snowmelt date or temperature) using binomial generalized linear mixed models with SI as the response, snowmelt date or degree-days accumulated from 1 March to 30 April as the predictor, 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). Outliers were retained because they did not change the significance of any variables.

Results

Climatic variation and flowering and insect phenology

April surface 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) varied significantly among years (Table S5). The highest recorded mean April surface temperature (mean across plots ± s.d. = 5.8 ± 4.5°C) and the earliest snowmelt (April 10 ± 1.4 days) both occurred in 2017. Mean April surface temperature was lowest (3.3 ± 4.7°C) and snowmelt was latest (April 20 ± 1.3 days) in 2018. Regional air temperatures from the Ottawa weather station were strongly correlated with daily mean surface temperatures recorded in our study plots over the same time period (Pearson r = 0.93, N = 93 days × 6 years). Based on the regional data, the variation in mean spring air 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 (Figure S3).

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; Fig. S1), with a mean flowering duration of 15.3 ± 3.9 days (mean ± s.d. across plots and years). The *T. grandiflorum* flowering period was 20.5 ± 4.5 days, from early to late May (Fig. 1). The three bee taxa, *Andrena*, *Lasioglossum*, and *Nomada* spp., have similar activity phenologies and were active for approximately three weeks, from mid-April to early May (Fig. 1).

Taxon-level analyses of flower and bee phenology

Logistic regressions described well the relationships between cumulative proportion of flowering or activity and accumulated surface 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 1). For *Nomada* spp., degree-day-based models had lower AIC values than models using days since snowmelt or day of year (Table 1). For *Andrena* and *Lasioglossum*, cumulative activity was best described by day of year or accumulated surface degree-days (models differ by <2 AIC units; Fig. 3; Table 1). 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 1).

Plot-level analyses of flower and bee phenology

Surface degree-day accumulation was a better phenological predictor than snowmelt day, regional surface temperature, or air temperature for most taxa (Table S6). For *Anemone* spp., first, peak, and last flowering days at the plot level were negatively correlated with accumulated surface degree-days (from 1 March until mean date of the phenological event), with flowering starting and ending earlier in warmer springs (Table 2). Conversely, for *T. grandiflorum*, first day, last day, and flowering period were best described by snowmelt date (Table S6; recall that day of year was not included in this analysis), although peak flowering day was negatively correlated with temperature (Table 2). Flowering period was not predicted by temperature in either plant taxon.

Models including only degree-day accumulation accounted for most of the variation in *Anemone* spp. flowering phenology but not that of *T. grandiflorum* (Table S6).

Lasioglossum spp. and *Nomada* spp. peak activity days were associated with surface temperature, with greater accumulation of heat units accelerating peak activity (Table 2), but first and last dates and activity period were not. No aspect of plot-level *Andrena* phenology was predicted by temperature (Table 2). Linear mixed models including accumulation of surface degree-days were generally better than models containing air or regional temperature and/or snowmelt date (Table S6), but accumulation of surface degree-days still failed to predict most of the variation in bee phenology (Table 2).

Variation in phenology response across taxa

The phenologies of the five taxa showed similar responses to snowmelt date and surface degree-day accumulation from 1 March to 30 April (i.e., no taxon by environmental predictor interactions, Fig. 4, Table 3). 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).

Temporal overlap between flower and bee phenology

The phenologies of the three focal bee taxa combined (*Andrena*, *Nomada*, and *Lasioglossum* spp.) overlapped 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 our study (*Anemone* × bees $X^2_{4,24}=0.3$, $P=0.99$; *Trillium* × bees $X^2_{4,49}=0.5$, $P=0.97$). Temporal overlap between the activity of bees and flowering ranged across plots and years from 0.40 to 0.87 (15.4 ± 4.4 days) for *Anemone vs.* 0.01 to 0.36 (7.8 ± 4.6 days) for *T.*

grandiflorum. There was no relationship between environmental variables and overlap between either plant taxon and bees (Tables S7–S8).

