

# Multitrophic interactions mediate the effects of climate change on herbivore abundance

Ayla Robinson<sup>1,2</sup> · David W. Inouye<sup>2,3</sup> · Jane E. Ogilvie<sup>2,4</sup> · Emily H. Mooney<sup>2,5</sup>

Received: 20 March 2017 / Accepted: 13 August 2017 / Published online: 11 September 2017  
© Springer-Verlag GmbH Germany 2017

**Abstract** Climate change can influence the abundance of insect herbivores through direct and indirect mechanisms. In this study, we evaluated multitrophic drivers of herbivore abundance for an aphid species (*Aphis helianthi*) in a sub-alpine food web consisting of a host plant (*Ligusticum porteri*), mutualist ants and predatory lygus bugs (*Lygus* spp.). We used a model-selection approach to determine which climate and host plant cues best predict year-to-year variation in insect phenology and abundance observed over 6 years. We complemented this observational study with experiments that determined how elevated temperature interacts with (1) host plant phenology and (2) the ant-aphid mutualism to determine aphid abundance. We found date of snowmelt to be the best predictor of yearly abundance of aphid and lygus bug abundance but the direction of this effect differed. Aphids achieved lower abundances in early snowmelt years likely due to increased abundance of lygus bug predators in

these years. Elevating temperature of *L. porteri* flowering stalks reduced their quality as hosts for aphid populations. However, warming aphid colonies on host plants of similar quality increased population growth rates. Importantly, this effect was apparent even in the absence of ants. While we observed fewer ants tending colonies at elevated temperatures, these colonies also had reduced numbers of lygus bug predators. This suggests that mutualism with ants becomes less significant as temperature increases, which contrasts other ant-hemipteran systems. Our observational and experimental results show the importance of multitrophic species interactions for predicting the effect of climate change on the abundances of herbivores.

**Keywords** Herbivory · Ant-aphid mutualism · Phenology · Warming experiment

## Introduction

Climate change has the potential to alter herbivore abundance in natural and managed systems. Changes in temperature or other abiotic factors have well-documented direct effects on herbivore abundance (Bale et al. 2002). For example, extended growing seasons allow multivoltine insect herbivores to complete more generations per year (Forrest 2016). Multitrophic interactions are also important determinants of herbivore abundance (Hairston et al. 1960), and climate change phenomena have the potential to alter top-down and bottom-up processes that affect herbivore abundance (Bale et al. 2002). Alteration of bottom-up processes includes climate-induced changes in both host plant abundance (e.g., Boggs and Inouye 2012) and quality (e.g., Jamieson et al. 2015). For example, elevated temperature can affect the primary and secondary plant metabolites in

---

Communicated by Amy Austin.

✉ Emily H. Mooney  
emooney@uccs.edu

<sup>1</sup> Ohio State University, Columbus, OH 43210, USA

<sup>2</sup> Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA

<sup>3</sup> Department of Biology, University of Maryland, College Park, MD 20742, USA

<sup>4</sup> Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA

<sup>5</sup> Department of Biology, University of Colorado Colorado Springs, Colorado Springs, CO 80918, USA

host plants that mediate insect herbivory (Jamieson et al. 2012, 2015). Alteration of top-down processes includes a variety of changes in predator–prey relationships. For example, elevated temperature can reduce escape performance in herbivorous reef fish allowing for increased predation (Allan et al. 2015). Climate change may also alter indirect species interactions that determine herbivore abundance. Barton and Ives (2014a) found that drought increased herbivore abundance through the effects of apparent competition.

Responses that alter the timing of interactions among herbivores and their host plants or natural enemies can also affect herbivore abundance. The match/mismatch hypothesis states that herbivore abundance is largely driven by the extent of overlap between herbivore recruitment and seasonal peaks in host plant quality or abundance (reviewed in Durant et al. 2007). For example, snow geese achieve lower body mass in early snowmelt years, which have reduced overlap between gosling development and high-quality plant phenological phases (Doiron et al. 2015). Warming experiments have also demonstrated the effects of phenological mismatch on herbivore abundance. Elevated temperature increased phenological overlap between deciduous trees and lepidopteran herbivores (Schwartzberg et al. 2014). When combined with decreases in herbivore development time, the increased overlap may accelerate increases in insect abundance with elevated temperatures (Schwartzberg et al. 2014). Shifts in the timing of interactions across multiple trophic levels may also affect herbivore abundance (Miller-Rushing et al. 2010), and phenological tracking may deteriorate at higher trophic levels, such that herbivores—but not their predators—keep pace with plants (Both et al. 2009). Using a long-term observational dataset from the Arctic, Mortensen et al. (2015) showed how the effects of shifting phenology may propagate across trophic levels to affect species abundance.

We investigated how elevated temperature may interact with multitrophic interactions—including host plant phenology—to determine aphid abundance. Our study system consisted of the host plant *Ligusticum porteri* (Apiaceae) and the phloem-feeding herbivore *Aphis helianthi* (Hemiptera: Aphididae). Like other insect herbivores, aphid populations have responded to climate change; these responses include both changes in abundance patterns such as greater overwinter survival and shifts in phenology such as earlier arrival at monitoring stations (Harrington et al. 2007; Bell et al. 2015). Simultaneous changes are also taking place in the species with which aphids interact. Advanced host plant phenology induced by warming experiments can increase aphid population growth rates although the direct effects of temperature are difficult to distinguish from those due to phenology (Gillespie et al. 2013). In addition to host plant-mediated effects, 40% of aphid species are tended by ants as a part of a protection mutualism (Ness et al. 2007).

Warming experiments have shown how interactions with ants can mediate how aphid abundance responds to climate change (Barton and Ives 2014b; Marquis et al. 2014). Changing interactions among aphids and their predators may be equally important. Harmon et al. (2009) increased the frequency of heat shock on the pea aphid, *Acyrtosiphon pisum*, which increased predation strength from *Coccinella septempunctata* but decreased *Harmonia axyridi* predation strength, demonstrating the complexity and unpredictability of ecological interactions under climate change. These interactions may also be mediated by phenology; aphid abundance can increase when aphids arrive on host plants in advance of their predators (Fuchs et al. 2016).

