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# Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate

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## Abstract

Variation in species' responses to abiotic phenological cues under climate change may cause changes in temporal overlap among interacting taxa, with potential demographic consequences. Here, we examine associations between the abiotic environment and plant–pollinator phenological synchrony using a long-term syrphid fly–flowering phenology dataset (1992–2011). Degree-days above freezing, precipitation, and timing of snow melt were investigated as predictors of phenology. Syrphids generally emerge after flowering onset and end their activity before the end of flowering. Neither flowering nor syrphid phenology has changed significantly over our 20-year record, consistent with a lack of directional change in climate variables over the same time frame. Instead we document interannual variability in the abiotic environment and phenology. Timing of snow melt was the best predictor of flowering onset and syrphid emergence. Snow melt and degree-days were the best predictors of the end of flowering, whereas degree-days and precipitation best predicted the end of the syrphid period. Flowering advanced at a faster rate than syrphids in response to both advancing snow melt and increasing temperature. Different rates of phenological advancements resulted in more days of temporal overlap between the flower–syrphid community in years of early snow melt because of extended activity periods. Phenological synchrony at the community level is therefore likely to be maintained for some time, even under advancing snow melt conditions that are evident over longer term records at our site. These results show that interacting taxa may respond to different phenological cues and to the same cues at different rates but still maintain phenological synchrony over a range of abiotic conditions. However, our results also indicate that some individual plant species may overlap with the syrphid community for fewer days under continued climate change. This highlights the role of interannual variation in these flower–syrphid interactions and shows that species-level responses can differ from community-level responses in nonintuitive ways.

*Keywords:* climate change, hoverfly, mismatch, phenology, pollinator, Rocky Mountain Biological Laboratory, synchrony, syrphidae

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## Introduction

Plant–pollinator interactions are critical for proper ecosystem services and function (Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998; Waser & Ollerton, 2006; Klein *et al.*, 2007; Ollerton *et al.*, 2011), and there is mounting evidence of declining pollinators, pollination services, and plants that depend on pollinators at local and regional scales (Biesmeijer *et al.*, 2006; Thomson, 2010; Pauw & Hawkins, 2011). Climate change is one potential disruptor of plant–pollinator interactions, especially in relation to climate-driven temporal and spatial mismatches between plants and pollinators (Parmesan & Yohe, 2003; Potts *et al.*, 2010; Burkle *et al.*, 2013). Despite widespread concern surrounding pollinator declines and the potential for temporal mismatches with nectar and pollen resources, there is limited information on the relative importance of factors controlling the phenology and abundance of insect pollinators (Hegland *et al.*, 2009). Elucidating the environmental drivers of plant and pollinator phenology will improve predictions of the future effects of climate change on ecosystem services like pollination.

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Flies are widely considered an important group of pollinators, especially in high-altitude environments (Larson *et al*., 2001). Within Diptera, syrphid flies (hoverflies), family Syrphidae, are often cited as the most effective pollinators and are documented as pollinators in a variety of ecological communities worldwide (reviewed in Larson *et al*., 2001). Adult syrphid flies feed on pollen and nectar (Fig. 1) (Holloway, 1976; Haslett, 1989a; Rotheray & Gilbert, 2011), and pollen is particularly important because females require it for ovarian development (Schneider, 1969). Syrphid species range from pollen generalists to pollen specialists (Haslett, 1989b). Among species that are pollen generalists, the guts of individual flies often contain pollen from only one plant species (Kearns, 1992), suggesting that individuals could be quite effective pollinators. Even when individuals visit flowers of multiple plant species, syrphid flies can contribute to plant reproductive success (McGuire & Armbruster, 1991). In addition, whereas bees tend to carry more pollen on their bodies than flies, flies can in some cases compensate for this difference by making more visits to flowers (*sensu* Kearns & Inouye, 1994).

The activity period of adult insects is especially relevant to pollination services, but almost no information exists regarding phenological cues for adult syrphid flies (see Graham-Taylor *et al*., 2009). A general progression of insect phenology within temperate habitats is as follows: photoperiod typically induces insect larval diapause in the fall or winter, which is then terminated in the spring after a sufficient chilling period (i.e. vernalization) or sufficient amount of temperature accumulation has occurred, after which temperature regulates the rate of development and therefore the timing of adult emergence in the spring (Tauber & Tauber, 1976; Bale *et al*., 2002; Denlinger, 2002; Bosch & Kemp, 2003; White *et al*., 2009; Forrest & Thomson, 2011). Temperature predicts the emergence of adult insects in the spring, with warmer temperatures advancing spring emergence (Sparks & Yates, 1997; Gordo & Sanz, 2006; Ellwood *et al*., 2012). Precipitation can also affect insect phenology (Forister & Shapiro, 2003; Graham-Taylor *et al*., 2009), and timing of snow melt seems to be an important predictor of springtime insect emergence at high latitudes and altitudes (Høye & Forchhammer, 2008).

**Fig. 1** A syrphid fly (Syrphidae) foraging on a flower at the Rocky Mountain Biological Laboratory.

If flies and the plants with which they interact respond to different combinations of cues, or if they exhibit different magnitudes of response to the same cues, they may become mismatched through time as those cues change. Similar to their insect pollinators, plant phenology is sensitive to temperature (Fitter & Fitter, 2002), and precipitation or timing of snow melt in high-altitude and high-latitude plant communities also influence flowering phenology (Dunne *et al*., 2003; Høye *et al*., 2007a; Gordo & Sanz, 2010; Lambert *et al*., 2010). Even if interacting taxa respond to different cues, their responses may be in the same direction and of a similar magnitude so that changes in temporal synchrony are unlikely, pointing to the need for long-term records to investigate phenological cues of interacting organisms. Such datasets that contain organisms known to interact at the same location are rare, especially for plant–pollinator interactions (Harrington *et al*., 1999; Hegland *et al*., 2009). Here, we utilize a 20-year record of syrphid fly and flowering phenology in the Colorado Rocky Mountains to investigate phenological cues and the potential for changes in phenological synchrony between syrphid flies and the plant species they visit. We specifically investigate (i) whether the onset and end of the activity periods of syrphids and flowers have changed over our 20-year record; (ii) the climatic cues associated with syrphid and flowering phenology (temperature, precipitation, and timing of snow melt); and (iii) shifts in phenological synchrony, or the number of days of temporal overlap between syrphids and flowers.