Discussion

Temperature (surface degree-day accumulation) was the best overall predictor of phenology in the hardwood-forest understory taxa we studied. However, temperature-sensitivity differed among taxa: flowering phenology of one wildflower was strongly associated with temperature, while the other species' phenology was best described by photoperiod. Bee phenology was more difficult to predict from the climatic variables we analysed, but peak activity dates of two out of three genera were correlated with temperature. Despite the interannual variation in environmental conditions and in species' sensitivities to environmental variables, temporal overlap between bees and flowers remained similar over the years of this study and was not significantly associated with variability in temperature or snowmelt date.

Drivers of flowering phenology

Flowering phenology of the two wildflower taxa was associated with different environmental factors. As is the case for many temperate-region species (Fitter and Fitter 2002; Tooke and Battey 2010; Chuine et al. 2010; Cook et al. 2012; Schwartz 2013; Guo et al. 2015), phenology of early-flowering *Anemone* spp. was strongly associated with temperature, with springtime degree-days predicting the onset, peak, and end of flowering. The phenology of early-flowering plant species is often 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 our study, with early-flowering *Anemone* spp. more responsive than later-flowering *T. grandiflorum*. Flowering phenology of *Trillium grandiflorum* was better explained by day of year than by temperature or snowmelt date, suggesting that photoperiod is the main environmental trigger for its flowering phenology. Nevertheless, even in *T. grandiflorum*, 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 for different reasons: *Anemone* spp. because first and last days of flowering responded similarly to variation in temperature; *T. grandiflorum* because its first and last days were both relatively insensitive to variation in temperature.

Flowering phenology of vernalization-sensitive plants can be modulated by fall and winter temperature in the previous year, with exposure to temperatures below a certain threshold being necessary to release subsequent sensitivity to warm, springtime temperatures (Cook et al. 2012). Although we did not explicitly test the effect of chilling temperatures on flowering phenology, varying exposure to cold in the preceding winter may be responsible for some of the unexplained variation in plant phenology in our study. 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 we did not investigate here.

Temperature and photoperiod are considered the primary triggers of phenological events in many short-lived herbs and trees in temperate forests (Diekmann 1996; Fitter and 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 (Lambert et al. 2010; Cooper et al. 2011; Inouye and Wielgolaski 2013; Wielgolaski and Inouye 2013). Temperature and snowmelt date are almost always confounded in nature (as observed in this study), making it difficult to separate the 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 surface degree-day accumulation was a better predictor of phenology than snowmelt date for all taxa in this study, at least based on the taxon-level analyses. Conversely, in studies that find snowmelt date to be the best predictor of phenology, temperature tends to have been measured at weather stations, above the snowpack and potentially some distance from the study plots (e.g. Iler et al. 2013; Inouye et al. 2002)—in other words, in a microhabitat quite different from that occupied by the plants—while snowmelt was measured more locally. Interestingly, in our study, the only case where timing of snowmelt outperformed local surface temperature as a predictor of phenology was in the plot-level analysis with *T. grandiflorum* (Table S6), for which regional and air temperatures were equally good (and for which the taxon-level analysis suggests that photoperiod is actually the primary cue).

Drivers of bee activity phenology

The phenology of bees in our study was only weakly associated with the environmental variables we measured, but taxon- 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. This contrasts 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 at describing the phenology of *Andrena* and *Lasioglossum* spp., as 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; Yocum et al. 2016; Bennett et al. 2018). 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 we did not consider here, such as precipitation, soil temperature, prior chilling, and body condition, may also play a role (Bosch and Kemp 2003, 2004; Ellwood et al. 2012; Schenk et al. 2018b; Olliff-Yang and Mesler 2018). In future, more attention should focus on the effect of soil temperature on phenology of bees and other insects that overwinter below-ground. Recent studies have shown that bumble bee emergence from hibernation and bee nesting activity are correlated with soil temperature (Olliff-Yang and Mesler 2018; Kudo and Cooper 2019), suggesting that below-ground temperatures reaching a specific threshold promotes bee activity. In addition, the lack of a strong phenological response of bees to springtime 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, transient environmental conditions such as temperature, precipitation, and wind speed on the day of sampling can influence bee activity (Kevan and Baker 1983) and may 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. We tried to minimize this problem by sampling only on days without precipitation, with cloud-cover <50% and daytime air temperature reaching >10°C. Nevertheless, fluctuation in the number of bees captured, due to environmental conditions on the day of sampling, could have limited the ability of the models to predict bee phenology based on accumulated degree-days, which are relatively insensitive to sampling-day temperature.