In this study system, changes in aphid abundance on *L. porteri* are likely to be responsive to changes in host plant phenology as well interactions with other arthropods. *Aphis helianthi* colonizes flowering stalks of *L. porteri* during distinct phenological stages, from anthesis in July through fruit set and plant senescence in August (Addicott 1981). Multitrophic interactions also determine the local abundance of *A. helianthi*. Past experimental work in this system demonstrates that aphid colonies without mutualist ants are vulnerable to predator-driven extinction (Mooney et al. 2016). In this study, we used a six-year dataset to examine year-to-year variation in the abundance and phenology of both aphids and the insects that are their predators and mutualists. Specifically, we evaluated the relative importance of host plant phenology and climate cues as drivers of these insect responses. Snowmelt date is the primary determinant of host plant phenology, but we also included temperature and precipitation in our evaluation. Using two manipulative experiments, we determined how elevated temperature interacts with (1) host plant phenology and (2) the ant-aphid mutualism to determine aphid abundance. The objective of these manipulations was to understand how elevated temperature might affect the multitrophic factors that determine aphid abundance.

## Materials and methods

### Study species

The aphid *A. helianthi* colonizes the flowering stalks and infrequently the leaves of *L. porteri* (Apiaceae) as well as other host species (Addicott 1978, 1981). *Ligusticum porteri* is a rhizomatous perennial found in the subalpine zone throughout the Rocky Mountains (Terrell and Fennell 2008). Plants produce flowering stalks with one to several compound umbels, and anthesis occurs in late June through July (Iler et al. 2013). *Aphis helianthi* colonies are tended by several ant species (Addicott 1979), most commonly *Formica fusca*, *Formica rufa* and *Tapinoma sessile*. Besides *A.*

*helianthi*, the primary phloem-feeding insects are the flightless nymphs of *Lygus hesperus* (Hemiptera: Miridae) and other lygus bugs in the Tribe Mirini. Lygus bug adults are also predators of aphids (Agusti and Cohen 2000). Other common predators of *A. helianthi* are ladybird beetles (Coleoptera: Coccinellidae) (Kummel et al. 2013), and we less frequently observe hover fly larvae (Diptera: Syrphidae) and red spider mites (Sarcoptiformes: Acaridae) in this system (E. Mooney, unpublished data).

### Observational study

We observed arthropods in ten host plant (*L. porteri*) populations located within 1 km of the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA. Each year, we randomly selected ten plants along a 30 m transect in each of the populations ( $N = 100$ ). We visited plants biweekly (2011) or weekly (2012–2016) in June through August to count the numbers of aphids, ants and other arthropods on each of the focal plants. For these study years, we used temperature and precipitation data collected from a permanent weather station (billy barr) located immediately north of the Gothic town site (<http://www.wrcc.dri.edu/rmbl/>). Precipitation recorded in June and July is rain. The snowmelt dates are the date of first bare ground recorded at the weather station site (b.barr, Unpublished data). The host plant abundance and phenology data come from a long-term study of flowering phenology. These data consist of counts made every other day of host-plant flowering stalks with open inflorescences within permanent phenology plots located within 1 km of RMBL (described in Inouye 2008).

We separately evaluated three response variables for aphids, ants and lygus bugs across study years (2011–2016): (1) abundance on host plants during the second census in June, (2) maximum abundance on host plants, and (3) day of year at maximum abundance. We recorded insect abundance on a host plant basis, i.e., the count of host plants observed with the given insect. We chose data from the second census in June because it represents insect abundance nearest to host-plant anthesis (mean ordinal date: 172–178). Temperature, precipitation and snowmelt date are possible drivers of these insect abundance and phenology responses, with snowmelt date being the best predictor of host plant anthesis in this system (Iler et al. 2013). Along with these climate variables, we also examined host plant abundance and phenology as possible predictors of year-to-year variation in insect responses. For host plant abundance, we used the mean total number of *L. porteri* flowering stalks across permanent phenology plots. As an index for host plant phenology, we used the day of the year (ordinal date) of peak flowering, which we defined as the mean date that the permanent plots achieved their maximum number of flowering stalks. In models of June

insect abundance, we used mean temperature and precipitation data for June. In models of the maximum abundance and day of year at maximum abundance, we used the mean temperature and precipitation data for both June and July. We used linear regression to model separately each of the climate and host plant variables as predictors of each of the insect responses using the ‘glm’ function in the ‘stats’ package with Poisson-distributed errors. We compared regression models using  $\Delta\text{QAICc}$  scores computed using the ‘aictab’ function in the ‘AICcmodavg’ package (Mazerolle 2017). Models with  $\Delta\text{AICc}$  of two or less were considered to be similarly supported by the data. McFadden’s pseudo  $R^2$  values were obtained using the ‘pR2’ function in the ‘pscl’ package (Jackman 2017). We performed all analyses in R v. 3.3.2 (R Core Team 2016).

### Host plant warming experiment

To determine how elevated temperature may affect host plant quality, we experimentally warmed replicate host plant flowering stalks in four populations of *L. porteri* beginning in 24 June 2016. We randomly selected eight plants in each population along a 15-m transect tape, and we then used open-top warming chambers to elevate the temperature surrounding the flowering stalks of four plants in each population ( $n = 16$ ). Warming chambers consisted of a 4-mm clear polyethylene (Film-Gard, Evansville, IN, USA) cylinder (90 cm tall and 92 cm diameter) supported by metal tomato cages. As a control, metal tomato cages without polyethylene surrounded four other flowering stalks in each population ( $n = 16$ ). To determine how much the chambers increased the temperature surrounding plants, we placed data loggers (60 cm from soil surface) (HOBO, OnSet Computers, Bourne, MA, USA) on two randomly selected plants in each treatment. The loggers measured temperature every 5 min throughout the experiment, and the open-top chambers resulted in a temperature increase of 1.3°C (mean daily temperature  $\pm$  standard error: ambient = 15.3  $\pm$  10.2, warming = 16.6  $\pm$  11.4).

