

Temperature-Dependent Species Interactions Shape Priority Effects and the Persistence of Unequal Competitors

Tess Nahanni Grainger,* Adam Ivan Rego, and Benjamin Gilbert

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada

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ABSTRACT: The order of species arrival at a site can determine the outcome of competitive interactions when early arrivers alter the environment or deplete shared resources. These priority effects are predicted to be stronger at high temperatures, as higher vital rates caused by warming allow early arrivers to more rapidly impact a shared environment. We tested this prediction using a pair of congeneric aphid species that specialize on milkweed plants. We manipulated temperature and arrival order of the two aphid species and measured aphid population dynamics and milkweed survival and defensive traits. We found that warming increased the impact of aphids on the quantity and quality of milkweed, which amplified the importance of priority effects by increasing the competitive exclusion of the inferior competitor when it arrived late. Warming also enhanced interspecific differences in dispersal, which could alter relative arrival times at a regional scale. Our experiment provides a first link between temperature-dependent trophic interactions, priority effects, and dispersal. This study suggests that the indirect and cascading effects of temperature observed here may be important determinants of diversity in the temporally and spatially complex landscapes that characterize ecological communities.

Keywords: historical contingency, climate change, warming, herbivory, dispersal, milkweed.

Introduction

The order in which species establish in a community can determine coexistence outcomes and the trajectory of community assembly, through a process known as priority effects (Alford and Wilbur 1985; Drake 1991; Fukami 2015). Priority effects occur when early arrivers draw down a common resource (niche preemption) or change the environment (niche modification) in a way that alters the success of late arrivers (Vannette and Fukami 2014). While priority effects have traditionally been considered mainly in the context of

alternate stable states, recent research has demonstrated the important role that assembly history can play in structuring transient communities including ephemeral ponds, plant patches, and flower nectar microbes (Fukami and Nakajima 2011; Fukami 2015). The broad range of communities that can foster priority effects suggests that they are likely to have important and wide-reaching impacts on coexistence and diversity in a variety of ecological communities. As a result, emerging research seeks to understand the conditions that favor priority effects and to determine their impact on community assembly and coexistence (Fukami 2004; Kardol et al. 2013; Pu and Jiang 2015).

Any condition that increases the ability of early arrivers to quickly deplete resources, modify the environment, or both should amplify the importance of arrival order for competitive outcomes (Kardol et al. 2013; Fukami 2015). Theoretical and empirical studies have demonstrated that priority effects are most pronounced when competing species have high growth rates and high niche overlap and compete strongly for the same limited resource (Tilman 2004; Peay et al. 2012; Tucker and Fukami 2014; Vannette and Fukami 2014; Fukami 2015). As such, conditions that increase population growth rates of early arrivers or their per capita impact on the quantity or quality of a shared resource should strengthen priority effects (Chase 2003, 2010; Kardol et al. 2013; Rudolf and Singh 2013).

Temperature regulates population growth and feeding rates in ectothermic species (Brown et al. 2004; Dell et al. 2011), indicating that, below the threshold at which rising temperatures begin to reduce these rates, higher temperatures should result in stronger priority effects. Moreover, recent extensions of metabolic theory to species interactions predict that the stronger temperature dependence of herbivore vital rates, compared to those of their plant resources, should cause temperature to systematically alter plant-herbivore interactions (O'Connor et al. 2011). Specifically, the higher temperature sensitivity of respiration relative to photosynthesis and the resulting higher activation energies of herbivores compared to autotrophs (Allen et al.

* Corresponding author; e-mail: tess.grainger@mail.utoronto.ca.

ORCIDiS: Grainger, <http://orcid.org/0000-0002-6094-0526>; Gilbert, <http://orcid.org/0000-0002-4947-6822>.

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2005; López-Urrutia et al. 2006; Dell et al. 2011) causes herbivore feeding and population growth rates to outpace growth rates of primary producers as temperatures increase (O'Connor et al. 2009). This temperature asymmetry can cause herbivores to rapidly deplete their plant resource (Gilbert et al. 2014). Ultimately, faster resource depletion lowers herbivore abundances and fluctuations, reducing the maximum size that populations can reach (O'Connor et al. 2011; Dell et al. 2014; Gilbert et al. 2014).