Temporal overlap between wildflowers and ground-nesting bees

Overall, bee activity and flowering phenology appear to have responded in parallel to variation in climatic factors over the years of our study. First, both bees and plants responded at similar rates to springtime degree-days and snowmelt date, even though, 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 affect plants and bees similarly, and consequently do not affect their temporal overlap. Third, despite the observed interannual variation in temperature and snowmelt date, temporal overlap between bees and plants remained similar over the course of this study and was unaffected by these environmental factors. Nonetheless, if climates continue to warm, *T. grandiflorum* may experience reduced temporal overlap with solitary bees, since its phenology had a strong photoperiodic response, whereas solitary bees showed greater sensitivity to temperature.

In this study system, even if phenologies of the plants and solitary bees we studied respond differently to climate change, this may not entail fitness consequences for these taxa. Neither of the plant taxa is totally dependent on solitary bees for seed production. *Anemone* spp. flowers are capable of autogamy (Motten 1982), and *T. grandiflorum*, although reliant on pollinators for seed production, is primarily pollinated by queen bumblebees (Irwin 2000). However, out-crossing increases seed set in *Anemone* spp. (Bernhardt 1976), and solitary bees may play an increasingly important role in *T. grandiflorum* pollination in the future, as abundances and range sizes of some North American bumble bee species appear to be shrinking (Cameron et al. 2011; Kerr et al. 2015;

Soroye et al. 2020). In the context of declining bumble bee numbers, changes in overlap with solitary bees could further impair reproduction in this species.

Bees typically started their seasonal activity at the same time as or shortly after the flowering of *Anemone,* 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. 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 understorey floral resources by more than a few days and affect bee lifespan, reproduction, and (in social species) colony development (Kudo 2014; Schenk et al. 2018a).

Understanding the factors that shape the phenologies of co-occurring species allows us to predict some of the possible consequences of climate change. Ongoing data collection will eventually allow us to explore the influence of additional environmental factors, such as precipitation, canopy closure, temperature on the day of sampling, and soil temperature (Hegland et al. 2009; Ellwood et al. 2012; Kerr et al. 2015; Olliff-Yang and Mesler 2018). More generally, datasets such as ours, involving multi-year, multi-site sampling, are critical to identify phenological drivers and to understand the impact of climate variation on the temporal overlap of co-occurring organisms. Ultimately, this information can facilitate prediction of future phenological mismatches between interacting species.

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Tables

Table 1. 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 surface 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 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

Table 2. Response of flowering and bee activity phenology to surface 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	0.1
Activity period	0.00±0.02	41	0.09	0.923	0.001	0.66

Table 3. Effects of snowmelt date (Snow) and temperature (DDA; surface 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	27.6	1, 31	3.0	0.091
Taxon	44.1	4, 213	1.2	0.305
Snow × taxon	18.0	4, 213	0.5	0.737
DDA	36.6	1, 22	4.0	0.059
Taxon	164.7	4, 194	4.5	**0.002**
DDA × taxon	46.5	4, 194	1.3	0.287
	Peak flowering or activity day			
Snow	67.6	1, 46	4.3	**0.041**
Taxon	106.5	4, 216	1.7	0.156
Snow × taxon	63.9	4, 216	1.0	0.405
DDA	122.4	1, 186	8.0	**0.005**
Taxon	164.2	4, 195	2.7	**0.033**
DDA × taxon	102.2	4, 195	1.7	0.159
	Last flowering or activity day			
Snow	42.5	1, 45	2.8	0.100
Taxon	146.5	4, 222	2.4	< **0.05**
Snow × taxon	91.7	4, 223	1.5	0.196
DDA	53.4	1, 95	3.5	0.066
Taxon	321.9	4, 201	5.2	< **0.001**
DDA × taxon	97.3	4, 201	1.6	0.182

Figures

Figure 1. Flowering and activity phenology of two plant and three bee taxa in Gatineau Park. Data collected in ten plots over six years. 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. Note that the 2013 bees are included in the figure but were excluded from analyses due to low numbers collected.