We scored the phenological stage of both primary and terminal umbels of each flowering stalk every 2–3 days using a system adapted from Lindsey (1982). The mean of primary and terminal umbel scores determined the phenological stage (Table 1). Snowmelt date is the chief determinant of host plant phenology in this system, and we confirmed that warming treatments had no effect on phenology ( $P > 0.05$ ). At the same time as phenological scoring, we counted the numbers of ants, aphids and Lygus bugs on each flowering stalk. We repeated observations across the one-month study period (24 Jun–25 Jul 2016). Three flowering stalks failed to have umbels at anthesis, likely from the effects of frost damage (Inouye 2008), so the final data set included data from 29 plants. Because light affects insect abundance in this

**Table 1** Scoring criteria used to describe the phenology stages of the terminal and primary umbels of host plant (*Ligusticum porteri*) flowering stalks

Phenology score	Description
0	Compound umbel partially enclosed by bract; no separation of individual umbels. Tight flower buds
1	Compound umbel separated from bract; umbels are very close together and unable to be distinguished
2	Separated umbels; some floral cracking evident
3	Flowers in full anthesis on the exterior of umbels; flowers in the center of umbel are buds
4	All flowers in full anthesis
5	Petals fallen on exterior of umbel
6	All petals shed
7	Fruit developing
8	Fruit have elongated and widened

system, we measured light as photosynthetically active radiation above each flowering stalk using a light meter (LiCor Corporation, Lincoln, NE, USA) between 10:00 AM and noon on a cloudless day.

After we removed the open top chambers, we made two assessments of host plant quality: (1) fruit set by *L. porteri* and (2) aphid population relative growth rate. Fruit set is an important measure of plant quality because (1) *A. helianthi* colonizes the inflorescences of *L. porteri* at anthesis through the onset of fruit development (Addicott 1978) and (2) like most plants (Reviewed in Salopek-Sondi et al. 2002), *L. porteri* inflorescence stalks senescence if flowers fail to set fruit. We categorized fruit set (N/Y) based on phenological stage at the final census (25 Jul 2016); phenological stage scores of seven or greater indicated developing fruit on primary and/or terminal umbels. At this time, many flowering stalks were senescing; we used aphid population growth to detect differences in host plant quality among the non-senescent flowering stalks ( $n = 15$ ). On 27 Jul 2016, we added ten field-collected aphids to the terminal umbel of each non-senescent flowering stalks. These included both control plants ( $n = 7$ ) and those that had been enclosed in open top chambers ( $n = 8$ ). Because we removed the open top chambers prior to adding aphids, any differences in aphid population growth rates would reflect differences in host plant quality rather than the direct effects of temperature. We enclosed aphid colonies in fine mesh bags for 2 days, after which we removed the bags and counted the number of aphids every other day across the 12 day study period (24 Jul–1 Aug 2016). We calculated mean relative growth rate ( $RGR = \ln(n_2 - n_1)/t_2 - t_1$ ) of aphid colonies across the study period using these replicate censuses.

We used a repeated measures approach to determine whether the effects of warming and phenological stage interact to determine observed insect abundance on each flowering stalk. We created a linear mixed model in the ‘lme’ function in the ‘nlme’ package with plant identity as a random effect plus light as a covariate and the fixed effects of

warming and phenological stage (Pinheiro et al. 2016). We compared maximum likelihood models of variation in total insect abundance that included all possible covariate interactions (light  $\times$  warming  $\times$  phenological stage) to a model that included only additive effects of the covariate using the ‘anova’ function. Because the simpler model was not different from the non-additive model (likelihood ratio = 2.797,  $P = 0.424$ ), the final model included light as an additive covariate with phenological stage and warming as predictors of insect abundance. We separately analyzed data for ants, aphids and lygus bugs. We compared frequencies of seed set between ambient and elevated temperature plants using a Chi-square test. We also determined whether aphid population differed between warmed and ambient temperature flowering stalks using a general linear model; we included light as a covariate in this analysis.

### Aphid colony warming experiment

We applied a two-way factorial design to examine the effects of elevated temperature on ant–aphid interactions. To create aphid colonies, we introduced 10–15 field-collected aphids to the terminal umbel of each of 36 flowering stalks in one population of *L. porteri*. All flowering stalks were setting fruit (phenological stage >6) at the initiation of warming treatments on 24 Jul 2016. We used the open-top chambers described above to elevate the temperature surrounding the aphid colonies of 18 randomly selected colonies; another 18 colonies served as ambient temperature controls. Half of the aphid colonies in each temperature treatment had ants excluded using an insect barrier (Tanglefoot, Scotts-Miracle Gro Corporation, Marysville, OH, USA). Initially, we protected the aphid colonies from aerial predators with fine mesh bags for 3 days while they established. Every 2–4 days, we counted the number of aphids, ants and Lygus bugs on the host plant flowering stalks across the 18 day study period (24 Jul–11 Aug 2016). We calculated mean relative growth

rate ( $RGR = \ln(n_2 - n_1)/t_2 - t_1$ ) of aphid colonies across the study period using these replicate censuses.

We excluded one experimental aphid colony from the final data analysis because its host plant flowering stalk was broken. We moved one other aphid colony in the ant exclusion treatment to the non-exclusion treatment when its barrier failed. Using these data ( $N = 35$ ), we compared mean relative growth rates of aphid colonies using a linear model with ant and warming treatments as explanatory variables. We also compared the total numbers of ants and lygus bugs observed with aphid colonies using general linear models with ant and warming treatments as explanatory variables; we modeled these count data using the Poisson distribution. We obtained  $P$  values using the ‘anova’ function in the ‘stats’ package. We performed all of the above analyses were performed in R v. 3.3.2 (R Core Team 2016).

