OIKOS

Research article

Host plant phenology shapes aphid abundance and interactions with ants

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Oikos
2022: e09109
doi: 10.1111/oik.09109
Subject Editor: Kailen Mooney
Editor-in-Chief: Dries Bonte
Accepted 1 September 2022

Phenological mismatch can occur when plants and herbivores differentially respond to changing phenological cues, such as temperature or snow melt date. This often shifts herbivore feeding to plant stages of lower quality. How herbivores respond to plant quality may be also mediated by temperature, which could lead to temperature-by-phenology interactions. We examined how aphid abundance and mutualism with ants were impacted by temperature and host plant phenology. In this study system, aphids *Aphis asclepiadis* colonize flowering stalks of the host plant, *Ligusticum porteri*. Like other aphids, abundance of this species is dependent on ant protection. To understand how host plant phenology and temperature affect aphid abundance, we used a multiyear observational study and a field experiment. We observed 20 host plant populations over five years (2017–2021), tracking temperature and snow melt date as well as host plant phenology and insect abundance. We found host plant and aphid phenology to differentially respond to temperature and snow melt timing. Early snow melt accelerated host plant phenology to a greater extent than aphid phenology, which was more responsive to temperature. Both the likelihood of aphid colony establishment and ant recruitment were reduced when aphids colonized host plants at post-flowering stages. In 2019, we experimentally accelerated host plant phenology by advancing snow melt date by two weeks. We factorially combined this treatment with open top warming chambers surrounding aphid colonies. Greatest growth occurred for colonies under ambient temperatures when they occurred on host plants at the flowering stage. Altogether, our results suggest that phenological mismatch with host plants can decrease aphid abundance, and this effect is exacerbated by temperature increases and changes to the ant–aphid mutualism.

Keywords: aphid–ant mutualism, aphids, climate change, phenology

Introduction

Climate change can upend phenological synchronization between plants and insects (Burkle et al. 2013, Renner and Zohner 2018, Jactel et al. 2019). When this shift

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reduces herbivore fitness, trophic mismatch occurs (Kharouba and Wolkovich 2020). For example, defoliating caterpillars can emerge prior to host bud burst in spring (van Asch et al. 2007). In this case, a larval development fails to overlap with peak host abundance, leading to reduced larval survival. Other trophic mismatches occur when herbivory shifts to host plant stages of lower nutritional quality (Renner and Zohner 2018). Trophic mismatches with host plants – driven by either temperature or other phenological cues – are likely an important indirect effect of climate change on herbivore abundance (Abarca and Spahn 2021). Nevertheless, field studies of trophic mismatch in natural plant-herbivore systems remain relatively scarce and largely focus on temperature as the sole phenological cue (Renner and Zohner 2018, Abarca and Spahn 2021). However, the timing of snow melt in spring drives phenology in a range of systems (Sanders-DeMott and Templer 2017), and earlier loss of snow has widespread impacts on trophic interactions (Penczykowski et al. 2017). However, trophic mismatches between plants and insect herbivores driven by changes in snow melt timing are largely understudied (Penczykowski et al. 2017, Renner and Zohner 2018).

Aphids clearly demonstrate the impacts of warming temperatures on herbivore phenology (Zhou et al. 1995, Bale et al. 2002, Bell et al. 2015). For example, a 1°C increase in average winter temperatures can accelerate aphid migration in spring by as much as 19 days (Zhou et al. 1995). Earlier aphid migration may shift aphid colonization to lower quality host plant stages, and population declines in several aphid species have been attributed to such trophic mismatches (Crossley et al. 2021). However, host plant quality is just one of several biotic and abiotic factors that shapes aphid abundance. Notably, 40% of aphid species form mutualisms with ants (Ness et al. 2010). In these mutualisms, ants protect aphids from natural enemies while consuming sugar-rich honeydew excreted by aphids (Eubanks and Styrsky 2007). Studies of climate change impacts on the ant–aphid mutualism have largely focused on effects arising from elevated temperatures (Blanchard et al. 2019). In general, elevated temperatures increase aphid abundance except when thermal optima for development or reproduction are exceeded (Blanchard et al. 2019). Changes to the ant–aphid mutualism can offset such direct effects. For example, Barton and Ives (2014a) found that corn leaf aphids *Rhopalosiphum maidis* had increased colony growth at higher temperatures, but lower levels of ant protection, which left colonies vulnerable to natural enemy attack. These multitrophic temperature effects may overlap with trophic mismatches with host plant phenological stage to shape aphid abundance. However, such interactive effects of host plant phenology and temperature are not well represented by past studies of trophic mismatch for insect herbivores (Renner and Zohner 2018, Abarca and Spahn 2021, Samplonius et al. 2021).

In this study, we examined the interactive effects of host plant phenology and temperature on an aphid herbivore, *Aphis asclepiadis*. This aphid feeds within the inflorescences of *Ligusticum porteri* (Apiaceae), a common perennial of the Rocky Mountains (Addicott 1981). Ten years of monitoring shows that *A. asclepiadis* colony abundance on *L. porteri* is reduced by half when snow melt occurs just 10 days earlier in spring (Fig. 1; Mooney et al. 2021). Snow melt timing is also associated with host plant flowering phenology (Iler et al. 2013). Spring snow melt timing is advancing by an average of 3.5 days per decade, and flowering onset for *L. porteri* is advancing at a similar rate (CaraDonna et al. 2014). Host plant phenology determines quality as food sources for many aphid species (Guldemond et al. 1998, Stadler and Dixon 1998, Newton et al. 2009). Given these associations, we predicted that trophic mismatch with host plant flowering phenology would play a role in the observed correlation between snow melt timing and *A. asclepiadis* abundance. However, any changes in trophic matching with host plants would co-occur with elevated temperatures, as summers are rapidly warming in the Colorado Rocky Mountains (Rangwala and Miller 2012). Past experimental work in our study system demonstrates both the dependence of *A. asclepiadis* on mutualist ants (Mooney et al. 2016) and the sensitivity of this mutualism to increased temperatures (Robinson et al. 2017, Mooney et al. 2019). Therefore, we also investigated how temperature would interact with host plant phenology to shape aphid abundance and mutualism with ants.