Figure 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 surface 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% CIs (treating each observation as independent) are represented by the shaded areas.

Figure 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 surface degree-days (left), days since snowmelt (middle) and days since Jan. 1 (right) accumulated up to that date. Each taxon has a particular base temperature based on the best-fit model across all the years. Symbols, fitted curves, and CIs as in Fig. 2.

Figure 4. Phenological responses of two plant and three bee taxa to temperature (accumulated surface 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. Lines are 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).

Figure 1

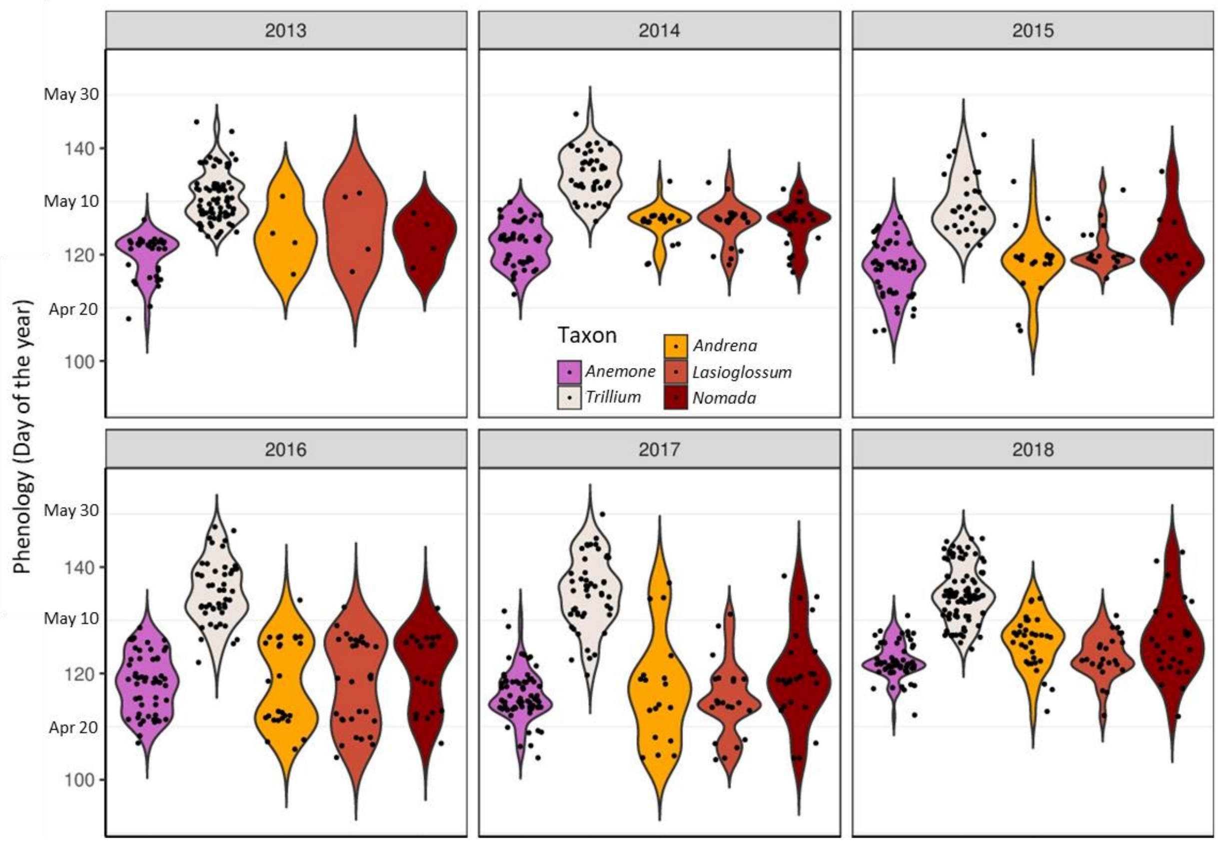

2013
2014
2015
2016
2017
2018
Phenology (Day of the year)
May 30
140
May 10
120
Apr 20
100
Taxon
Anemone
Trillium
Andrena
Lasioglossum
Nomada

Figure 2

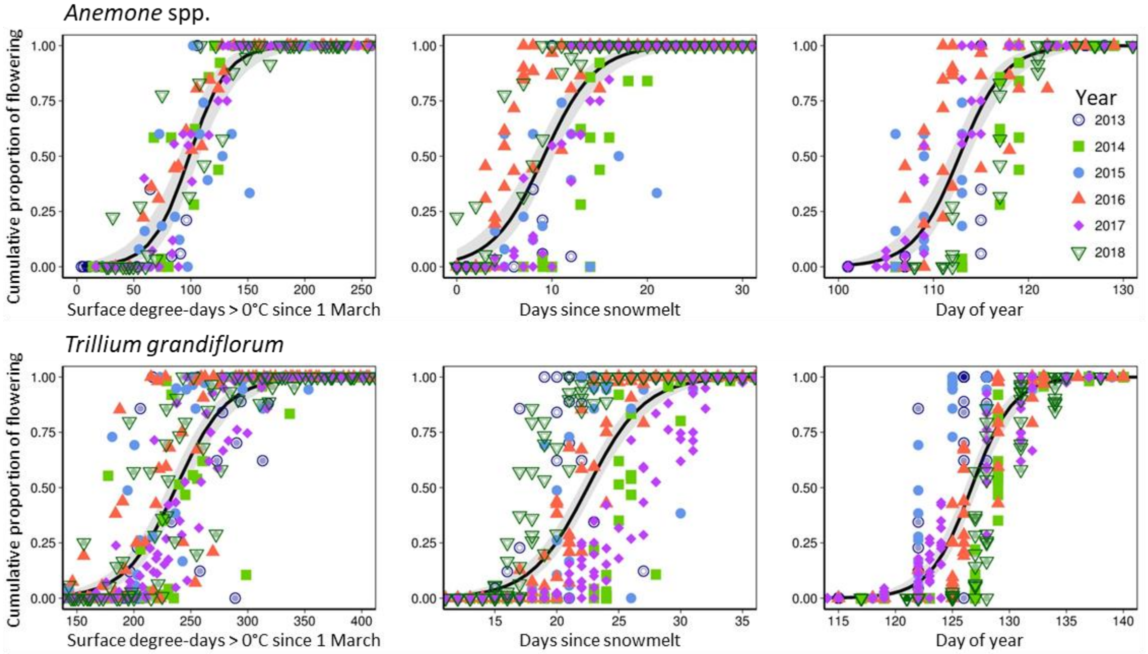

Anemone spp.
Cumulative proportion of flowering
1.00
0.75
0.50
0.25
0.00
Surface degree-days > 0°C since 1 March
Days since snowmelt
Day of year
Year
2013
2014
2015
2016
2017
2018
Trillium grandiflorum
Cumulative proportion of flowering
Surface degree-days > 0°C since 1 March
Days since snowmelt
Day of year