## Results

### What factors predict year-to-year variation in insect abundance and phenology on host plants?

Different explanatory variables best modeled year-to-year variation in the abundance of aphids, ants and lygus bugs at the last census in June (Table 2). Increased precipitation

in June was associated with decreased abundance of aphids on host plants ( $z = -1.725, P < 0.0001$ ). Earlier peak flowering by host plants was associated with decreases in the abundance of ants in June ( $z = -2.266, P = 0.023$ ). Earlier snowmelt dates were associated with increases in the abundance of lygus in June ( $z = -4.463, P < 0.0001$ ). While snowmelt date best modeled year-to-year variation in the maximum abundance of both aphids and lygus bugs (Table 3), the direction of the association differed (Fig. 1). Aphids achieved greater maximum abundances on host plants in years with later snowmelt dates ( $z = 9.045, P < 0.0001$ ), whereas lygus bugs achieved greater maximum abundance in years with earlier snowmelt dates ( $z = -2.785, P = 0.005$ ). Earlier peak flowering by host plants was similarly supported as a determinant of maximum lygus bug abundance ( $z = -2.469, P = 0.014$ ). Precipitation best modeled year-to-year variation in the maximum abundance of ants on host plants, and years with more summer precipitation were associated with more ants ( $z = 4.680, P < 0.0001$ ). We identified regressions with temperature, precipitation and host-plant abundance, and snowmelt date as the best for modeling year-to-year variation in the day of year at maximum abundance for aphids, ants and lygus bugs, respectively. However, these insect responses were not significantly associated with any of these variables ( $P > 0.05$ ).

**Table 2** Performance of linear regression models of year-to-year variation in June abundance as predicted by climate variables (temperature, precipitation and snowmelt date) and host plant phenology/

abundance; June abundance is the number of host plant flowering stalks with the specified insect during the last week of June across six study years

Model	Aphids			Ants			Lygus		
	$r^2$	$P$ value	$\Delta AICc$	$r^2$	$P$ value	$\Delta AICc$	$r^2$	$P$ value	$\Delta AICc$
Snowmelt date	0.074	0.207	5.560	0.055	0.119	3.475	<b>0.259</b>	<b>&lt;0.0001</b>	0
Temperature	0.005	0.736	7.039	0.027	0.278	4.733	0.221	<0.0001	2.846
Precipitation	<b>0.333</b>	<b>0.008</b>	<b>0</b>	0.009	0.517	5.492	0.127	0.002	9.874
Host plant abundance	0.205	0.036	2.742	0.051	0.133	3.654	0.074	0.018	13.861
Host plant phenology	0.000	0.996	7.153	<b>0.133</b>	<b>0.015</b>	<b>0</b>	0.120	0.003	10.402

Bold values indicate models with lowest  $\Delta AICc$  scores

**Table 3** Performance of linear regression models of year-to-year variation in maximum abundance as predicted by climate variables (temperature, precipitation and snowmelt date) and host plant phenol-

ogy/abundance; maximum abundance is the largest observed number of host plant flowering stalks with the specified insect during each of six study years

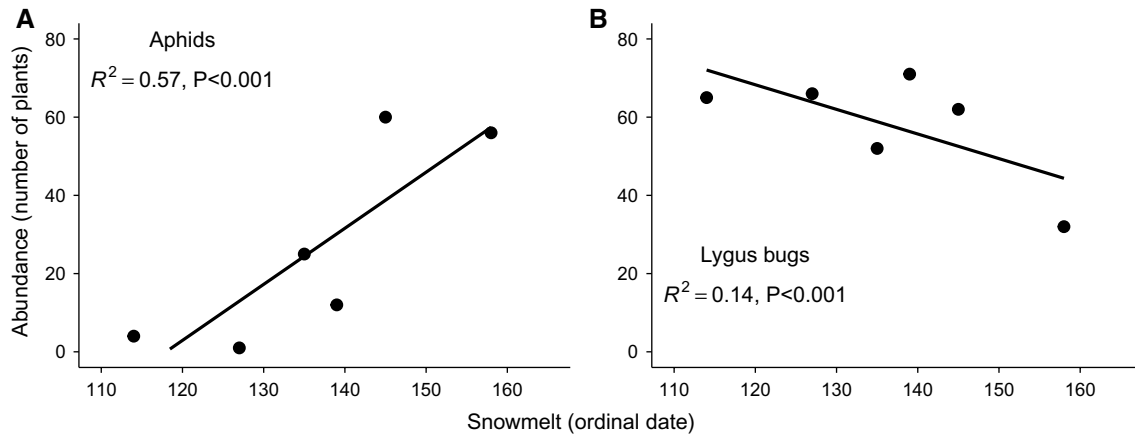
Model	Aphids			Ants			Lygus		
	$r^2$	$P$ value	$\Delta AICc$	$r^2$	$P$ value	$\Delta AICc$	$r^2$	$P$ value	$\Delta AICc$
Snowmelt date	<b>0.565</b>	<b>&lt;0.0001</b>	<b>0</b>	0.013	0.326	19.146	<b>0.142</b>	<b>0.005</b>	0
Temperature	0.096	<0.0001	78.145	0.112	0.004	11.942	0.011	0.448	7.187
Precipitation	0.222	<0.0001	57.101	<b>0.276</b>	<b>&lt;0.0001</b>	0	0.028	0.213	6.214
Host plant abundance	0.087	<0.0001	79.645	0.151	0.001	9.139	0.006	0.571	7.443
Host plant phenology	0.427	<0.0001	22.982	0.009	0.430	19.485	<b>0.110</b>	<b>0.014</b>	<b>1.765</b>

Bold values indicate models with lowest  $\Delta AICc$  scores

### How does elevated temperature interact with host plant phenology to determine aphid abundance?

While ant abundance on flowering stalks increased with greater light levels, ant abundance did not vary with either

phenological stage or temperature treatment (Table 4). For aphids, abundance was greatest on host plants during post-anthesis, but these colonies only occurred on ambient temperature flowering stalks (Fig. 2). Unlike ants and aphids, mean abundance of lygus bugs on flowering stalks did not