For trophic mismatch to take place, herbivores and host plants need to differentially respond to phenological cues (Kharouba and Wolkovich 2020). Therefore, our first objective was to track variation in aphid and host plant phenology. We recorded snow melt dates, temperatures and phenology in twenty host plant populations along an elevation gradient over four years. The elevation gradient served as a natural experiment such that temperature and snow melt timing varied among populations. Our second objective was to evaluate interactive effects of temperature and host plant phenology on key responses related to aphid colony abundance.

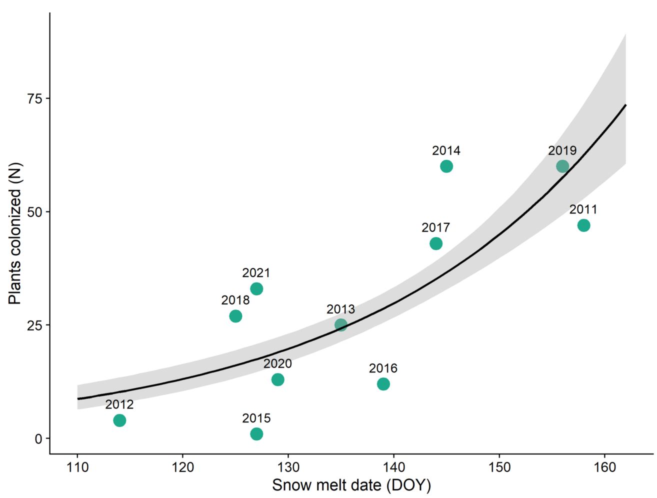

Figure 1. Year-to-year variation in colonization of host plant flowering stalks is associated with snow melt timing; figure was produced from data collected from 2011 to 2021 with methods described in Mooney et al. (2019).

Using observations collected over five years, we tested how the flowering stage at colonization affected colonization success and recruitment of ants across a range of temperatures. Overlapping variation in host plant defense can make studies of plant–insect interactions along elevation gradients difficult to interpret (Rasmann et al. 2014). Therefore, we also experimentally evaluated the interactive effects of temperature and host plant phenology on aphid abundance. To create host plants of different phenological stages, we manipulated the timing of snow melt by applying shade cloth to replicate plots. This approach has been successfully used to alter flowering phenology in many different plant communities (Steltzer et al. 2009, Wipf and Rixen 2010). Importantly, the moisture from the snow remains in the plot, which lessens the confounding effects of water stress. We then measured responses of aphid colonies in a factorial combination of host plant phenology and temperature treatments. Combining a five-year observational study with a manipulative experiment enabled a robust evaluation of temperature-by-host plant phenology interactions.

Material and methods

Observational study

Study sites and monitoring data

We monitored 20 populations of the host plant *Ligusticum porteri* in subalpine meadows and canopy gaps near the Rocky Mountain Biological Laboratory (RMBL) in Crested Butte, CO, USA from 2017 to 2021. These populations spanned an elevation gradient from 2774 to 3109 m a.s.l. We randomly selected ten flowering plants in each population in June of each year, then we censused the numbers of aphids, ants and other arthropods on flowering stalks on each plant for nine weeks. During the censuses, we also scored the flowering phenology of inflorescences as outlined in Robinson et al. (2017). Temperatures were logged at each site using a temperature sensor (HOBO, Onset Technology) at plant height (0.5 m) and shielded from solar radiation. We extracted mean temperatures from hourly records for each day of monitoring. In September of 2018–2020, we anchored a logger at the soil surface in each site. This allowed us to estimate snow melt date, which we determined as the day of year when logged temperatures first showed diurnal fluctuation (Lundquist and Lott 2008). We did not place a logger in 2016, so we do not have snow melt dates for populations in 2017.

Aphid and host plant phenology

We tested for differential responses of aphid and host plant flowering phenology to variation in temperature and snow melt date. We used temperature, snow melt date, aphid phenology and host plant flowering phenology observations from the 20 study populations in 2018, 2019, 2020 and 2021. For aphid phenology, our response variable was the ordinal date of the census when aphid colonies were first observed in each population. These initial colonies were small – median colony size of 3 individuals – suggesting that census date reflected date of colony initiation. For host plant phenology, our response variable was the ordinal date of first flowering in each population. To estimate date of first flowering from weekly observations, we regressed phenology scores on ordinal census date for each population in each year. Summarizing population level responses resulted in a data set of 80 total observations (20 populations $\times$ 4 years $=$ 80 observations of temperature, snow melt date and phenology). To test for differential responses of aphid and host plant phenology to temperature and snow melt date, we created mixed effect models using the *lmer* function from the 'lmerTest' package (Kuznetsova et al. 2017). Fixed effects included snow melt date, temperature, species (aphids and host plants) and all possible interactions. Significance testing of fixed effects in the model used Satterthwaite's degrees of freedom method (Kuznetsova et al. 2017). The model included the random effect of population to account for multiple observations from the same populations across study years (Qian 2017).