## Materials and methods

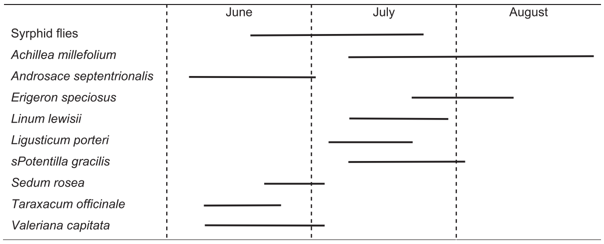
### *Study site and data collection*

Phenology data were collected at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (38°57.5′N, 106°59.3′W, 2900 m a.s.l.). The landscape surrounding the RMBL is a mosaic of mesic and wet meadows, dry rocky meadows, and mixed conifer forests. The growing season in this area is brief, with snow melt typically occurring in mid-May and snowfall beginning in late September to early October. To sample insect phenology at the RMBL, a Malaise trap (BioQuip Products, Inc. model 2875A: 1.2 m × 2.13 m tall; Rancho Dominguez, Compton, CA, USA) was set up weekly for 48 h, typically starting in early June and ending in mid-August. Malaise traps are an effective and commonly used sampling technique for syrphid flies (Keil & Konvicka, 2005; Petanidou *et al.*, 2011), and the number of individuals in the family Syrphidae was recorded in weekly samples from 1992 to 2011, excluding 2002 and 2010. Malaise trap phenology records are independent of flowering phenology and are therefore conducive to assessment of changes in phenological synchrony. Most evidence of phenological shifts in response to climate change comes from long-term records of first appearance, which may not accurately reflect shifts in the period of activity of an organism (Miller-Rushing *et al.*, 2008). We therefore focus on both the onset and end of flowering and syrphid activity and the number of days that the syrphid community overlaps with the flowering community. We focus on the community level because the most common syrphid morphospecies we observe in our samples visit multiple plant species (i.e. are generalized rather than specialized; Burkle, Inouye, and Iler personal observations).In 1973, a series of 2 × 2 m plots was established in and around the RMBL to monitor community flowering phenology (see Inouye, 2008 for a map of plots). The plots are generally located in two distinct habitats: relatively dry, rocky meadows (seven plots), and mesic or wet meadows (19 plots), which occur ca. 60 m lower in elevation than the dry meadows. The farthest distance between two plots is ca. 1 km (Miller-Rushing & Inouye, 2009). Depending on the species, either the number of flowers per stalk or number of flowering stalks (for species with numerous small flowers) was counted every other day throughout the growing season. The Malaise trap was located in a mesic–wet meadow between the rocky and mesic–wet meadow phenology plots in the RMBL Research Meadow. To determine which flowering species were most commonly visited by syrphids, we used data on syrphid–flower associations at the RMBL from Kearns (1992) and Burkle & Irwin (2009). There are at least 20 syrphid species at the RMBL (Kearns, 1992), while we estimate that our samples contain at least five to six common syrphid morphospecies that visit multiple plant species. We included plant species in the analysis if at least 15 syrphids were collected from them (Kearns, 1992) or at least 25 visits were recorded on them (Burkle & Irwin, 2009), for a total of nine species commonly visited by syrphids (Table 1). Temperature and precipitation data were obtained from a NOAA weather station located at an altitude of 2704 m in Crested Butte, CO, ca. 9.5 km south of our study site (http://www.ncdc.noaa.gov). Snow melt data for the study period were collected at a plot within 2 km of the research site and were recorded as day of first bare ground (B. Barr, unpublished data).

### *Analysis*

We used linear interpolation to determine the day of year when 10% and 90% of the flower and syrphid community were counted. To calculate community-level floral abundance, the number of flowers of the nine species commonly visited by syrphids was summed across all species on each day of the year. Following Høye *et al.* (2007b), the day on which 10% of samples were counted was estimated using linear interpolation between the latest census in which <10% of samples were counted and the earliest census in which >10% of samples were counted (separately for flowers and syrphids). The same procedure was followed to quantify the end of the activity period for each taxon. This provides a day of year value in each year for the onset (10%) and end (90%) of the activity period of the flower and syrphid communities. In five of the years sampled, the first syrphid sample in each of those years was greater than 10% of the total number of syrphids caught in that year (1992, 2004, 2006, 2007, and 2009). The day of year on which 10% of syrphids were sampled was calculated based on the rate of increase between the first sample and the date on which 20–25% of the syrphids were sampled. In one case, the first sample represented 34% of the syrphids caught in that year. Here, we used the rate of increase between 34% and 40% to estimate the day on which 10% of syrphids were sampled. This allowed us to analyze all 18 of the years for which syrphid phenology data are available. We employed timing of snow melt, temperature, and precipitation as potential explanatory variables of each phenological response variable in regression analysis. In addition, to determine whether temporal overlap between syrphids and flowers responds to climate, we calculated overlap in each year as the number of days between the taxa with the later onset and the taxa with the earlier end. Because heat accumulation is relevant to diapause termination and growth and development, we used degree-days as a measure of temperature as opposed to mean temperature. We calculated degree-days above 0 °C using mean daily temperatures, starting on March 1 because that is when temperatures start to warm above freezing at our site (Forrest & Thomson, 2011). Temperatures were summed across days when the mean temperature was above 0 °C from March 1 until the mean day of year for each phenological response (mean across years). Precipitation was summed across months of syrphid and flowering onset (June) and end (June through July); we used the months of June and July because in the spring months prior to June at our site, most precipitation falls as snow. The timing of snow melt, also a predictor in our analysis, is affected by amount of winter snowfall, dust accumulation from dust storms in the western US (Painter *et al.*, 2007), and spring temperatures. Growing degree-days

**Table 1** Phenology of the activity period of the syrphid fly community and flowering period of nine plant species commonly visited by syrphids at the Rocky Mountain Biological Laboratory. $N = 20$ years for all species except *Sedum rosea* ($N = 9$). The mean (across years) for the onset and end of each activity period is indicated by the start and end of each line



(GDDs) are significantly correlated with snow melt (S1); this covariation may affect parameter estimates but will not affect model selection. We included each of these three predictors in a simple linear regression model and in all possible combinations in multiple regression models, for a total of seven statistical models for each phenological response. The best models were selected based on lowest $\text{AIC}_c$ scores, which include a penalty term for additional parameters. Models within $\Delta\text{AIC}_c \leq 2$ are considered to be supported by the data (Anderson, 2008). We also looked for a threshold phenological response to snow melt in plants and syrphids, as previously observed for flowering in this system (Inouye, 2008) and in a snow manipulation experiment (Steltzer *et al.*, 2009). $\text{AIC}_c$ values were always lower for a simple linear snow melt model compared to a model also containing a quadratic snow melt term, and the quadratic terms were not significant. We therefore used only a first-degree snow melt term in subsequent multiple regression models.