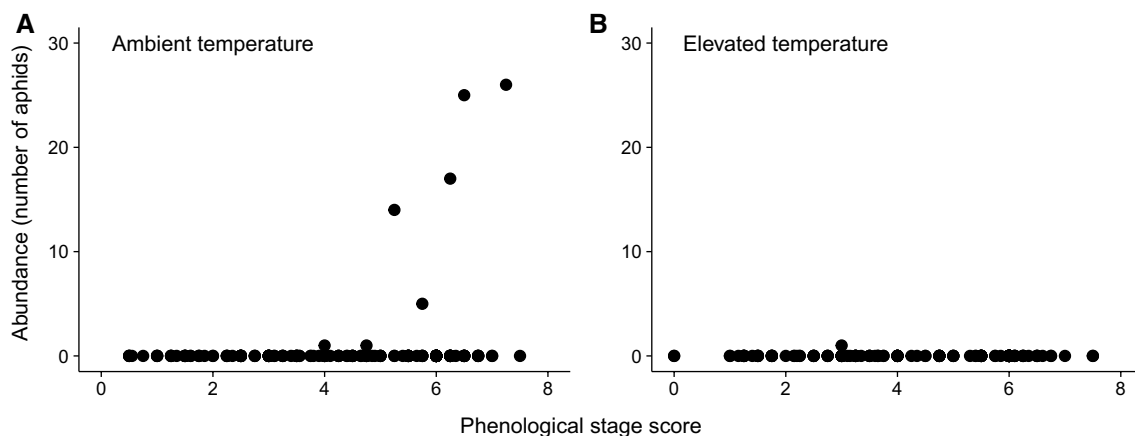
**Fig. 1** Maximum abundance of aphids (a) and lygus bugs (b) on host plant flowering stalks as predicted by snowmelt date; maximum abundance is the largest observed number of host plant flowering

stalks with each insect across six study years. Snowmelt date is the ordinal date of first observed bare ground for a weather station at the Rocky Mountain Biological Laboratory

**Table 4** Results from repeated measures analysis of covariance modeling how insect abundance (ants, aphid and lygus bugs) is predicted by light, host plant phenological stage and warming treatment

	Ants	Aphids	Lygus bugs
Intercept	$F_{1,207} = 4.364, P = 0.038$	$F_{1,207} = 4.790, P = 0.030$	$F_{1,207} = 82.124, P < 0.0001$
Light	<b><math>F_{1,77} = 18.073, P = 0.0001</math></b>	<b><math>F_{1,77} = 6.217, P = 0.015</math></b>	$F_{1,77} = 0.011, P = 0.916$
Phenological stage	$F_{1,59} = 1.953, P = 0.168$	<b><math>F_{1,59} = 6.170, P = 0.016</math></b>	<b><math>F_{1,59} = 10.523, P = 0.002</math></b>
Warming	$F_{1,207} = 0.138, P = 0.710$	$F_{1,207} = 3.665, P = 0.057$	$F_{1,207} = 2.196, P = 0.140$
Phenological stage $\times$ warming	$F_{1,207} = 0.550, P = 0.459$	<b><math>F_{1,207} = 5.896, P = 0.016</math></b>	$F_{1,207} = 0.099, P = 0.754$

Values in bold indicate significant ( $P < 0.05$ ) effects

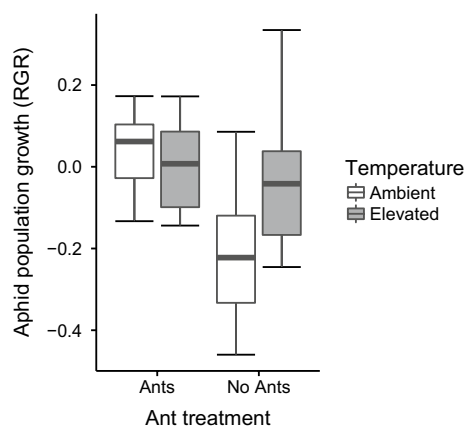


**Fig. 2** Aphid abundance on ambient (a) and elevated temperature (b) flowering stalks ( $n = 29$ ) of different phenological stage scores; see Table 1 for list of phenological stage scores

vary with light level. *Lygus* bug abundance increased with phenological stage in both elevated and ambient temperature flowering stalks. As assessed by the likelihood of fruit set, elevated temperature significantly reduced host plant quality ( $\chi^2 = 4.045$ ,  $P = 0.044$ ). Although fruit set was low overall (35.5%), ambient temperature flowering stalks were more likely to set fruit (53.3%) than elevated-temperature flowering stalks (18.8%). However, we found no difference in mean relative growth rate of aphid colonies on flowering stalks previously subjected to elevated temperature and those on flowering stalks that were at ambient temperature ( $F = 0.033$ ,  $P = 0.859$ ); the experimental colonies largely showed negative growth rates, and only one colony persisted through the entire study period.

### How does elevated temperature interact with ant mutualism to determine aphid abundance?

We found that warming increased aphid population growth rates similar to the effect of ant tending. Relative to ambient temperature aphid colonies, warming resulted in a 0.86-fold increase in mean population growth rate ( $F = 4.537$ ,  $P = 0.041$ ). Overall, aphid colonies tended by ants had 1.1-fold increase in mean population growth rate relative to untended colonies ( $F = 6.643$ ,  $P = 0.015$ ). We observed a trend ( $P < 0.10$ ) for the effect of ant tending on mean population growth to vary with the warming treatment applied to the aphid colony. Aphid colonies at ambient temperatures without ant tending had the lowest growth rates. However, warming these colonies tended to increase their growth rates to levels of colonies with ants (Fig. 3). Ant exclusions reduced by half the numbers of ants in aphid colonies relative to colonies without such exclusions ( $\chi^2 = 262.5$ ,  $P$

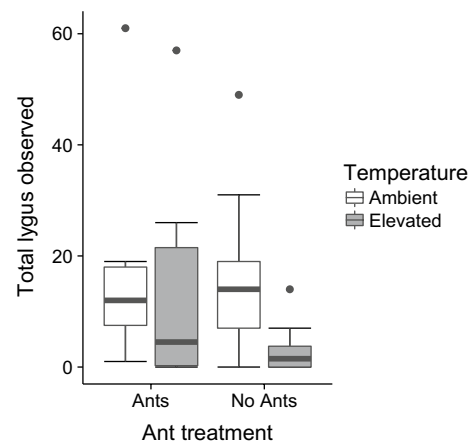


**Fig. 3** Variation in aphid population growth rate on ambient and elevated temperature aphid colonies with and without ant tending. Boxes show interquartile ranges with dark horizontal lines representing the median; whiskers extend to the most extreme data point which is no more than 1.5 times the length of the box away from the box

$\leq 0.0001$ ). Warming reduced the number of ants in aphid colonies by 0.3-fold relative to aphid colonies at ambient temperatures ( $\chi^2 = 4.801$ ,  $P = 0.028$ ). We also observed an interactive effect, but this was largely the result of warming treatments failing to influence the number of ants when exclusions were present. The treatments also had significant effects on the abundance of *lygus* bugs in aphid colonies. Warming reduced the number of *lygus* bugs by 0.5-fold relative to the number of *lygus* bugs at ambient temperature ( $\chi^2 = 56.204$ ,  $P < 0.0001$ ), and ant exclusion reduced the number of *lygus* bugs by 0.4-fold relative to the number of *lygus* when no ant exclusion was present ( $\chi^2 = 34.304$ ,  $P < 0.0001$ ). The decrease of *lygus* bugs with warming tended to be greater when ants were excluded from colonies than when aphid colonies were tended by ants ( $\chi^2 = 38.932$ ,  $P < 0.0001$ ; Fig. 4).