Aphid colony establishment, initial colony growth and ant recruitment

Across the five study years (2017–2020), aphids occurred on 503 host plants, with most colonies initiated on plants at flowering (n = 143) or post-flowering stages (n = 225). These counts exclude browsed or otherwise damaged host plants. Temperature during aphid colonization varied: we observed colonization at a low of 9.4°C to a high of 19.7°C. We used these observations to test for interactive effects of temperature and host plant phenology on two responses related to aphid abundance: colonization success and recruitment of ants. For the explanatory variable of temperature, we used the mean daily temperature recorded from the first census date through the second census date. For host plant flowering phenology, we focused on differences between flowering and post-flowering stages given that most aphids occurred on these stages. We scored plants as colonized if the aphid colony persisted until the next census week; this produced the response variable of colony establishment (Y/N). Based on this criterion, 170 host plants were colonized, and we used these colonization events to test for the interactive effects of temperature and host plant phenology on 1) aphid colony size at the second census and 2) ant recruitment. For ant recruitment, we used the total number of ants counted on aphid colonized host plants during the first and second census date.

To test for the effects of host plant phenology and temperature on the likelihood of colony establishment, aphid colony growth and ant recruitment, we used the 'lmerTest' package to create mixed effects models (Kuznetsova et al. 2017). Each model included a random effect of population to account for multiple observations from the same population in a given study year. Fixed effects included temperature, host plant phenology (flowering versus post flowering) and their interaction. For the models of establishment and ant recruitment, we used initial colony size as a covariate, given that larger colonies of *A. asclepiadis* are more likely both to persist and attract mutualist ants (Addicott 1979). We used a repeated measures approach to model aphid colony growth as the change in colony size between the first and second census date. In this model, we included an additional random effect to account for repeated observations of colony size on the same host plant. Likewise, we used the number of ants as a covariate in the model of aphid colony size to account for the influence of ants as mutualists in this system (Mooney et al. 2016). The model for establishment (Y/N) was created with the *glmer* function, specifying binomially-distributed errors, whereas the model for aphid colony size and ant recruitment specified Poisson-distributed errors (Qian 2017). Poisson distribution of errors for these count responses produced the best overall model fits based on AIC values. We performed post hoc contrasts using function from the 'emmeans' package (Lenth 2019). For significant ($p < 0.05$) interactions involving continuous predictors, we used the *emtrends* function to contrast slopes between relatively higher (mean plus one standard deviation) and relatively lower values (mean minus one standard deviation).

Experimental study

Snow melt manipulation

To create host plants with accelerated phenology, we altered snow melt timing on replicate plots containing *L. porteri*. On 12 October 2018, we marked eight, 16 m^2 plots containing at least 10 flowering *L. porteri* in a subalpine meadow near RMBL with PVC poles. The meadow was located at 2889 m a.s.l., placing it near the midpoint of elevation gradient described above. Each plot was randomly assigned to either the ambient or early snow melt treatment. We anchored a temperature logger (HOBO, Onset Technology) at the soil surface in the center of all plots. On 27 April 2019, we spread shade cloth (EasyShade 50% Black Bulk Shade Cloth UV Resistant) across the early snow melt treatment plots. We removed the shade cloth on 16 May 2019. We determined snow melt date in each plot from logged temperatures as described above. Application of shade cloth accelerated snow melt date. Snow melt for plots with shade cloth occurred on 15 May 2019 (mean ordinal date: 135 $\pm$ 1.2 SE) and snow melt for ambient plots occurred on 1 June 2019 (mean ordinal date: 152 $\pm$ 0.5 SE).

Host plant flowering phenology

We tracked phenological responses of host plants to the snow melt treatment. Each week from June through July, we scored flowering phenology for all host plants with flowering stalks using a 0–8 scale (Robinson et al. 2017). We determined how flowering phenology scores tracked from June through July varied with snow melt treatment using a repeated-measures approach (Qian 2017). For this analysis, we used only the plants whose flowering stalks were not deer browsed or damaged (n = 80). Using the 'lmerTest' package, we constructed a mixed effects model with the fixed effects of snow melt treatment (ambient or accelerated) and day of year plus the random effect of plant nested within plot (Kuznetsova et al. 2017).

Aphid colony growth

We created experimental aphid colonies on 26 July 2019, to test for the effects of host plant phenology on aphid colony growth. Host plants under ambient and accelerated snowmelt conditions showed differences in flowering phenology. On this date, host plants in ambient snow melt plots were still flowering (mean phenology score = 5.2 $\pm$ 0.1) when we added experimental aphid colonies while host plants in the accelerated snow melt treatment had entered the post-flowering stage (mean phenology score = 6.9 $\pm$ 0.1). We added 10 field-collected apterous (wingless) aphids to the terminal inflorescences of 8 plants in each plot (n = 64). Host plants whose flowering stalks were deer browsed, damaged or senescent were not included. To exclude predators during colony establishment, we enclosed the aphids in a fine-mesh bag and created a stem guard using tape coated in an insect barrier (Tree Tanglefoot, Contech Enterprises). After two days, colonies had established on 60 host plants.

We used a subset of successful colonies (n = 48) to test for the interactive effects of temperature and host plant phenology on the change in aphid colony size over time and interactions with ants. For these colonies, we removed stem barriers and mesh bags on 29th July. At this time, we randomly assigned half of these colonies (n = 24) to experimental warming. We surrounded these colonies on flowering stalks with an open-top warming chamber (OTC). The OTC was the same dimensions as used in past experiments (Robinson et al. 2017, Mooney et al. 2019), and we individually adjusted the height of each chamber to entirely surround the flowering stalk and colony. The duration of the warming period captured initial colony growth and ant recruitment on host plants at different stages of flowering phenology. Longer-term warming would impact host plant quality directly (Robinson et al. 2017), and *A. asclepiadis* colonies will begin to show declines in growth when censused over multiple weeks (Mooney and Agrawal 2008). We placed one temperature logger in an OTC and one at the same height under ambient conditions. Ambient temperatures were a mean of 14.9°C $\pm$ 0.03, and temperatures in the OTC were a mean of 15.9°C $\pm$ 0.04. Given the OTC design, daytime temperature differences were more pronounced, with temperatures averaging 3°C warmer inside the chamber. We censused the number of aphids every two to three days until 5 August 2019. During the censuses, we also counted the number of ants tending colonies or natural enemies interacting with the colonies. The counts excluded ants and natural enemies not in direct contact with the aphid colony. The censuses captured few interactions with natural enemies, with only 11 coccinellid beetles, syrphid flies and parasitoid wasps counted in total.