Data were included for 2002 and 2010 flower analysis, while these years are missing in the syrphid analysis; model selection and results do not differ if we remove these years from the flower analysis (results not shown). In addition, there was one outlier in relation to snow melt for both onset and end of flowering (2004 and 1994, respectively, based on Bonferroni-corrected *P*-values of studentized residuals). Their removal did not alter model selection results but increases the effect size of snow melt and the importance of GDD. However, the most important predictor is still snow melt when these outliers are removed. We retain the outliers because we have no reason to remove them other than to improve model fit.

We used ANCOVAS to test for a different magnitude of response between flowers and syrphids to important climate variables determined from the above analysis. Taxon (syrphid vs. flower categories), climate, and the interaction between taxon and climate were the explanatory variables. A significant interaction term indicates that the slope of the linear relationship between phenological response and climate differs between taxa. Removal of the outliers mentioned above does not affect the tests for differences between slopes.

Because community-level trends may obscure species-specific changes in phenology, we also analyzed changes in temporal overlap (no. days) between flowering of each individual plant species and the syrphid community (species-level syrphid data are unavailable). We followed the same multiple regression approach outlined above, using temporal overlap for each plant species as the response variable and year and abiotic variables as predictors. All analyses were conducted in R v. 2.11.1 (R Development Core Team, 2008, http://www.r-project.org/).

## Results

### *Change through time*

None of the climate predictors has changed significantly through time over our 20-year dataset (snow melt: $R^2 = 0.03$, $F_{1,18} = 0.58$, $P = 0.46$; GDDs to flowering onset: $R^2 = 0.0$, $F_{1,18} = 0.0$, $P = 0.96$; GDDs to syrphid onset: $R^2 = 0.0$, $F_{1,18} = 0.0$, $P = 0.99$; GDDs to flowering end: $R^2 = 0.10$, $F_{1,18} = 1.97$, $P = 0.18$; GDDs to syrphid end: $R^2 = 0.05$, $F_{1,18} = 0.95$, $P = 0.34$; June–July total precipitation: $R^2 = 0.04$, $F_{1,18} = 0.80$, $P = 0.38$). Consistent with trends in climate, there was no change in the onset or end of the syrphid activity period from 1992 to 2011 (onset: $R^2 = 0.02$, $F_{1,16} = 0.25$, $P = 0.63$, 2.3 ± 4.7 days earlier per decade; end: $R^2 = 0.08$, $F_{1,16} = 1.38$, $P = 0.26$, 4.7 ± 4.0 days earlier per decade) or in the onset or end of the flowering period ($R^2 = 0$, $F_{1,18} = 0.066$, $P = 0.80$, 1.7 ± 6.6 days earlier per decade; $R^2 = 0.0$, $F_{1,18} = 0.021$, $P = 0.89$, 0.78 ± 5.4 days later per decade).

The duration of the adult syrphid activity period occurs within the flowering period in most years, with syrphids emerging after flowering commences and ending before flowering ends (Fig. 2; Table 1). The number of days that the syrphid activity period overlaps with the flowering community has not changed significantly ($R^2 = 0.08$, $F_{1,16} = 1.36$, $P = 0.26$, 4.4 ± 3.7 fewer days of overlap per decade). Similarly, there is no change in phenological overlap through time for eight of the nine plant species (results not shown), and for only one species, *Ligusticum porteri* (Porter's licorice root), is there a slight trend toward fewer days of overlap at a rate of 3.0 ± 1.7 fewer days per decade ($R^2 = 0.17$, $F_{1,16} = 3.20$, $P = 0.10$).

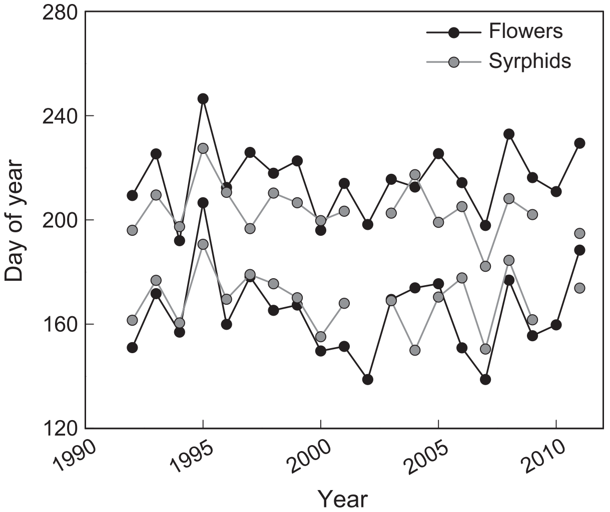


**Fig. 2** Interannual variation in the timing of the syrphid community and flowering of plant species visited by syrphids from 1992 to 2011 (syrphid data were unavailable in 2002 and 2010). The beginning (bottom set of lines) and end (top set of lines) of the season for each taxon is the day on which 10% and 90% of the yearly total samples were counted, respectively.