### Discussion

We found contrasting responses to changing climate cues between an aphid herbivore and its predator over six study years. Early snowmelt years are associated with low aphid abundance but high *lygus* bug predator abundance. This result suggests that changes in the timing of snowmelt are influencing top-down control in this system. Mechanistically, advanced snowmelt likely allows *lygus* bug predators to emerge earlier from overwintering sites (Khattat and Stewart 1980) and then achieve larger population sizes through successive generations on host plants (Leferink and Gerber 1997; Lu et al. 2010). *Lygus* bugs then can facultatively switch from feeding on host plants to soft-bodied insects



**Fig. 4** Variation in *lygus* bug abundance on ambient and elevated temperature aphid colonies with and without ant tending. Boxes show interquartile ranges with dark horizontal line representing the median; whiskers extend to the most extreme data point which is no more than 1.5 times the length of the box away from the box; outliers are shown as individual data points

like aphids (Hagler et al. 2010). We would suspect similar alteration of top-down control might occur in other systems. For example, timing of snowmelt is also a key predictor of insect phenology in arctic (Avila-Jiménez and Coulson 2011) and alpine communities (Van De Velde et al. 2016). In an arctic system, Dollery et al. (2006) found greater aphid abundances in later-exposed positions along a transect with variable snowmelt dates. In a warming experiment that induced earlier snowmelt, warmed plots had reduced aphid abundance relative to control plots, and the authors partially attributed this effect to greater numbers of predators and parasites with warming (Dollery et al. 2006). However, advanced snowmelt also reduces soil moisture, which can affect aphid abundances through effects on host plant water status and quality, i.e., bottom-up control (Dollery et al. 2006). Reduced host plant quality and increased predator abundance may together explain the very low abundance of aphids seen in early snowmelt years. Top-down and bottom-up effects combine shape year-to-year population dynamics for insect herbivores in systems similarly affected by climate change (Avila-Jiménez and Coulson 2011).

Rising temperatures are predicted to increase aphid abundance in a given year, largely through the direct effects of temperature on development time (Bale et al. 2002). However, recent studies have placed doubt on predicted changes in abundance or distribution of species that are based on temperature's direct effects alone (Wiszniewski et al. 2013; Ehrlén and Morris 2015). Our experimental results confirm that elevated temperature has host plant-mediated effects on herbivore abundance. Experimental warming of host plants over 1 month reduced fruit set in their terminal and primary umbels, and this represents an important reduction in host plant quality. Reproductive organs are attractive aphid-feeding sites (Jandricic et al. 2014), but plants direct phloem sap elsewhere following fruit abscission (Stephenson 1981). Aphids likely detected differences—using any number of quality cues (Döring 2014)—because no aphids colonized flowering stalks subjected to elevated temperatures. Our results suggest that elevated temperature reduces host plant quality for aphids, with potential implications for the species that depend on aphids or their honeydew (Sagata and Gibb 2016). Effects mediated by resource quality are important—if relatively understudied—components of how food webs will be impacted by climate change (Rosenblatt and Schmitz 2016).

We also detected effects of elevated temperature on interactions at other trophic levels. Given the ant–aphid mutualism, we would expect predator abundance to be greater when we excluded ants from aphid colonies. This prediction may be slightly apparent for colonies at ambient temperatures (Fig. 4), but we observed the opposite of this effect at elevated temperatures, i.e., more *Lygus* bug predators in colonies with ants than those without ants. Elevated temperature

also reduced the number of ants tending experimental aphid colonies. Barton and Ives (2014b) also found that ants were both less abundant and less aggressive towards aphid predators at elevated temperatures. These results suggest that elevated temperatures suppress predator abundance independent of the ant–aphid mutualism. While direct effects of temperature on aphid development time would also be a factor, predator suppression may explain why aphid colonies achieved similar growth rates regardless of whether they were tended by ants. This result is in contrast to findings by Zhou et al. (2017) who observed increased temperatures to strengthen the protection mutualism between ants and mealybugs. As these authors point out, relatively few studies have examined the effects of elevated temperature on ant–hemipteran interactions (Zhou et al. 2017). Future work may allow for a consensus, but at this point, the possible outcomes of warming on these interactions appears to be system specific. This consensus—or lack thereof—may be particularly relevant when predicting the impacts of climate change on the abundance and distributions mutualistic species (Van der Putten et al. 2010). In our results, we see that warming alone may allow for increases in aphid abundances—by suppressing predator abundance—even when aphids lack mutualist partners. This is significant given the outsize role that ant tending usually plays in the distribution and abundance of this aphid species (Mooney et al. 2016) and others (Müller and Godfray 1999).

## Conclusions

Our observational and experimental results confirm the importance of multitrophic species interactions for predicting the effects of climate change on herbivore abundance. In a recent review, Rosenblatt and Schmitz (2016) emphasize the simultaneous alteration of top-down and bottom-up effects to predict the effects of climate change on food webs. In our system, later snowmelt dates are likely simultaneously reducing predator populations while increasing host plant quality; the overall result are years with high herbivore abundance. Years of very low herbivore abundance may be similarly the products of simultaneous effects on food webs. Specifically, if early snowmelt years also have high temperatures during the growing season, then initial increases in predator abundance would be combined with reduced host plant quality. Shorter term warming could allow aphid populations to expand even in the absence of mutualist ants. These dramatic shifts in herbivore abundance are examples of what Rosenblatt and Schmitz (2016) term 'ecological surprises'. The effects of such shifts can propagate across food webs, and as snowmelt timing advances more, community composition or even ecosystem-level changes become possible (Mortensen et al. 2015).