We used the remaining colonies (n = 12) to determine the effects of host plant phenology on the change in aphid colony size in the absence of ants and natural enemies, i.e. the bottom–up effects of host plant phenology. Given the limited sample size, we could not evaluate the interactive effects of temperature and host plant phenology without ants and natural enemies. We kept this subset of colonies inside of mesh bags with stem barriers intact. These colonies occurred on three flowering and three post-flowering host plants in four plots (n = 12). We censused the number of aphids every two to three days until 5 August 2019, removing bags during counts and replacing them immediately afterwards.

We used a repeated measures approach to model the growth change of experimental aphid colonies across census dates. For ant and predator-free colonies, model terms included host plant phenology (flowering versus post flowering) plus the random effects of plant nested within plot. For colonies with ants and natural enemies, the model included a factorial combination of host plant phenological stage (flowering versus post flowering) and temperature (ambient versus elevated) as fixed effects plus the random effects of plant nested within plot. Also for these colonies, we used counts of tending ants as a covariate to account for the roles of ants mutualists (Mooney et al. 2016). However, we observed ants tending only two colonies on host plants at the post-flowering stage. Given this multicollinearity, we evaluated a reduced model for aphid colony growth that excluded interaction terms among ant abundance and host plant phenological stage. We used the *glmer* function in the package 'lmerTest' to construct these models and perform significance testing. The models of aphid colony growth specified Poisson-distributed errors, as these produced the best fit as evaluated by comparing AIC values (Qian 2017). We performed post hoc contrasts using the 'emmeans' package as previously detailed (Lenth 2019).

Ant recruitment and honeydew deposition

We also tested for the effects of host plant phenology and temperature on ant recruitment and honeydew deposition by aphid colonies. We measured ant recruitment as the total number of ants counted tending aphid colonies across each census date. On 1 August, we quantified honeydew production from six randomly selected aphid colonies in each treatment combination (n = 24). We placed 100-cm^2 squares of aluminum foil around the host plant stem directly below each colony. The foil squares remained in place for 24 h, during which time ants were excluded as described above for colony establishment. We counted the number of honeydew droplets from digital images of the foil squares using an analysis program (Schneider et al. 2012).

We tested for variation in ant recruitment and honeydew deposition using colony size as a covariate, given that larger aphid colonies will attract more ants and produce more honeydew. For both responses, we included the fixed effects of host plant phenological stage (flowering versus post flowering) and temperature treatment (ambient versus elevated) plus all covariate interactions. For ant recruitment, the model included the random effect of plant nested within plot. However, the influence of host plant phenological stage on the number of tending ants produced nearly complete separation (Buckley 2015). Therefore, we fit the ant recruitment model using the *bglmer* function from the 'blme' package to impose zero-mean normal priors on the fixed effect of host plant phenology (Chung et al. 2013). For honeydew deposition, we used a generalized linear model with negative binomially distributed errors, which produced the lowest AIC value. We fit this model using the *neg.bin* function of the 'MASS' package (Venables and Ripley 2002). We performed all analyses using R ver. 4.1.3 (<www.r-project.org>).

Results

Observational study

Aphid and host plant phenology

Phenology of aphids and their host plants differentially responded to snow melt date and temperature, i.e. we observed a significant temperature-by-snow melt date-by species interaction (F-value = 7.117, $p = 0.009$). Significant two-way interactive effects indicated differential phenological responses of aphids and host plants to both temperature (F-value = 9.803, $p = 0.003$) and snow melt date (F-value = 8.838, $p = 0.004$). Later snow melt dates delayed the onset of host plant flowering to a greater extent than the arrival of aphids in populations (Fig. 2). Post hoc comparison of slopes showed that flowering onset advanced by a mean of 0.455 $\pm$ 0.061 days for each day of earlier snow melt. For aphids, colonization of host plants advanced by a mean of 0.217 $\pm$ 0.061 days for each day of earlier snow melt. Phenological responses to temperature were also species specific. Warmer temperatures in June accelerated arrival of aphids into populations more so than flowering phenology. One degree of warmer temperatures in June advanced aphid colonization by a mean of 2.239 $\pm$ 0.506 days. For host plants, one degree of temperature increase in June accelerated flowering by 0.156 $\pm$ 0.499 days.

Aphid colony establishment, initial colony growth and ant recruitment

The likelihood of colony establishment was positively associated with initial colony size, but this association was modified by host plant phenological stage (Table 1A). Overall, colonies were twice as likely to establish if they occurred on a host plant at the flowering stage (z-ratio = 3.604, $p < 0.001$). We observed a trend ($p < 0.10$) indicating an initial colony size-by-temperature-by-stage interaction. To parse this interaction, we used separate post hoc slope contrasts for flowering versus post-flowering host plants that compared the association of initial colony size with establishment likelihood at lower versus higher temperatures. On flowering plants, colonies with larger initial sizes were equally likely to establish regardless of temperature (z-ratio = 0.243, $p = 0.808$). When post-flowering host plants were colonized, temperature significantly altered the association between initial colony size and establishment likelihood (z-ratio = −2.616, $p = 0.009$). On plants at the post-flowering stage, colonies with larger initial sizes were 23.3% more likely to establish at higher versus lower relative temperatures.

Among the successfully established aphid colonies, we observed similar interactive effects of host plant phenological stage and temperature on colony growth (Table 2A). Overall, colonies grew 232% more between census dates when they occurred on flowering versus post-flowering host plants, but temperature additionally modified this pattern.