### *Phenological responses to climate*

Phenology was strongly associated with climate (Table 2). Timing of snow melt was the best predictor of the onset of both the flowering and syrphid period (Table 2). Both flowers and syrphids emerged earlier as snow melt advanced (Fig. 3a). A few multiple regression models containing snow melt fell within $\Delta \mathrm{AIC_C}$ of 2 relative to the simplest and best model containing only snow melt (Table 2); GDDs and precipitation accounted for some variation in flowering and syrphid onset when timing of snow melt was held constant, but these predictors were not significant (Table 3). The best model of the end of flowering contains snow melt and GDDs, and both were independently good predictors of the end of flowering (Table 2); flowering ends earlier as snow melt advances and as GDDs increase (Fig. 3c, d). The model containing snow melt, GDDs, and precipitation was also supported, but likely only because snow melt and GDDs were in the model; the effect of precipitation on the end of flowering was insignificant (Table 2and 3). In contrast, the best model of the end of

**Table 2** Linear regression models of the onset and end of the flowering and syrphid period in response to climate variables: timing of snow melt (snow, the day of year of first bare ground), growing degrees-days (GDD, from March 1 until the mean of each phenological response), and total precipitation (precip) during the month of onset (June) through end (June–July)

| | Flowering onset | | | Syrphid onset | | | Flowering end | | | Syrphid end | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model | $R^2$ | $P$ | $\Delta \mathrm{AIC_c}$ | $R^2$ | $P$ | $\Delta \mathrm{AIC_c}$ | $R^2$ | $P$ | $\Delta \mathrm{AIC_c}$ | $R^2$ | $P$ | $\Delta \mathrm{AIC_c}$ |
| Snow | 0.82 | <0.0001 | 0 | 0.68 | <0.0001 | 0 | 0.69 | <0.0001 | 2.5 | 0.23 | 0.044 | 3.0 |
| GDD | 0.62 | <0.0001 | 14.7 | 0.57 | 0.0003 | 5.0 | 0.69 | <0.0001 | 2.6 | 0.33 | 0.013 | 0.6 |
| Precip | 0.01 | 0.66 | 34.0 | 0.08 | 0.25 | 18.8 | 0.03 | 0.49 | 25.5 | 0.09 | 0.23 | 6.1 |
| Snow + GDD | 0.82 | <0.0001 | 2.2 | 0.69 | 0.0002 | 1.8 | 0.76 | <0.0001 | 0 | 0.33 | 0.051 | 3.2 |
| Snow + precip | 0.83 | <0.0001 | 1.4 | 0.71 | <0.0001 | 0.63 | 0.74 | <0.0001 | 1.6 | 0.39 | 0.025 | 1.4 |
| GDD + precip | 0.63 | 0.0002 | 16.8 | 0.66 | 0.0003 | 3.6 | 0.70 | <0.0001 | 4.4 | 0.44 | 0.014 | 0 |
| Snow + GDD + precip | 0.83 | <0.0001 | 2.2 | 0.74 | 0.0002 | 1.9 | 0.79 | <0.0001 | 0.5 | 0.44 | 0.037 | 2.7 |

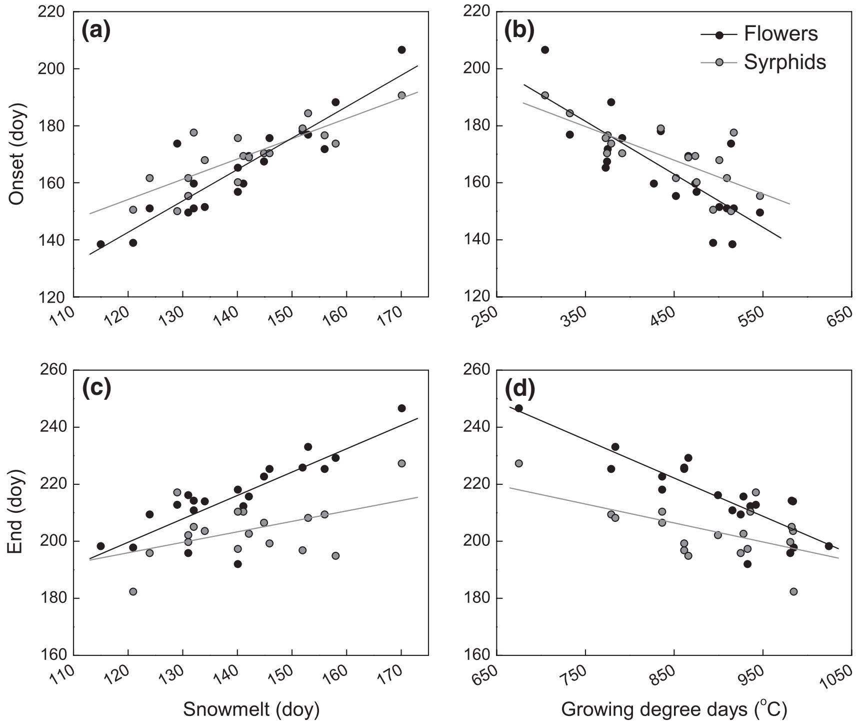


**Fig. 3** Variation in syrphid and flowering phenology in relation to timing of snow melt (day of year) and temperature, shown as accumulated growing degree-days (°C), for the (a, b) onset and (c, d) end of the flower (black lines) and syrphid (gray lines) community. Linear relationships are from simple linear regression. Slopes are significantly different from one another in all panels (see Table 4).

**Table 3** Effect sizes for individual climate predictors of flowering and syrphid phenology used in multiple regression models. Timing of snow melt (snow, the day of year of first bare ground), growing degrees-days (GDD, from March 1 until the mean of each phenological response), and total precipitation (precip) during the month of onset (June) through end (June–July)