**Acknowledgements** A Research and Creative Work grant to EM through the University of Colorado Colorado Springs supported this research. The National Science Foundation grants DEB-9408382, IBN-9814509, DEB-0238331, DEB-0922080, and DEB-1354104 provided funding to DI for the plant phenology and abundance observations. We also thank the Rocky Mountain Biological Laboratory for hosting and permitting this research. Fieldwork included help from Gretchen Kraeger, Cheryl Sandrow and Brittany Smith.

**Author contribution statement** EM, DI and JO designed and performed the observational study. AR and EM conceived and designed the manipulative experiments. EM and AR performed the manipulative experiments. AR and EM analyzed the data. AR wrote the original version of the manuscript, and EM and DI revised and edited the final submitted version.

## References

- Addicott JF (1978) Niche relationships among species of aphids feeding on fireweed. *Can J Zool* 56:1837–1841. doi:[10.1139/z78-250](https://doi.org/10.1139/z78-250)
- Addicott JF (1979) A multispecies aphid–ant association: density dependence and species-specific effects. *Can J Zool* 57:558–569. doi:[10.1139/z79-066](https://doi.org/10.1139/z79-066)
- Addicott J (1981) Synonymy of *Aphis heraclella* Davis 1919 with *Aphis helianthi* Monell 1879 (Homoptera: Aphididae). *Can Entomol* 113:167–169
- Agusti N, Cohen A (2000) *Lygus hesperus* and *L. lineolaris* (Hemiptera: Miridae), phytophages, zoophages, or omnivores: evidence of feeding adaptations suggested by the salivary and midgut digestive enzymes. *J Entomol Sci* 35:176–186
- Allan BJM, Domenici P, Munday PL et al (2015) Feeling the heat: the effect of acute temperature changes on predator–prey interactions in coral reef fish. *Conserv Physiol* 3:cov011. doi:[10.1093/conphys/cov011](https://doi.org/10.1093/conphys/cov011)
- Avila-Jiménez ML, Coulson SJ (2011) Can snow depth be used to predict the distribution of the high Arctic aphid *Acyrtosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen? *BMC Ecol* 11:25. doi:[10.1186/1472-6785-11-25](https://doi.org/10.1186/1472-6785-11-25)
- Bale JS, Masters GJ, Hodkinson ID et al (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob Chang Biol* 8:1–16. doi:[10.1046/j.1365-2486.2002.00451.x](https://doi.org/10.1046/j.1365-2486.2002.00451.x)
- Barton BT, Ives AR (2014a) Species interactions and a chain of indirect effects driven by reduced precipitation. *Ecology* 95:486–494. doi:[10.1890/13-0044.1](https://doi.org/10.1890/13-0044.1)
- Barton BT, Ives AR (2014b) Direct and indirect effects of warming on aphids, their predators, and ant mutualists. *Ecology* 95:247–253
- Bell JR, Alderson L, Izera D et al (2015) Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *J Anim Ecol* 84:21–34. doi:[10.1111/1365-2656.12282](https://doi.org/10.1111/1365-2656.12282)
- Boggs CL, Inouye DW (2012) A single climate driver has direct and indirect effects on insect population dynamics. *Ecol Lett* 15:502–508. doi:[10.1111/j.1461-0248.2012.01766.x](https://doi.org/10.1111/j.1461-0248.2012.01766.x)
- Both C, van Asch M, Bijlsma RG et al (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol* 78:73–83. doi:[10.1111/j.1365-2656.2008.01458.x](https://doi.org/10.1111/j.1365-2656.2008.01458.x)
- Doiron M, Gauthier G, Lévesque E (2015) Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Glob Chang Biol* 21:4364–4376. doi:[10.1111/gcb.13057](https://doi.org/10.1111/gcb.13057)
- Dollery R, Hodkinson ID, Jónsdóttir IS (2006) Impact of warming and timing of snow melt on soil microarthropod assemblages associated with Dryas-dominated plant communities on Svalbard. *Ecography (Cop)* 29:111–119. doi:[10.1111/j.2006.0906-7590.04366.x](https://doi.org/10.1111/j.2006.0906-7590.04366.x)
- Döring TF (2014) How aphids find their host plants, and how they don't. *Ann Appl Biol* 165:3–26
- Durant JM, Hjermmann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res* 33:271–283
- Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecol Lett*. doi:[10.1111/ele.12410](https://doi.org/10.1111/ele.12410)
- Forrest JR (2016) Complex responses of insect phenology to climate change. *Curr Opin Insect Sci* 17:49–54
- Fuchs B, Breuer T, Findling S et al (2016) Enhanced aphid abundance in spring desynchronizes predator–prey and plant–microorganism interactions. *Oecologia* 183:1–10. doi:[10.1007/s00442-016-3768-1](https://doi.org/10.1007/s00442-016-3768-1)
- Gillespie MAK, Jónsdóttir IS, Hodkinson ID, Cooper EJ (2013) Aphid–willow interactions in a high Arctic ecosystem: responses to raised temperature and goose disturbance. *Glob Chang Biol* 19:3698–3708. doi:[10.1111/gcb.12284](https://doi.org/10.1111/gcb.12284)
- Hagler JR, Jackson CG, Blackmer JL (2010) Diet selection exhibited by juvenile and adult lifestages of the omnivores Western tarnished plant bug, *Lygus hesperus* and tarnished plant bug, *Lygus lineolaris*. *J Insect Sci* 10:127. doi:[10.1673/031.010.12701](https://doi.org/10.1673/031.010.12701)
- Hairston N, Smith F, Slobodkin L (1960) Community structure, population control, and competition. *Am Nat* 94:421–425. doi:[10.1086/282146](https://doi.org/10.1086/282146)
- Harmon JP, Moran NA, Ives AR (2009) Species response to environmental change: impacts of food web interactions and evolution. *Science* 323:1347–1350. doi:[10.1126/science.1167396](https://doi.org/10.1126/science.1167396)
- Harrington R, Clark SJ, Welham SJ et al (2007) Environmental change and the phenology of European aphids. *Glob Chang Biol* 13:1550–1564. doi:[10.1111/j.1365-2486.2007.01394.x](https://doi.org/10.1111/j.1365-2486.2007.01394.x)
- Iler A, Inouye D, Hoye TT et al (2013) Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Glob Chang Biol* 19:2348–2359. doi:[10.1111/gcb.12246](https://doi.org/10.1111/gcb.12246)
- Inouye D (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362
- Jackman S (2017) pscl: classes and methods for R developed in the Political Science Computational Laboratory. United States Studies Centre, University of Sydney. Sydney, New South Wales, Australia. R package version 1.5.1. <https://github.com/atahk/pscl/>
- Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL (2012) Consequences of climate warming and altered precipitation patterns for plant–insect and multitrophic interactions. *Plant Physiol* 160:1719–1727. doi:[10.1104/pp.112.206524](https://doi.org/10.1104/pp.112.206524)
- Jamieson MA, Schwartzberg EG, Raffa KF et al (2015) Experimental climate warming alters aspen and birch phytochemistry and performance traits for an outbreak insect herbivore. *Glob Chang Biol* 21:2698–2710. doi:[10.1111/gcb.12842](https://doi.org/10.1111/gcb.12842)
- Jandricic SE, Mattson NS, Wraight SP, Sanderson JP (2014) Within-Plant Distribution of *Aulacorthum solani* (Hemiptera: Aphididae), on Various Greenhouse Plants With Implications for Control. *J Econ Entomol* 107:697–707. doi:[10.1603/EC13428](https://doi.org/10.1603/EC13428)
- Khattat AR, Stewart RK (1980) Population fluctuations and interplant movements of *Lygus lineolaris*. *Ann Entomol Soc Am* 73:282–287. doi:[10.1093/aesa/73.3.282](https://doi.org/10.1093/aesa/73.3.282)
- Kummel M, Brown D, Bruder A (2013) How the aphids got their spots: predation drives self-organization of aphid colonies in a patchy habitat. *Oikos* 122:896–906. doi:[10.1111/j.1600-0706.2012.20805.x](https://doi.org/10.1111/j.1600-0706.2012.20805.x)
- Leferink JHM, Gerber GH (1997) Development of adult and nymphal populations of *Lygus lineolaris* (Palisot de Beauvois), *L. elisus*