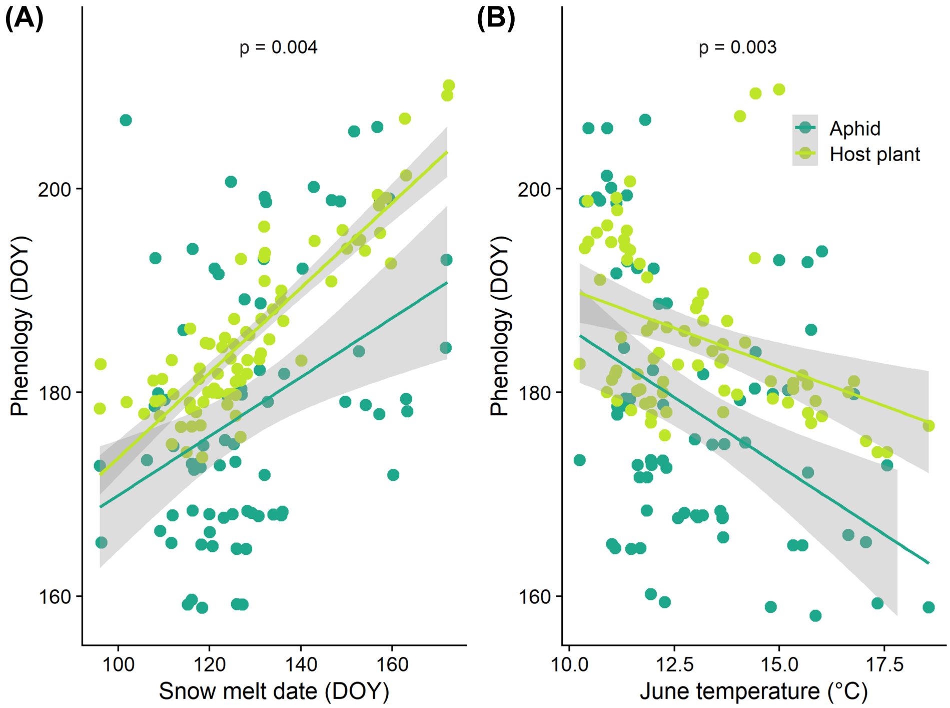

Figure 2. Associations of aphid and host plant phenology with snow melt date (A) and temperature in June (B) observed across 20 sites from 2018 to 2021; aphid phenology is the day of year of first colony appearance; host plant phenology is the day of year when populations reached a mean phenological score of 4, indicating flowering had begun. p-values indicate results from post hoc tests for heterogeneity of slopes between species responses to each climate variable.

Post hoc slope contrasts showed that when colonies occurred on host plants at the post-flowering stage, growth was 38% greater at lower temperatures than at higher temperatures (z-ratio = 6.422, $p < 0.001$). In contrast, temperature had no effect on growth between census dates when colonies occurred on host plants at the flowering stage ($p > 0.05$). Other significant interactive effects suggested that ant abundance mediated how colony growth responded to both temperature and host plant flowering stage. When ants were relatively scarce on flowering stalks, temperature mediated colony growth between census dates (z-ratio = 6.027, $p < 0.001$). In this case, colonies grew 136% more at lower temperatures than at higher temperatures. When ants were relatively abundant on flowering stalks, temperature did not mediate colony growth between census dates ($p > 0.05$). Ant abundance also mediated how aphid colony growth responded to host plant flowering stage. Post hoc slope contrasts showed that host plants at the flowering stage supported aphid colony growth regardless of ant abundance ($p > 0.05$). For colonies on host plants at the post-flowering stage, ant abundance significantly mediated colony growth (z-ratio = −11.680, $p < 0.001$). In this case, higher ant abundances boosted colony growth by 308% relative to colonies on flowering stalks with lower ant abundances.

Host plant phenological stage and temperature also impacted ant recruitment to aphid colonized flowering

Table 1. Statistical results for the effects of host plant phenological stage and temperature on (A) the likelihood of colony establishment 1) and the number of ants recruited to colonized flowering stalks 2) observed in 20 host plant populations from 2017 through 2021, and (B) the number of ants recruited to experimental aphid colonies 1) and aphid honeydew production 2) on host plants in the snow melt experiment.

	(A) Observational study				(B) Snow melt experiment			
	1) Establishment likelihood		2) Ant recruitment		1) Ant recruitment		2) Honeydew production	
Model term	z-ratio	p-value	z-ratio	p-value	z-ratio	p-value	z-ratio	p-value
Aphid colony size	3.088	0.002	9.494	< 0.001	0.143	0.887	0.934	0.350
Temperature	1.798	0.072	7.198	< 0.001	2.047	0.041	−2.049	0.040
Host plant phenological stage	−3.604	< 0.001	−5.527	< 0.001	−2.049	0.041	−2.402	0.016
Colony size × Temperature	−0.243	0.808	−2.783	0.005	0.84	0.401	1.571	0.116
Colony size × Phenological stage	−0.604	0.546	−3.426	0.001	−1.071	0.284	2.043	0.041
Temperature × Phenological stage	−0.165	0.869	−0.613	0.540	0.245	0.807	1.861	0.0627
Colony size × Temperature × Phenological stage	1.928	0.054	1.555	0.120	0.844	0.399	−2.146	0.0319

Table 2. Statistical results for the effects of host plant phenological stage and temperature on the change in aphid colony size censused on (A) colonized host plants observed in 20 populations from 2017 to 2021 and (B) experimental aphid colonies created on host plants in the snow melt experiment.