| Response | Model | Coefficient | Estimate ± SE | *T* | *P* |
|---|---|---|---|---|---|
| Flowering onset | Snow | Snow | 1.1 ± 0.12 | 9.03 | <0.0001 |
| | GDD | GDD | −0.19 ± 0.35 | −5.4 | <0.0001 |
| | Precip | Precip | 1.19 ± 2.68 | 0.45 | 0.66 |
| | Snow + GDD | Snow melt | 1.0 ± 0.23 | 4.37 | 0.0004 |
| | | GDD | −0.023 ± 0.045 | −0.52 | 0.61 |
| | Snow + precip | Snow melt | 1.13 ± 0.13 | 9.01 | <0.0001 |
| | | June precipitation | −1.15 ± 1.18 | −0.97 | 0.34 |
| | GDD + precip | GDD | −0.19 ± 0.035 | −5.33 | <0.0001 |
| | | June precipitation | 0.98 ± 1.69 | 0.58 | 0.57 |
| | Snow + GDD + precip | Snow melt | 1.08 ± 0.25 | 4.328 | 0.0005 |
| | | GDD | −0.011 ± 0.048 | −0.24 | 0.82 |
| | | June precipitation | −1.05 ± 1.27 | −0.83 | 0.42 |
| Syrphid onset | Snow | Snow | 0.71 ± 0.12 | 5.79 | <0.0001 |
| | GDD | GDD | −0.12 ± 0.025 | −4.64 | 0.0003 |
| | Precip | Precip | 2.14 ± 1.79 | 1.20 | 0.25 |
| | Snow + GDD | Snow melt | 0.55 ± 0.23 | 2.39 | 0.031 |
| | | GDD | −0.034 ± 0.042 | −0.82 | 0.42 |
| | Snow + precip | Snow melt | 0.69 ± 0.12 | 5.69 | <0.0001 |
| | | June precipitation | 1.36 ± 1.05 | 1.30 | 0.21 |
| | GDD + precip | GDD | −0.12 ± 0.024 | −5.03 | 0.0002 |
| | | June precipitation | 2.17 ± 1.13 | 1.93 | 0.073 |
| | Snow + GDD + precip | Snow melt | 0.46 ± 0.23 | 2.03 | 0.062 |
| | | GDD | −0.048 ± 0.041 | −1.17 | 0.26 |
| | | June precipitation | 1.63 ± 1.06 | 1.54 | 0.15 |
| Flowering end | Snow | Snow | 0.82 ± 0.13 | 6.36 | <0.0001 |
| | GDD | GDD | −0.13 ± 0.019 | −6.33 | <0.0001 |
| | Precip | Precip | 0.74 ± 1.04 | 0.71 | 0.49 |
| | Snow + GDD | Snow melt | 0.45 ± 0.20 | 2.22 | 0.041 |
| | | GDD | −0.067 ± 0.031 | −2.18 | 0.043 |
| | Snow + precip | Snow melt | 0.83 ± 0.12 | 6.81 | <0.0001 |
| | | June–July precipitation | 0.97 ± 0.55 | 1.75 | 0.098 |
| | GDD + precip | GDD | −0.12 ± 0.020 | −6.17 | <0.0001 |
| | | June–July precipitation | 0.44 ± 0.60 | 0.74 | 0.47 |
| | Snow + GDD + precip | Snow melt | 0.52 ± 0.20 | 2.53 | 0.022 |
| | | GDD | −0.057 ± 0.031 | −1.86 | 0.081 |
| | | June–July precipitation | 0.74 ± 0.53 | 1.39 | 0.18 |
| Syrphid end | Snow | Snow | 0.37 ± 0.17 | 2.19 | 0.044 |
| | GDD | GDD | −0.067 ± 0.024 | −2.80 | 0.013 |
| | Precip | Precip | 0.95 ± 0.76 | 1.26 | 0.23 |
| | Snow + GDD | Snow melt | −0.022 ± 0.31 | −0.071 | 0.94 |
| | | GDD | −0.069 ± 0.047 | −1.48 | 0.16 |
| | Snow + precip | Snow melt | 0.42 ± 0.16 | 2.71 | 0.016 |
| | | June–July precipitation | 1.28 ± 0.65 | 1.98 | 0.067 |
| | GDD + precip | GDD | −0.068 ± 0.23 | −3.04 | 0.0084 |
| | | June–July precipitation | 1.04 ± 0.61 | 1.70 | 0.11 |
| | Snow + GDD + precip | Snow melt | 0.12 ± 0.30 | 0.41 | 0.69 |
| | | GDD | −0.053 ± 0.045 | −1.16 | 0.27 |
| | | June–July precipitation | 1.12 ± 0.66 | 1.70 | 0.11 |

the syrphid period contained GDDs and precipitation (Table 2). The end of the syrphid period shifts toward earlier dates as GDDs increase and precipitation decreases (Fig. 3d; Table 3); a simple model containing only GDDs performs almost as well as the multiple regression model containing both predictors (Table 2).

This suggests that precipitation has a slight effect on the end of the syrphid period when GDDs are held constant. Based on the above results, we investigated whether flowers and syrphids responded at different rates to both snow melt and GDDs, separately. Flowering onset and end advanced at a faster rate than syrphid onset and end in response to increasing GDDs and earlier snow melt, as indicated by significant interaction terms between taxa and each of the predictors (Table 4; Fig. 3).

Snow melt was the best predictor of overlap between the syrphid and flower community, with GDDs and precipitation showing very slight evidence of importance only after the effect of snow melt was held constant (see Table S2 for model selection results). There were 4.6 ± 1.4 more days of overlap between the syrphid and flower community with every day that snow melt advanced ($R^2 = 0.41$, $F_{1,16} = 11.23$, $P = 0.0041$; Fig. 4). This led us to examine whether the duration of the syrphid activity and floral bloom periods, calculated as the number of days between onset and end, was longer in years of early snow melt, which may explain this pattern. Indeed, the duration of flowering extended as snow melt date advanced ($R^2 = 0.21$, $F_{1,18} = 4.90$, $P = 0.04$), and syrphids were also present for more days as snow melt date advanced, although this trend was not as strong ($R^2 = 0.19$, $F_{1,16} = 3.75$, $P = 0.071$). Duration extends in years of early snow melt because onset advances at a faster rate than end in response to advancing snow melt (Table 3).

Overlap of individual plant species with the syrphid community was associated with climatic predictors for five of the nine plant species (Fig. 5; Table 5; see Table S3 for full set of model selection results). When a relationship exists, temporal overlap (no. days) between syrphids and these species generally shows a positive relationship with precipitation, a negative relationship with snow melt, and a positive relationship with temperature (Fig. 5; Table 5; but see *Sedum rosea* overlap and snow melt). Multiple factors seem to affect overlap between syrphids and *Linum lewisii* (Lewis flax), *Potentilla gracilis* (slender cinquefoil), and *Achillea millefolium* (common yarrow); while the effect of snow melt on overlap with *P. gracilis* has the most support, precipitation is the most common factor in supported models for overlap with *L. lewisii* and *A. millefolium* (Table 5).