This influence of temperature on plant-herbivore interactions should have a predictable two-pronged effect on how early-arriving herbivores impact late arrivers, by changing both the quantity and quality of the plant resource that late arrivers encounter. First, early-arriving herbivores are predicted to reduce plant resources more rapidly at higher temperatures, increasing niche preemption. Second, when stronger top-down pressure from herbivores prompts an increase in the induction of plant defenses (Underwood 2000), late arrivers will feel the negative impacts of stronger niche modification. Despite the potential for higher temperatures to strengthen priority effects in plant-herbivore systems by systematically altering trophic dynamics, this hypothesis has yet to be explored empirically.

Temperature can also impact priority effects on a broader metacommunity scale if dispersal dynamics are temperature dependent, by altering the order in which species colonize resource patches or the length of time between colonization events by different species (O'Connor et al. 2007; Altermatt et al. 2008). Temperature-dependent dispersal emerges through a variety of mechanisms, from changes in per capita dispersal success to shifts in local dispersal cues (Travis et al. 2013). In herbivorous insects, for example, crowding and low resource quality can induce higher dispersal rates, as individuals leave in search of better habitat (Zera and Denno 1997; Benard and McCauley 2008). As a result, the temperature dependence of plant-herbivore interactions is expected to increase dispersal at higher temperatures by precipitating a decline in resource quantity and quality. When these temperature-induced shifts in dispersal change species' arrival order or increase the time between colonization by different species, they have the potential to alter priority effects at a regional scale. An integration of dispersal into research on priority effects would thus provide a more complete picture of how warming will change species interactions and coexistence in patchy landscapes.

We tested the effects of temperature on priority effects using two congeneric aphid species that specialize on milkweed: *Aphis nerii* and *Aphis asclepiadis*. The patchy distribution of milkweed plants causes the initiation of local aphid populations to be constrained by dispersal among plants, such that aphid species rarely arrive at a plant at the same time. These aphid species have high niche overlap (both feed exclusively on milkweed phloem), rapid popula-

tion growth rates that are sensitive to temperature (Agrawal et al. 2004), and can reach large population sizes capable of depleting their ephemeral plant resource to the point of death. Milkweed also has physical defenses that can be affected by aphid feeding, making priority effects through niche modification a potential determinant of competitive interactions (Agrawal 2004a; Woods et al. 2012). Finally, previous research has demonstrated that these two species are competitively unequal, and that priority effects may play a role in their ability to coexist. Compared to *A. asclepiadis*, *A. nerii* produces more offspring, has higher feeding rates, is more dispersive, is less affected by competition, and is preyed upon less (Mooney et al. 2008; Smith et al. 2008). However, *A. asclepiadis* can produce frost-tolerant eggs capable of overwintering in cold northern climates, whereas *A. nerii* is obligately parthenogenic and must disperse north from warmer overwintering sites each summer (Groeters 1989; Mooney et al. 2008). Although the arrival times of these species vary from year to year and across their shared range, earlier arrival could give *A. asclepiadis*, the putatively inferior competitor, an advantage that helps these two species coexist (Mooney et al. 2008).

In our experiment, we manipulated temperature and the order of arrival of aphid species to test hypotheses about four related processes that together shape the local and regional coexistence of two unequal competitors. We hypothesized that a stronger temperature dependence of insects relative to plants would result in several consequences of higher temperatures: (1) higher aphid population growth rates and lower aphid maximum population sizes; (2) a stronger, aphid-induced decline in both plant quantity (less growth and greater mortality) and quality (greater induction of defensive traits); (3) stronger priority effects, as early arrivers exert a stronger impact on milkweed; and (4) higher dispersal rates, as aphids leave to avoid low-resource conditions. We show that predictable consequences of temperature on herbivores and plants alter priority effects and dispersal rates to shape competitive outcomes. These results have broad implications for understanding the local and regional coexistence of competing species under climate change.

Methods

Natural History

Common milkweed *Asclepias syriaca* (hereafter milkweed) is a native perennial commonly found in old field habitats across eastern North America. Milkweed is chemically defended with neurotoxic cardenolides and physically defended with trichomes covering the leaf surface and latex that is expelled when leaves are damaged. Milkweed physical defenses (trichomes and latex) occur constitutively and can be induced by herbivory (Van Zandt and Agrawal 2004; Ali and

Agrawal 2014). As a result of its defenses, milkweed hosts only a small group of specialist herbivorous insects that includes two aphid congeners (*Aphis asclepiadis* and *Aphis nerii*) that feed on phloem and coexist on milkweed (Mooney et al. 2008; Smith et al. 2008). Both aphid species reproduce through parthenogenesis and produce both unwinged morphs that are largely sedentary and winged morphs capable of actively dispersing between plants, with winged morphs more readily produced in crowded conditions (Groeters 1989).