- Van Duzee, and *L. borealis* (Kelton) (Heteroptera: Miridae) in relation to seeding date and stage of plant development on canola (Brassi.). *Can Entomol* 129:777–787
- Lindsey AH (1982) Floral phenology patterns and breeding systems in *Thaspium* and *Zizia* (Apiaceae). *Syst Bot* 7:1–12. doi:10.2307/2418648
- Lu Y, Wu K, Jiang Y et al (2010) Mirid bug outbreaks in multiple crops. *Science* (80-) 328:1151–1154. doi:10.1126/science.1187881
- Marquis M, Del Toro I, Pelini SL (2014) Insect mutualisms buffer warming effects on multiple trophic levels. *Ecology* 95:9–13. doi:10.1890/13-0760.1
- Mazerolle MJ (2017) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. <https://cran.r-project.org/package=AICcmodavg>. Accessed 5 Sept 2017
- Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. *Philos Trans R Soc B Biol Sci* 365:3177–3186. doi:10.1098/rstb.2010.0148
- Mooney EH, Phillips JS, Tillberg CV et al (2016) Abiotic mediation of a mutualism drives herbivore abundance. *Ecol Lett* 19:37–44. doi:10.1111/ele.12540
- Mortensen LO, Schmidt NM, Høye TT et al (2015) Analysis of trophic interactions reveals highly plastic response to climate change in a tri-trophic High-Arctic ecosystem. *Polar Biol* 39:1–12
- Müller CB, Godfray HCJ (1999) Predators and mutualists influence the exclusion of aphid species from natural communities. *Oecologia* 119:120–125. doi:10.1007/s004420050767
- Ness J, Mooney K, Lach L (2007) Ants as mutualists. In: Lach L, Parr C, Abbott K (eds) *Ant ecology*. Oxford University Press, Oxford, p 432
- Pinheiro J, Bates D, DebRoy S et al (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-131. <https://CRAN.R-project.org/package=nlme>. Accessed 5 Sept 2017
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Rosenblatt AE, Schmitz OJ (2016) Climate change, nutrition, and bottom-up and top-down food web processes. *Trends Ecol Evol* 31:965–975. doi:10.1016/j.tree.2016.09.009
- Sagata K, Gibb H (2016) The effect of temperature increases on an ant-hemiptera-plant interaction. *PLoS One* 11:e0155131. doi:10.1371/journal.pone.0155131
- Salopek-Sondi B, Kovač M, Prebeg T, Magnus V (2002) Developing fruit direct post-floral morphogenesis in *Helleborus niger* L. *J Exp Bot* 53:1949–1957. doi:10.1093/jxb/erf047
- Schwartzberg EG, Jamieson MA, Raffa KF et al (2014) Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia* 175:1041–1049. doi:10.1007/s00442-014-2960-4
- Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annu Rev Ecol Syst* 12:253–279. doi:10.1146/annurev.es.12.110181.001345
- Terrell IB, Fennell A (2008) Osha: bear Root. *Nativ Plants J* 10:111–118
- Van De Velde H, Nijs I, Bonte D (2016) Warming affects different components of plant-herbivore interaction in a simplified community but not net interaction strength. *Oikos* 126:285–295. doi:10.1111/oik.03415
- Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philos Trans R Soc Lond B Biol Sci* 365:2025–2034. doi:10.1098/rstb.2010.0037
- Wisz MS, Pottier J, Kissling WD et al (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol Rev Camb Philos Soc* 88:15–30. doi:10.1111/j.1469-185X.2012.00235.x
- Zhou A, Qu X, Shan L, Wang X (2017) Temperature warming strengthens the mutualism between ghost ants and invasive mealybugs. *Sci Rep* 7:959. doi:10.1038/s41598-017-01137-0