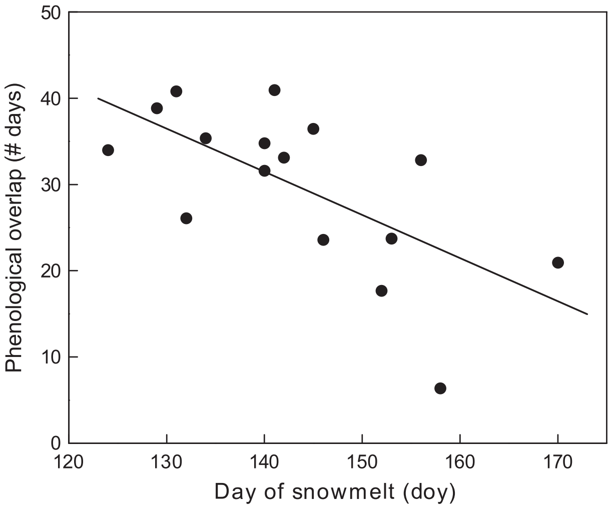


**Fig. 4** Phenological overlap between syrphid flies and flowers is best predicted by timing of snow melt, shown as day of year (Table S2). Phenological overlap is the number of days that both the syrphid and flower community are active (based on date in each year when 10–90% of syrphids and flowers were sampled).

## Discussion

There has been no change in flowering phenology, syrphid phenology, or temporal overlap among flowers and syrphids over our 20-year record (1992–2011), consistent with a lack of directional change in climate variables that we examined over the same time frame.

**Table 4** Differences in the rate (i.e., slope) of shifts in flower and syrphid phenology in response to snow melt (snow) and growing degree-days from March 1−mean of the end of the syrphid activity period (GDD). Results are from ANCOVAS with timing (onset and end) of the activity period (day of year) as a continuous response variable. Degrees of freedom = 3, 34 for each analysis

| | Onset | | | End | | |
|---|---|---|---|---|---|---|
| Model | Estimate ± SE | $t$ | $P$ | Estimate ± SE | $t$ | $P$ |
| Intercept | 10.7 ± 16.3 | 0.65 | 0.52 | 101.4 ± 19.5 | 5.2 | <0.0001 |
| Snow | 1.1 ± 0.12 | 9.5 | <0.0001 | 0.82 ± 0.13 | 5.9 | <0.0001 |
| Taxa | 58.3 ± 24.6 | 2.4 | 0.024 | 50.7 ± 29.4 | 1.7 | 0.094 |
| Taxa × Snow | −0.39 ± 0.17 | −2.2 | 0.031 | −0.45 ± 0.21 | −2.2 | 0.037 |
| Intercept | 88.1 ± 10.6 | 8.3 | <0.0001 | 336.09 ± 18.7 | 18.0 | <0.0001 |
| GDD | 0.18 ± 0.025 | 7.3 | <0.0001 | −0.13 ± 0.021 | −2.7 | <0.0001 |
| Taxa | 37.2 ± 15.3 | 2.4 | 0.021 | −73.1 ± 27.2 | −6.5 | 0.011 |
| Taxa × GDD | −0.078 ± 0.035 | −2.2 | 0.034 | 0.068 ± 0.030 | 2.2 | 0.033 |

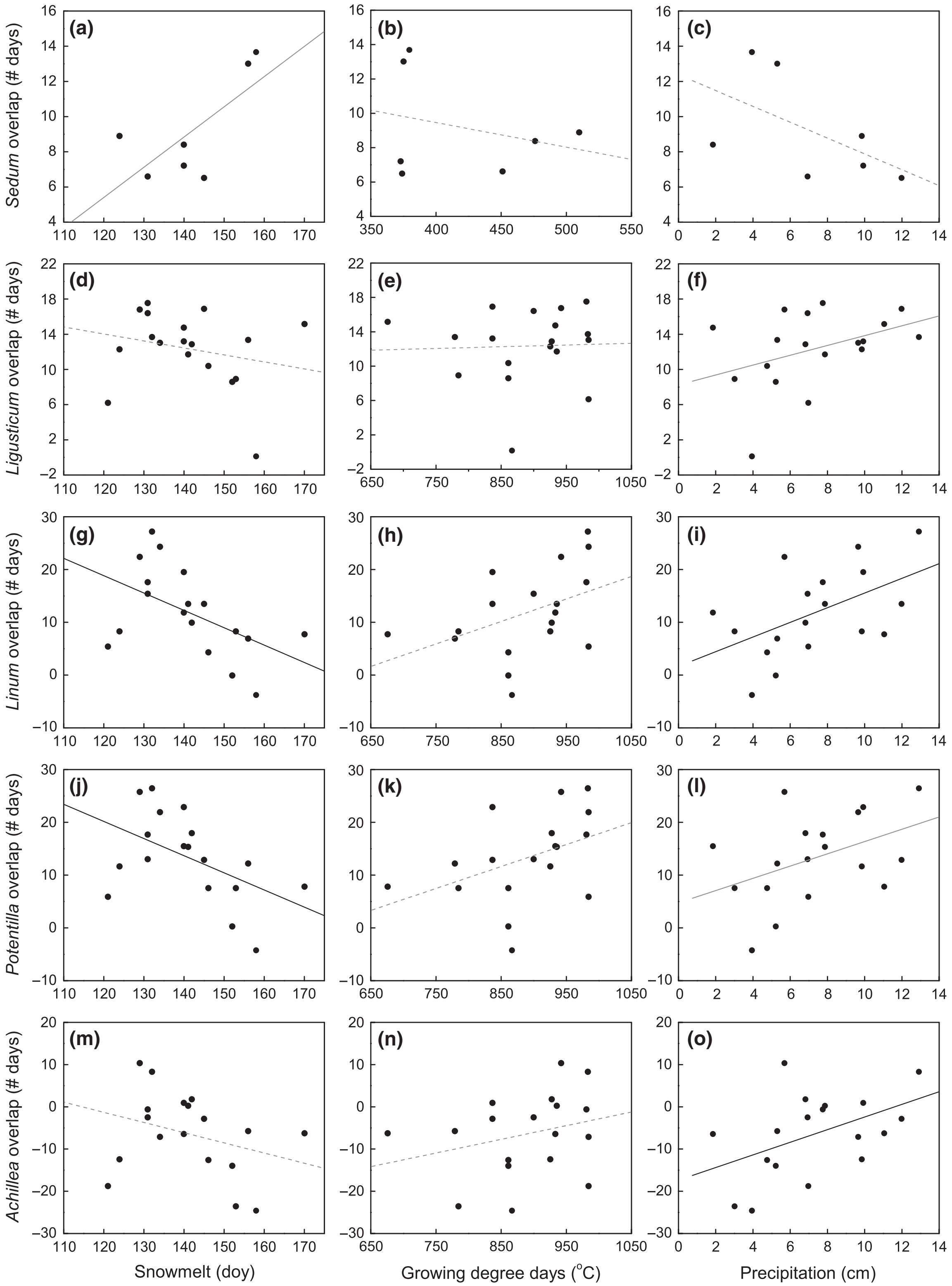


**Fig. 5** Relationships between phenological overlap of individual plant species with the syrphid community (no. days) and abiotic predictors. Linear relationships are from simple linear regression. Results are only shown for species with evidence of a linear relationship between at least one climate variable and overlap ($P \leq 0.10$; Table 5). Solid lines indicate independent effects of each predictor on overlap for relationships with the most support in model selection (lowest $\Delta AIC_c$ values; models with an asterisk in Table 5). Black lines indicate significant linear relationships ($P < 0.05$) and gray lines nonsignificant linear relationships.