Figure 3

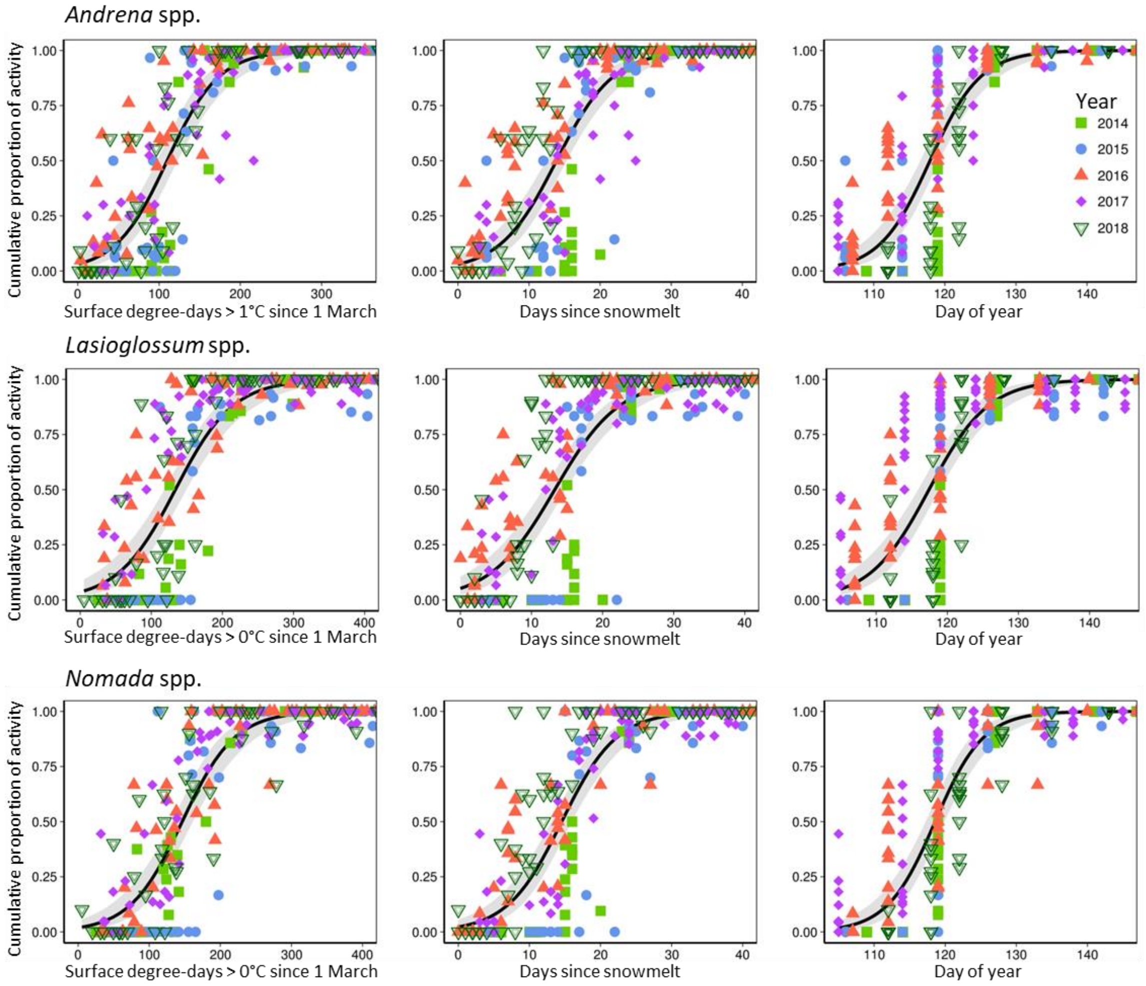
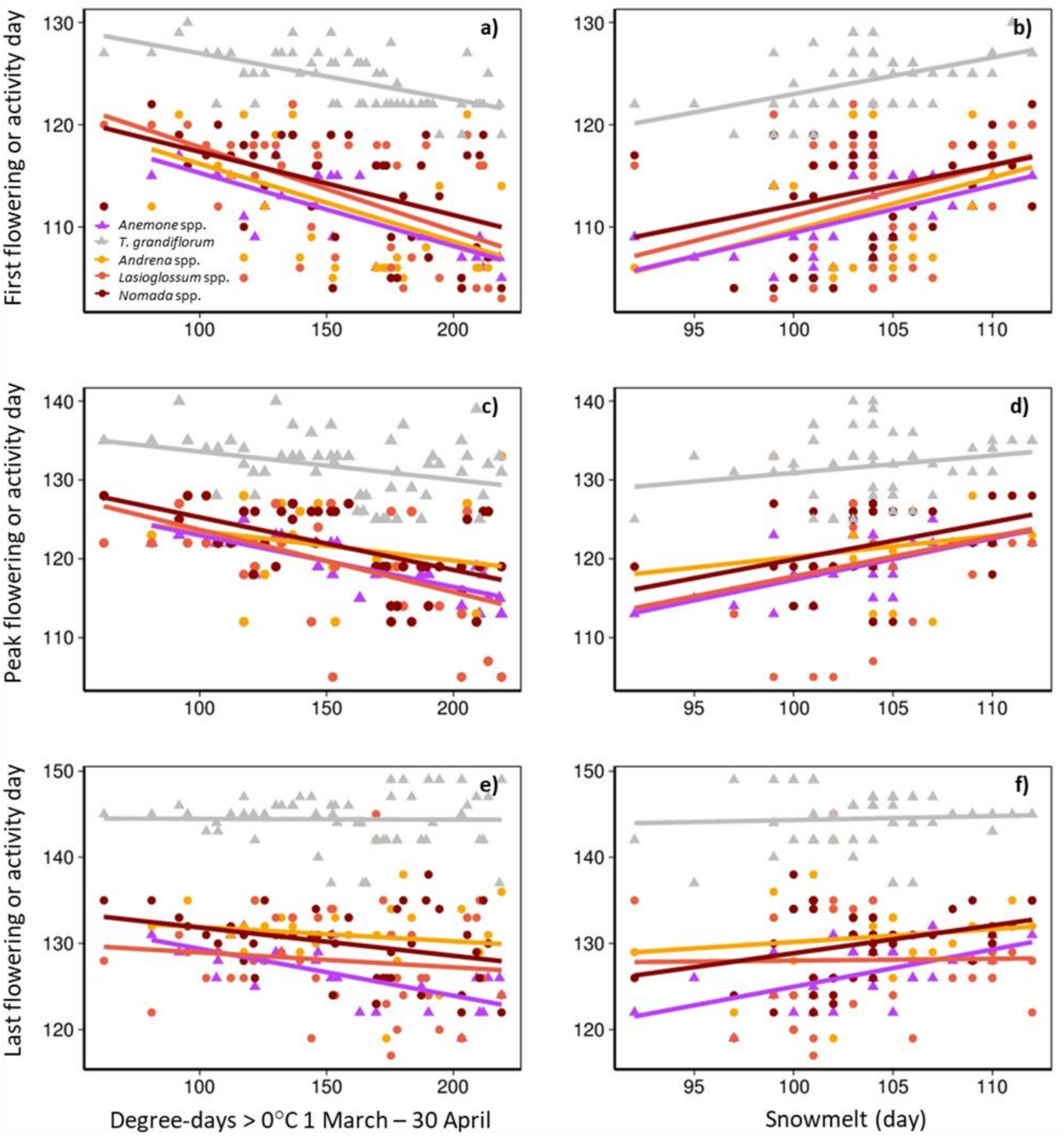

Andrena spp.
Lasioglossum spp.
Nomada spp.
Cumulative proportion of activity
1.00
0.75
0.50
0.25
0.00
Surface degree-days > 1°C since 1 March
Surface degree-days > 0°C since 1 March
Days since snowmelt
Day of year
0
100
200
300
400
10
20
30
40
110
120
130
140
Year
2014
2015
2016
2017
2018

Figure 4


First flowering or activity day
Peak flowering or activity day
Last flowering or activity day
a)
b)
c)
d)
e)
f)
Anemone spp.
T. grandiflorum
Andrena spp.
Lasioglossum spp.
Nomada spp.
130
120
110
140
150
100
150
200
95
100
105
110
Degree-days > 0°C 1 March – 30 April
Snowmelt (day)