	(A) Observational study		(B) Snow melt experiment	
Model term	z-ratio	p-value	z-ratio	p-value
Census day	26.603	< 0.001	32.412	< 0.001
Ants	4.881	< 0.001	−1.031	0.302
Temperature	1.610	0.107	−0.752	0.452
Host plant phenological stage	0.620	0.536	−1.282	0.200
Census day × Ants	0.784	0.433	−1.772	0.076
Census day × Temperature	0.656	0.512	−6.431	< 0.001
Census day × Phenological stage	−5.500	< 0.001	−3.293	0.001
Ants × Temperature	−1.126	0.260	0.796	0.426
Ants × Phenological stage	1.025	0.305	NA	NA
Temperature × Phenological stage	0.154	0.877	0.419	0.675
Census day × Ants × Temperature	8.091	< 0.001	2.247	0.025
Census day × Ants × Phenological stage	9.698	< 0.001	NA	NA
Census day × Temperature × Phenological stage	−5.104	< 0.001	4.962	< 0.001
Ants × Temperature × Phenological stage	1.366	0.172	NA	NA
Census day × Ants × Temperature × Phenological Stage	0.011	0.991	NA	NA

stalks. As expected, host plant flowering stalks with larger aphid colonies recruited more ants than those with smaller aphid colonies. Although the overall model did not indicate significant interactive effects of host plant phenological stage and temperature, these factors individually modified this ant recruitment pattern (Table 1A). For host plant phenological stage, ant recruitment to colonies of a given size was 116% greater when these colonies occurred on host plants at the flowering stage versus those at the post-flowering stage. In the case of temperature, ant recruitment to colonies of a given size was 31% greater at lower temperatures than at higher temperatures.

Experimental study

Host plant flowering phenology

Host plant flowering phenology responded to the experimental manipulation of snow melt date. Our phenological stage scoring captured advances in flowering phenology over time (day of year: t-value = 47.613, $p < 0.001$). Across all observation dates, host plants in ambient snow melt plots had phenological scores delayed by 34% relative to plants in accelerated snow melt plots (snow melt treatment: t-value = −3.313, p = 0.001). Changes in phenology over time also varied with snow melt treatment (day of year × snow melt treatment: t-value = 4.145, $p < 0.001$). Post hoc slope contrasts showed that phenology advanced by a 12% greater rate for plants in the accelerated snow melt plots as compared to those than in ambient snow melt conditions.

Aphid colony growth

When protected from ants and natural enemies, growth of experimental aphid colonies showed direct effects of host plant flowering phenology. Overall, these experimental aphid colonies grew across census dates (census day: z-ratio = 20.236, $p < 0.001$). However, host plant flowering phenology influenced aphid colony growth (census day × flowering stage: z-ratio = −3.656, $p < 0.001$). As found in the observational study, plants at the flowering stage supported greater levels of aphid colony growth than plants at the post-flowering stage. The experimental aphid colonies showed 34% greater growth across census dates on host plants at the flowering stage versus those at the post-flowering stage. When colony sizes were pooled across census dates, we did not observe an overall main effect of host plant flowering phenology (flowering stage: z-ratio = 0.925, p = 0.355).

Aphid colonies open to ants and natural enemies also increased in size across the census dates (Table 2B). Again, colony growth was greater on host plants at the flowering stage, and the effects of temperature on aphid colony growth was also mediated by host plant phenological stage (Fig. 3A). As in the observational study, warmer temperatures tended to reduce aphid colony growth. For experimental colonies on flowering host plants, temperature treatment significantly affected colony growth across census dates (z-ratio = 6.250, $p < 0.001$). In this case, experimental warming reduced growth by 46% relative to colonies at ambient temperature conditions. There was a trend for this same temperature effect for experimental colonies on host plants at the post-flowering stage (z-ratio = −1.934, p = 0.053). This phenological stage-by-temperature interaction slightly contrasts with that found in the observational study, where colonies on host plants at the post-flowering stage showed the most pronounced effects of temperature on growth. Although we could not evaluate the influence of ant tending on this broader interactive effect, we found evidence that ants mediated how aphid colony growth responded to the temperature treatment. When colonies had relatively few tending ants, the temperature treatment significantly impacted colony growth (z-ratio = 4.202, $p < 0.001$), with colonies growing 33% more at ambient temperatures than with warming. When colonies had relatively more tending ants, we did not observe an effect of temperature treatment on colony growth across census dates ($p > 0.05$).

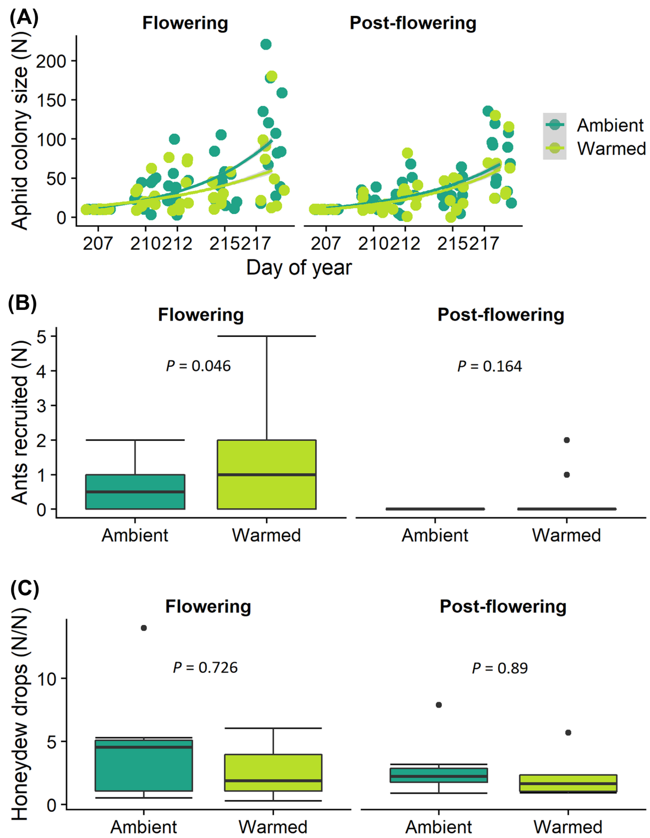

Figure 3. Host plant phenological stage and temperature treatment influenced (A) the growth of experimental aphid colonies, (B) the number of tending ants recruited and (C) per capita honeydew production (droplets/aphid) in the snow melt experiment.