Experimental Setup

We grew milkweed plants from seed obtained from a commercial nursery (Prairie Moon Nursery, Winona, MN; detailed methods in the appendix, available online). We started aphid colonies from individuals collected from the Koffler Scientific Reserve (44°03'N, 79°53'W) and maintained colonies at room temperature (~21°C).

In two growth chambers, we conducted a 5-week experiment that crossed two temperatures (20.1° and 22.2°C mean daily temperature, described below) with five levels of competition and a control: (1) *A. nerii* alone, (2) *A. asclepiadis* alone, (3) both species added simultaneously, (4) both species with *A. nerii* added 2 weeks before *A. asclepiadis*, (5) both species with *A. asclepiadis* added 2 weeks before *A. nerii*, and (6) milkweed with no aphids as a control. This resulted in a total of 12 treatments, each replicated between eight and 11 times, for a total of 120 plants. We placed potted plants within cages to contain aphids (fig. A1; figs. A1–A3 are available online) and implemented our warming treatment at the individual plant level to avoid chamber effects. To raise the temperature of our warmed cages, we used 50-W light bulbs painted black (so that heat but not light was emitted), and we left the light bulbs unplugged in our cool treatment (fig. A1). To quantify dispersal, we secured a 10 × 12.5-cm yellow sticky card (Plant Products, Ancaster, Ontario) at the end of the cage opposite the plant (approximately 45 cm away from the plant) to catch dispersing aphids. Throughout the experiment, we monitored the temperature and humidity inside cages and the soil moisture in potted plants (see appendix). Warming increased the temperature by an average of 2.1°C (from 20.1° to 22.2°C mean daily temperatures; fig. A2). These temperatures are well below the critical thresholds, often called optimal temperatures (e.g., Dell et al. 2011), for our species (El Din 1976; Agrawal et al. 2004) and were selected because they approximate both interannual temperature fluctuations at our field site and the projected temperature increase under climate change (IPCC 2014; see appendix).

In treatments with a single species, we added six adult individuals of that species on day 1 of the experiment. In treatments that had species arriving together, three individ-

uals each of *A. nerii* and *A. asclepiadis* were added on day 1 of the experiment. For each of the priority treatments, we added three individuals of the early-arriving species to the plant on day 1 of the experiment and added three individuals of the late-arriving species on day 14; this 2-week lag was selected to approximate typical lags in colonization of a given plant between these species and corresponds to the amount of time required for these species to begin increasing the production of winged individuals in a population (see Results). All treatments (except no-aphid controls) therefore had six aphids added in total. One day after each aphid population was introduced to its experimental unit, we replaced any aphids that had died overnight or had become winged adults and removed any nymphs produced overnight. We did this because the aphids we added were sometimes damaged by handling, were gravid, or were in the early undetectable stages of wing development, and we wanted to ensure that all added aphids were healthy unwinged adults.

Plant and Aphid Responses

We measured the impact of aphids and temperature on the following plant responses: growth, mortality, trichome density, and latex production (see appendix). To quantify plant growth and latex production, we measured the change in plant height (Agrawal 2004b) or latex exudation by first measuring these responses 1 day before the experiment started and then repeating measurements 3 weeks into the experiment (on day 21), when 98% of the plants were still alive. We also measured trichome density on leaf tips 3 weeks into the experiment. We quantified plant mortality as whether plants died (>50% of leaves senesced) by the end of the experiment. Plant mortality was assumed to be herbivore induced, as all but one of the control plants (no aphids added) remained healthy throughout the experiment and did not lose any leaves.

To quantify aphid population dynamics, we counted all aphids on each plant and recorded the number of winged and unwinged individuals twice a week, for a total of 10 surveys. To get an indirect measure of long-distance dispersal potential, we counted the number of winged individuals on each plant. To get a direct measure of short-distance dispersal, we photographed the sticky card in each cage at each survey and later counted the number of individuals of each species that had landed on the card between each survey point. Because cards remained in the cages throughout the experiment and were not replaced, and aphids decayed and turned black within a few days of landing on the cards, the two species were indistinguishable when both occurred on the same card. We therefore restricted our measurement of dispersal to treatments in which each species was alone (see

detailed methods in the appendix). We ran the experiment for 5 weeks, which is roughly the length of time that our two aphid species interact during a growing season.