**Table 5** Temporal overlap (no. days) between syrphids and flowering of individual plant species. Results are only shown for species with evidence of a relationship between climate variables and overlap ($P \leq 0.10$). Only models within $\Delta AIC_c < 2$ are shown here. For a full list of results, see Table S3. $N = 18$ years for all species except *S. rosea* ($N = 7$ years). Species are listed in order of flowering throughout the growing season. Snow = timing of snow melt (doy); GDD = growing degree-days; from March 1– mean of each phenological response, precip = total precipitation.

| Species | Model | Slope ± 1SE | $R^2$ | *F* | *P* |
|---|---|---|---|---|---|
| *S. rosea* | *Snow | 0.17 ± 0.076 | 0.50 | 5.09 | 0.074 |
| *L. porteri* | *June–July precip | 0.56 ± 0.32 | 0.16 | 3.05 | 0.10 |
| *L. lewisii* | *Snow | −0.28 ± 0.13 | 0.45 | 6.10 | 0.012 |
|  | *June–July precip | 1.17 ± 0.52 |  |  |  |
|  | GDD | 0.04 ± 0.019 | 0.44 | 5.88 | 0.013 |
|  | June–July precip | 1.34 ± 0.52 |  |  |  |
| *P. gracilis* | *Snow | −0.28 ± 0.13 | 0.37 | 4.45 | 0.03 |
|  | *June–July precip | 0.94 ± 0.56 |  |  |  |
|  | Snow | −0.32 ± 0.14 | 0.25 | 5.43 | 0.033 |
|  | GDD | 0.04 ± 0.02 | 0.35 | 4.03 | 0.04 |
|  | June–July precip | 1.11 ± 0.56 |  |  |  |
| *A. millefolium* | *June–July precip | 1.50 ± 0.70 | 0.22 | 4.62 | 0.047 |
|  | GDD | 0.03 ± 0.025 | 0.29 | 3.06 | 0.077 |
|  | June–July precip | 1.46 ± 0.69 |  |  |  |
|  | Snow | −0.18 ± 0.17 | 0.28 | 2.88 | 0.087 |
|  | June–July precip | 1.36 ± 0.71 |  |  |  |

*Indicates model with the lowest $\Delta AIC_c$ value.

However, over longer time frames since the 1970s, abiotic variables at our study site have changed in accordance with regional climate projections: earlier snow melt and increasing temperatures (Lambert *et al.*, 2010; Iler *et al.*, 2013a). The strong relationships between phenology and climate in this study allow us to comment not only on phenological relationships between syrphids and flowers under future climate change at our site but also on the effects of interannual variability in the abiotic environment on phenology. Interannual variability in climate is expected to increase (IPCC, 2007), which implies some years with longer temporal overlap between syrphid and flower communities at our site (early snow melt years) and some years with less overlap (late snow melt years). Over shorter timescales, interannual variation is likely to be more relevant to phenological synchrony at our site, while directional climate change will play a larger role over longer timescales. The demographic consequences of climate-induced phenological shifts are largely unknown, but interannual variation in temporal overlap may have a larger effect on the fitness of interacting species than long-term directional change (Miller-Rushing *et al.*, 2010).

Syrphid and flowering phenology were associated with different abiotic cues. The timing of snow melt seems to restrict the start of the season for both flowers and syrphids, whereas a combination of temperature, precipitation, and snowmelt seem to determine the end of their period of temporal overlap. Earlier snow melt was strongly associated with advanced flowering onset, as shown for other plant species at the RMBL and other high-altitude or high-latitude sites (Price & Waser, 1998; Inouye *et al.*, 2002, 2003; Dunne *et al.*, 2003; Høye *et al.*, 2007a,b; Inouye, 2008). Syrphid onset was also earlier in years of advanced snow melt, whereas the syrphid period ended earlier in warmer and drier years. The end of flowering was advanced in years of early snow melt and warmer temperatures, which may reflect an effect of temperature on floral longevity because individual flowers tend to have shorter lifetimes when temperatures are warmer (Yasaka *et al.*, 1998; Bynum & Smith, 2001; Lundemo & Totland, 2007). Furthermore, experimentally advanced spring snow melt leads to drier soils in the summer, also a potential direct consequence of warming, which could limit the duration of flowering through effects of soil moisture and may explain why both snow melt and temperature were good predictors of the end of flowering (Harte *et al.*, 1995; Dunne *et al.*, 2003). Temperature and the timing of snow melt are correlated with one another, and it remains currently unclear which of these abiotic factors has a stronger effect on flowering. The relative importance of phenological cues like snow melt is also likely to vary among insect taxa at the same location (Høye & Forchhammer, 2008); for example, snow melt was not a strong predictor of the emergence phenology of wasps and solitary bees at the RMBL (Forrest & Thomson, 2011).