Ant recruitment and honeydew deposition

The overall counts of ants tending experimental aphid colonies were low: most colonies had two or fewer tending ants observed during the census period (Fig. 3B). However, we found effects that mirrored those for ant recruitment to flowering stalks in the observational study, with lower levels of ants tending colonies under warmed conditions and on host plants at the post-flowering stage. Host plant phenological stage influenced the number of ants recruited to host plants (Table 1B). Regardless of colony size, colonies on host plants at the post -flowering stage recruited very few tending ants. In contrast, colonies on host plants at the flowering stage recruited more tending ants. Temperature treatment also affected the number of ants recruited to the experimental aphid colonies. Regardless of colony size, the warming treatment increased counts of tending ants relative to ambient conditions. Both host plant phenology and temperature also impacted honeydew deposition by aphid colonies (Table 1B). Overall, honeydew deposition was 22% greater for colonies on host plants at the flowering stage (Fig. 3C). Temperature did not affect honeydew deposition by colonies on host plants at the flowering stage ($p > 0.05$), but there was a trend for warmer temperatures to reduce honeydew production for colonies on plants at the post-flowering stage (z-ratio = 1.698, $p = 0.089$).

Discussion

Desynchronization of phenological responses is a key component of phenological mismatches between herbivores and host plants (Kharouba and Wolkovich 2020), and our results indicate that such desynchronization occurs for *A. asclepiadis* feeding on its host plant *L. porteri*. We show that flowering phenology of *L. porteri* is responsive to snow melt timing, while aphid arrival on host plants is more tied to temperatures during colonization. These results are not unexpected: prior research in this study area has consistently shown that early snow melt accelerates *L. porteri* flowering (Iler et al. 2013, CaraDonna et al. 2014), and more broadly, seasonal phenology of aphids has long been tied to temperatures (Zhou et al. 1995). The desynchronization that we demonstrate may be present for other aphids and host plants, given the range of systems where snow melt timing is a key phenological cue (Penczykowski et al. 2017), the many aphid species that feed within inflorescences (Kundu and Dixon 1995), and the diversity of plant species that show accelerated flowering phenology (Rafferty and Nabity 2017). Phenological mismatches are largely understood to be driven by differential responses between consumers and resources to temperature (Visser and Gienapp 2019, Abarca and Spahn 2021). However, our system uniquely shows how snow melt timing can combine with temperature conditions to shift aphid colonization to earlier or later host plant phenological stages. For example, *A. asclepiadis* would encounter *L. porteri* entirely at the post-flowering stage when early snow cover loss is combined with cooler temperatures during colonization. While snow melt timing and temperature are often correlated, they may also change independently of one another as reduced snowpack and other factors can separately accelerate loss of snow cover in spring (Steltzer et al. 2009, Musselman et al. 2017, Painter et al. 2018).

We found that host plant phenological stage can influence aphid abundance, with advantages to colonizing host plants at the flowering stage demonstrated in both the observational and experimental portions of the study. Initial colony growth was greatest on host plants at the flowering stage, and this was evident both for colonies with ants and natural enemies and where these associations were excluded. This suggests bottom–up differences in host plant quality for *A. asclepiadis* between the flowering and post-flowering stages of *L. porteri*. Nutritional differences in phloem sap (e.g. C:N) could underlie this effect (Douglas 2006), although few studies have directly assessed changes in phloem sap across flowering stages (Corbesier et al. 2001, Dinant et al. 2010, Chrétien et al. 2022). Aphids generally benefit by feeding on actively growing tissues such as expanding leaf buds or developing flower stems (Kundu and Dixon 1995, Guldemond et al. 1998, Hardy et al. 2015, White 2015). Given that climate change is broadly accelerating plant phenology, shifts to older host plant stages could impact abundance for a wide range of aphid species. This sensitivity to host plant phenology was suggested by results from a recent survey of 88 aphid species (Crossley et al. 2021). Aphids with life cycles dependent upon timed transitions to specific host plants were most likely to show population losses in the last 10–50 years (Crossley et al. 2021). In our study system, reduced likelihood of colony establishment and initial growth on plants at the post-flowering stage is consistent with low overall abundance of *A. asclepiadis* colonies in years when early snow melt accelerates flowering phenology. Field studies in greater variety of systems are needed to assess the role of phenological matching in aphid population declines.

Our results also show increased recruitment of ants to colonies on host plants at the flowering stage, which could enhance these bottom–up effects. We counted more ants on host plants at the flowering stage in both the observational and experimental studies. One important caveat is that counts of ants from the observational study may include ants feeding on floral nectar, as ants are common floral visitors in many species of Apiaceae (Koul et al. 1993). However, we limited ant counts from the experimental study to those engaged in tending behavior toward aphids, and more ants tending aphid colonies on flowering host plants in these results as well. One key mechanism for this result is honeydew production, which was also greatest for colonies on host plants at the flowering stage. However, the relationship between ant tending and honeydew production can be self-reinforcing as greater ant attendance itself can elicit more honeydew production (Völkl et al. 1999, Fischer and Shingleton 2001). In this way, we cannot determine whether increased honeydew production was the cause or the effect of higher levels of ant tending for colonies on host plants at the flowering stage. An alternative explanation was that ants 'came for the flowers but stayed for the aphids', i.e. ant foraging for floral nectar enhanced their discovery of the experimental aphid colonies. Such an effect would be novel, given previous research showing that plant available nectar competes with aphids for ant mutualists (Engel et al. 2001, Katayama et al. 2013, Levan and Holway 2015). Despite the ambiguity of mechanism in the present study, our results demonstrate the influence of host plant flowering phenology on ant recruitment. Given widespread shifts in plant phenology, our result adds an important dimension to the understanding of how climate change may affect the ant–aphid mutualism (Blanchard et al. 2019, Vidal et al. 2021).