Statistical Analysis

To determine the impact of temperature on aphids (hypothesis 1), we analyzed the effect of temperature on the population growth rates and maximum population size of each species when grown alone (in the absence of interspecific competition). For these analyses, we used only single-species treatments, which all had starting densities of six aphids, as other treatments could be influenced by their lower starting conspecific density. Aphid populations in our analyses include all aphids of a single species on one plant (experimental unit) and do not include dispersed individuals (as species could not be distinguished in interspecific competition treatments). To determine the effect of temperature on the population growth rates of each species, we constructed a four-parameter logistic model with a fixed lower asymptote (the other parameters were the upper asymptote, midpoint, and scale), using the *nlme* function, with replicate included as a random effect in a random-slope, random-intercept analysis. We fixed the lower asymptote of our models at the initial population size of six aphids (the number of aphids initially added to each plant) and truncated the data for each plant to include all sampling times up to and including the population maximum to avoid modeling the subsequent population decline. We corrected for heteroscedasticity in the error term by using the weights function to scale the error with the sample date and by allowing this scaling to differ between temperature treatments. The inverse of the scale parameter of the logistic model describes the steepness of the curve at the inflection point and corresponds to the population growth rate in the absence of density dependence (Paine et al. 2012). For this analysis, parameter estimates for *A. asclepiadis* depended on the starting values for the parameters. We therefore used the starting values that led to the closest match between the observed data (numbers through time and maximum population size) but note that varying the starting values did not qualitatively change our results.

We calculated maximum population size as the maximum number of aphids reached in each population and determined the date at which each population peaked. We ran separate linear models for each species, with temperature as the predictor variable and log maximum population size or date of population peak as the response variable.

To test the impact of temperature and aphids on plants (hypothesis 2), we analyzed the effect of temperature and aphid population size on two plant responses indicative of resource quantity (plant growth and death) and two re-

sponses indicative of plant quality (latex exudation and trichome density). For all plant analyses, population size was the maximum number of aphids reached on a plant, with all individuals from both species summed. For this analysis, our goal was to test the impact of aphid abundances and warming on milkweed responses, as per our hypotheses, rather than focus on the effects of our competitive treatments (i.e., arrival order and aphid species identity) on plant responses. Additionally, because aphid abundances were also affected by competitive treatment, plants within competitive treatments were not independent for this measure. For these reasons, we analyzed plant responses using the mean values of aphid maximum population size for each of our 12 treatments as our aphid predictor and the mean values of our plant responses for each treatment as our response. We used separate linear models to analyze plant growth, latex, and log (trichomes), with temperature and aphid population size as the predictor variables. We used a binomial generalized linear model (GLM) to analyze plant survival, with temperature and aphid population size as the predictor variables and mortality by the end of the experiment as a binary response variable. We also ran planned post hoc comparisons on control plants (without aphids) to assess the effect of warming on plant responses in the absence of aphids and determine whether observed warming effects on plant responses were direct effects or were driven by aphid feeding.

To determine whether priority effects were present and whether they were influenced by warming (hypothesis 3), we analyzed the effect of temperature and arrival order on the maximum population size and population persistence of each aphid species separately. For each species, we included all six multispecies treatments: three levels of arrival order (arrived 2 weeks before its competitor [early], at the same time [same time], or 2 weeks after its competitor [late]) crossed with two temperature levels (cool and warm). Although early and late treatments had lower initial densities (three aphids of one species added on the first day and three aphids of the other species added 2 weeks later) than the same-time treatment (three aphids of each species added on the first day), our aphid responses (maximum population size and population persistence) were selected to be insensitive to small differences in starting densities. For maximum population size, we used linear models with temperature and arrival order as predictor variables and the log of the maximum population size reached by that population as the response variable. For *A. asclepiadis* population persistence, we used a binomial GLM with temperature and arrival order as predictors and persistence (whether that population declined to 0 by the end of the experiment) as a binary response (see appendix). We did not analyze *A. nerii* persistence, as all populations persisted until plant death or the end of the experiment.

To specifically test whether higher temperatures strengthen priority effects, we ran two additional analyses. We were interested in additive and interactive effects of temperature and arrival order; however, because persistence was analyzed with a logistic regression that estimates log odds ratios and the maximum population size analysis was log transformed, interactive effects cannot be quantified using the linear model and binomial GLM described above. We therefore performed a planned comparison of persistence in early- and late-arrival treatments across our two temperatures on a linear scale, testing solely for an interaction between temperature and arrival order. For this analysis, we used a generalized least squares (gls function in the nlme package) model, with a separate variance fitted for each treatment combination using the weights function.