Syrphid and flowering phenology also respond at different rates to the same cues: the timing of snow melt and GDDs. Despite these different rates of response, there are more days of temporal overlap between the syrphid and flowering community in years of early snow melt. This increasing temporal overlap seems to be a consequence of an extended duration of both flowering and syrphid activity when snow melt is early. Other observational and experimental work at the RMBL also found evidence of an extended duration of flowering under early snow melt conditions (Price & Waser, 1998; Dunne *et al.*, 2003). Flight duration of butterflies was extended during a series of warm years in the United Kingdom, indicating extended activity in other insect pollinators with climate change (Roy & Sparks, 2000). Maintenance of temporal synchrony between syrphids and flowers could therefore continue for some time if the climate continues to change as predicted, especially for pollen generalists and generalist-pollinated plants, consistent with empirical evidence that complete decoupling of bees and their floral resources is also unlikely (Bartomeus *et al.*, 2011; Forrest & Thomson, 2011; Rafferty & Ives, 2011; but see Kudo *et al.*, 2004; Thomson, 2010; Burkle *et al.*, 2013). Our results indicate that the greatest risk of altered community-level synchrony under climate change occurs at the end of the activity period of syrphids and flowers (Fig. 3), where syrphids would need to switch to later-flowering plants to maintain synchrony, such as *Heliomeris multiflora* (showy goldeneye). At the same time, the end of the syrphid period was the most variable and difficult to predict of our phenological responses, again highlighting the role of interannual variation over directional change in this study. The regional trend of a longer growing season in the temperate zone of the Northern Hemisphere (Myneni *et al.*, 1997; Menzel & Fabian, 1999) suggests the potential for longer temporal overlap of other plant–pollinator interactions. However, such an effect will depend on local environmental drivers of phenology; in the Arctic, spatial variation in flowering responses to warming has led to shorter flowering seasons in association with a declining abundance of insect visitors (Høye *et al.*, in press).

In contrast to community-level flowering results, we find evidence of the potential for decreasing phenological synchrony of some individual plant species with syrphids if abiotic conditions shift in the directions predicted under climate change. One might expect to find phenological mismatch in plant–pollinator communities at the very beginning or end of the flowering season, where pollinators and flowers are not buffered by earlier or later species, respectively (Kudo & Ida, in press). Surprisingly, we find no evidence of changes in synchrony with syrphids in relation to the abiotic environment for the first three species to flower (*A. septentrionalis*, *T. officinale*, and *V. capitata*). Instead, species flowering in the middle and end of the season show changes in synchrony with variation in the abiotic environment. *Ligusticum porteri*, *L. lewisii*, *P. gracilis*, and *A. millefolium* all overlap with syrphids for fewer days as summer precipitation decreases, and *S. rosea* overlaps with syrphids for fewer days as snow melt advances. However, for two of these species (*L. lewisii* and *P. gracilis*), abiotic factors could have opposing effects on overlap with the syrphid community under continued climate change. Advancing snow melt and warming temperatures should lead to increasing synchrony with syrphids, compared to precipitation declines leading to decreased synchrony. Over shorter timescales, interannual variability in climate is also more likely to impact these species-level plant–pollinator interactions than directional changes in climate, highlighting the high level of phenological variability in this community (Iler *et al.*, 2013b).

Our results are limited to species caught in the Malaise trap, which represent a subsample of the RMBL syrphid community. We cannot rule out the possibility of interspecific variation among syrphids in the phenological cues to which they respond or changes in overlap of individual syrphid species with the flowering community. Indeed, based on our analysis of temporal overlap between syrphids and individual plant species, we expect species-specific variation in patterns of temporal overlap. Furthermore, our study focuses on food availability for adult syrphid flies because this relates to their pollination activity on flowers. Syrphid phenology may ultimately be a product of interactions among the nutritional and habitat requirements of larvae, floral resource availability, and predation. The availability of aphids for species with aphidophagous larvae, the availability of water-logged soil that is required for larval development of some species, and the timing of the flight period of Hymenopteran models that many syrphids mimic are all important components of the syrphid life cycle (Howarth & Edmunds, 2000). Syrphid flies are widely thought to be Batesian mimics of Hymenoptera (Waldbauer, 1988; Dittrich *et al.*, 1993; Azmeh *et al.*, 1998; Howarth *et al.*, 2004), and most of the Syrphidae identified at the RMBL mimic stinging Hymenoptera (Fig. 1; Kearns, 1992).

An important caveat when interpreting our results is that the degree of change in temporal overlap necessary to cause fitness consequences for plants and syrphids is unknown (e.g., reproductive losses because of mistimed pollen availability for syrphids or pollen vectors for plants). This represents a key gap in our understanding of climate change–induced shifts in the phenology of species interactions. Occasional fitness losses for long-lived perennial plant species because of low syrphid pollination will probably have weaker demographic consequences compared to syrphids that complete their reproductive cycle in 1–2 years. For species closely dependent on one another, even a small amount of phenological asynchrony can lead to fitness losses (van Asch *et al.*, 2007). Syrphid pollen specialists at our site are therefore likely to face a higher risk of fitness losses because of changes in synchrony with limited floral resources, a hypothesis supported by declining population trends for syrphids with a narrow range of adult and larval food sources (Biesmeijer *et al.*, 2006). On the other hand, some syrphid species are multivoltine (Stubbs & Falk, 2002), and climate change could therefore increase the number of generations per year (*sensu* Tobin *et al.*, 2008) as our results suggest is possible under continued advancement of snow melt. Furthermore, increasing temporal overlap between interacting taxa may not necessarily correspond to increased fitness, especially if an extended duration of flowering at the community-level leads to reduced total floral abundance or changes in the distribution of resources throughout the growing season (Aldridge *et al.*, 2011). At our site, we find no evidence of changes in the timing of peak flowering relative to peak syrphid abundance (results not shown).

Understanding the potential for disparate shifts among interacting species is crucial for advancing our knowledge of ecological responses to recent climate change (Parmesan, 2007). Indeed, altered timing of species interactions is implemented in some of the few cases of extinction and population declines in association with climate change (Burkle *et al.*, 2013; Cahill *et al.*, 2013; Høye *et al.*, in press). Our results suggest that syrphid flies and the flowering community they visit at the RMBL are unlikely to experience widespread temporal asynchrony in the foreseeable future, despite the fact that syrphids and the plants they visit respond to different abiotic factors and respond to abiotic factors at different rates. We do, however, find evidence of fewer days of temporal overlap between syrphids and individual plant species in response to abiotic conditions, and these plant species flower at various times throughout the growing season. These results demonstrate that species-level phenological responses can differ from community-level responses in nonintuitive ways and highlight the role of interannual variation in climate on phenology.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Correlation matrix of all predictor variables used to analyze associations between the abiotic environment and phenological responses.
**Table S2.** Model selection for analysis of number of days of overlap between syrphids and flowers, using linear regression.
**Table S3.** Temporal overlap between syrphids and flowering of individual plant species (# days).