Host plant phenological stage also altered how aphid colony growth responded to temperature. Higher temperatures reduced aphid colony growth, an effect we have documented in past manipulations with our study system (Robinson et al. 2017, Mooney et al. 2019). However, at which host plant phenological stage this temperature effect was most apparent differed between the observational and experimental portions of this study. Higher temperatures reduced colony growth most on host plants at the post-flowering stage in the observational study, but in the experimental study, this effect were most apparent for colonies on host plants at the flowering stage. These contrasting effects may be due to the inherent constraints present in both study portions. In the observational study, daily mean temperatures during colony growth varied broadly from 9.4 to 19.7°C. Across such broad temperature ranges, aphid demographic responses can be non-linear, with both relatively cooler and warmer temperatures reducing development time and other vital rates (Davis et al. 2006, Hough et al. 2017, Grainger et al. 2018). Given the observational nature of these data, growth of colonies on plants at the post-flowering stage may have been more concentrated towards the warmer end, where the negative effects of high temperature appear. In contrast, experimental warming allowed us to track colony growth under ambient and incrementally elevated temperature conditions, i.e. 14.9 versus 15.9°C, for both host plant phenological stages. In this case, negative effects of elevated temperatures were revealed for colony growth on host plants at the flowering stage. Elevated temperatures reduced colony growth to a lesser extent on host plants at the post-flowering stage, perhaps because colony growth was constrained by reduced host plant quality at this phenological stage. Similar interactive effects are present in other plant–herbivore systems, where indirect effects of climate change on host plant quality overrides direct responses to temperature (Jamieson et al. 2017). Overall, these results underscore the importance of changing host plant phenology and quality when assessing the impacts of climate change on insect abundance.

We also found evidence that ants further mediated the effects of temperature on aphid colony growth, and this interactive effect was consistent when we observed temperature variation along the elevation gradient and when we applied experimental warming. In both cases, warmer temperatures reduced aphid colony growth across census dates when relatively few ants were present. When more ants were counted on colonized flowering stalks or tending colonies, this effect of temperature on colony growth was less apparent. Past field experiments in this system have also shown that mutualist ants can negate the impacts of elevated temperature on *A. asclepiadis* population growth (Robinson et al. 2017, Mooney et al. 2019). In addition to protecting colonies from predators, ants can have cascading effects on aphid demographic rates such as boosting longevity and fecundity (Flatt and Weisser 2000, Yao 2014). These benefits may be sufficient to override demographic consequences from physiological stress induced by high temperatures. However, temperature also has important direct effects on ants that alters their behavior as mutualists (Barton and Ives 2014b, Blanchard et al. 2019). In this system, experimental warming reduced ant tending behavior towards *A. asclepiadis* aphids (Mooney et al. 2019). We found evidence of a similar effect from observations of colonized host plants, which recruited fewer ants per capita at higher temperatures regardless of host plant phenological stage. Unfortunately, the pervasive impact of host plant phenology on ant recruitment limited our ability to assess how temperature affects ant–aphid interactions across different host plant stages. Follow up experiment in this and other systems should independently manipulate ant access to aphid colonies on host plants of varying phenological stages and at different temperatures. Given that 40% of all aphid species form associations with ants (Ness et al. 2010), the combined influences of host plant phenology and temperature on aphid abundance likely depends upon the how these factors also affect this mutualism.

Conclusions

Our results show that phenological mismatch with host plants can contribute to the low abundances of *A. asclepiadis* colonies that we observed in early snow melt years. Such phenological mismatches with host plants are likely an important contributor to insect population declines (Abarca and Spahn 2021), but these have been assessed in relatively few plant–herbivore systems to date (Renner and Zohner 2018). Insects that feed on or within inflorescences such as *A. asclepiadis* may be especially susceptible to these mismatches, given the pervasive impacts of warmer temperatures on flowering phenology of many plants (Rafferty and Nabity 2017). Our results also illustrate how temperature can exacerbate differences in aphid colony establishment and growth due to host plant phenological stage, perhaps because warmer temperatures reduce ant recruitment. Field studies in other systems clearly demonstrate that species interactions moderate how aphid abundance responds to climate change (Grainger and Gilbert 2017, Grainger et al. 2018, Nelson et al. 2019). Acceleration of host plant phenology is another key component of how climate change can reshape the species interactions that govern aphid abundance.

Acknowledgements – We thank A. Shapiro for help with data collection. We are also grateful to the Research Committee and Science Director Jennie Reithel at the Rocky Mountain Biological Laboratory for permitting this research.
Funding – This research was supported by a grant from the National Science Foundation Division of Environmental Biology to EM (NSF DEB no. 1655914). Additional funding for CD came from the Colorado College Hevey Fund.

Author contributions

Emily Mooney: Funding acquisition (lead); Investigation (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Alexander Mitchell**: Investigation (supporting); Methodology (supporting); Writing – original draft (supporting). **Maria Mullins**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting). **James Den Uyl**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Charlotte DiBiase**: Investigation (supporting); Methodology (supporting); Writing – original draft (supporting). **M. Shane Heschel**: Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Writing – original draft (supporting).

Data availability statement

Experimental data are available from the Dryad Digital Repository: <https/:doi.org/10.5061/dryad.1ns1rn8xg> (Mooney et al. 2022). Long-term monitoring data are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/02b87002ed19d183ee95442f3f3940ae> and <https://doi.org/10.6073/pasta/4d12833442bafba9ce10c4fd20bb12ab>.

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