To test whether dispersal rates depend on temperature (hypothesis 4), we analyzed the effect of temperature on the proportion of winged individuals and per capita dispersal to sticky cards in single-species treatments over the course of the entire experiment. We used binomial GLMs, with temperature and time (survey date) as predictor variables, winged/unwinged or dispersed/not dispersed as binary response variables, and plant as a random factor. We included both time and time squared (with time centered at zero) in the models to allow the model to capture nonlinear trends in dispersal over time.

We included chamber in all analyses, and as we found no significant effects of chamber, we do not report these results. For all analyses, we started with the most complex models and dropped all nonsignificant higher-order interactions. All statistical analyses were performed in R (version 3.0.3). All data used in our analyses are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3qn05> (Grainger et al. 2017).

Results

Hypothesis 1: The Impact of Temperature on Aphids

In single-species treatments, *Aphis nerii* had higher growth rates and reached higher maximum population sizes than *Aphis asclepiadis* (fig. 1) and warming advanced population peaks by ~11 days for *A. asclepiadis* ($F_{1,18} = 11.26$, $P = .003$; fig. 1A) and ~6 days for *A. nerii* ($F_{1,18} = 13.40$, $P = .002$; fig. 1B). Warming increased population growth rates for *A. nerii* ($F_{1,84} = 8.91$, $P = .0037$; fig. 1C) but had no effect on *A. asclepiadis* growth rates ($F_{1,117} = 1.57$, $P = .21$; fig. 1D). As predicted, maximum population sizes were lower under warmed conditions for both species (*A. nerii*: $F_{1,17} = 11.37$, $P = .004$; *A. asclepiadis*: $F_{1,18} = 7.66$, $P = .013$; fig. 1E, 1F). Although most aphid populations (87% for each species) peaked before the experiment ended (fig. 1A, 1B; growth curves for all treatments in fig. A3), four out of 10 *A. asclepiadis* populations in cool conditions were still increasing

at the end of the experiment. Therefore, both the timing of these population peaks and the maximum population sizes would have been higher if the experiment had continued longer, and our results likely underestimate the impact of warming on these measures for *A. asclepiadis*.

Hypothesis 2: The Impact of Temperature and Aphids on Milkweed Plants

Across treatments, plant growth was negatively associated with aphid abundances ($F_{1,9} = 5.95$, $P = .037$) but was not affected by temperature ($F_{1,9} = 0.13$, $P = .72$; fig. 2A). More than one-third of plants (44 out of 120) died, and plant mortality increased with aphid abundance ($F_{1,9} = 12.21$, $P = .007$) and warming ($F_{1,9} = 11.22$, $P = .008$; fig. 2B). There was no effect of warming on mortality for control plants ($P > .05$), indicating that aphids killed plants and that this effect was intensified at higher temperatures (fig. 2B). Trichome density increased with aphid abundance ($F_{1,9} = 6.62$, $P = .030$) and warming ($F_{1,9} = 12.76$, $P = .006$), and there was no effect of warming on trichomes for control plants ($P > .05$), indicating that the increased trichome production with warming was contingent on the presence of aphids (fig. 2C). Although latex was unaffected by aphid abundances ($F_{1,9} = 1.07$, $P = .34$) or temperature ($F_{1,9} = 1.56$, $P = .24$), in no-aphid control plants the change in latex exudation was higher in warm (1.10 ± 0.46 mg, 95% confidence interval [CI]) than cool (0.12 ± 0.39 mg, 95% CI) conditions, indicating that warming increased latex exudation in the absence of aphids (fig. 2D).

Hypothesis 3: The Impact of Temperature on Priority Effects

In multispecies treatments, the maximum population size reached by *A. nerii* depended on temperature ($F_{1,53} = 6.52$, $P = .013$) and arrival order ($F_{2,53} = 4.47$, $P = .016$), with the smallest populations occurring in warmed and late-arrival conditions (figs. 3A, A3). However, post hoc contrasts showed that there was no interaction between temperature and arrival order for *A. nerii* maximum population size ($P = .80$; table A1, available online; fig. 3A), indicating that temperature did not alter the impact of priority effects on maximum population size for this species. Arrival order ($F_{2,53} = 20.24$, $P < .001$), but not temperature ($F_{1,53} = 2.05$, $P = .16$), affected the maximum population size reached by *A. asclepiadis*; early arrival resulted in larger maximum population sizes (fig. 3B), and there was a marginal interaction between temperature and arrival order for *A. asclepiadis* ($P = .053$; table A1; fig. 3B). Given the number of statistical comparisons performed, we do not further interpret this marginally significant interaction.

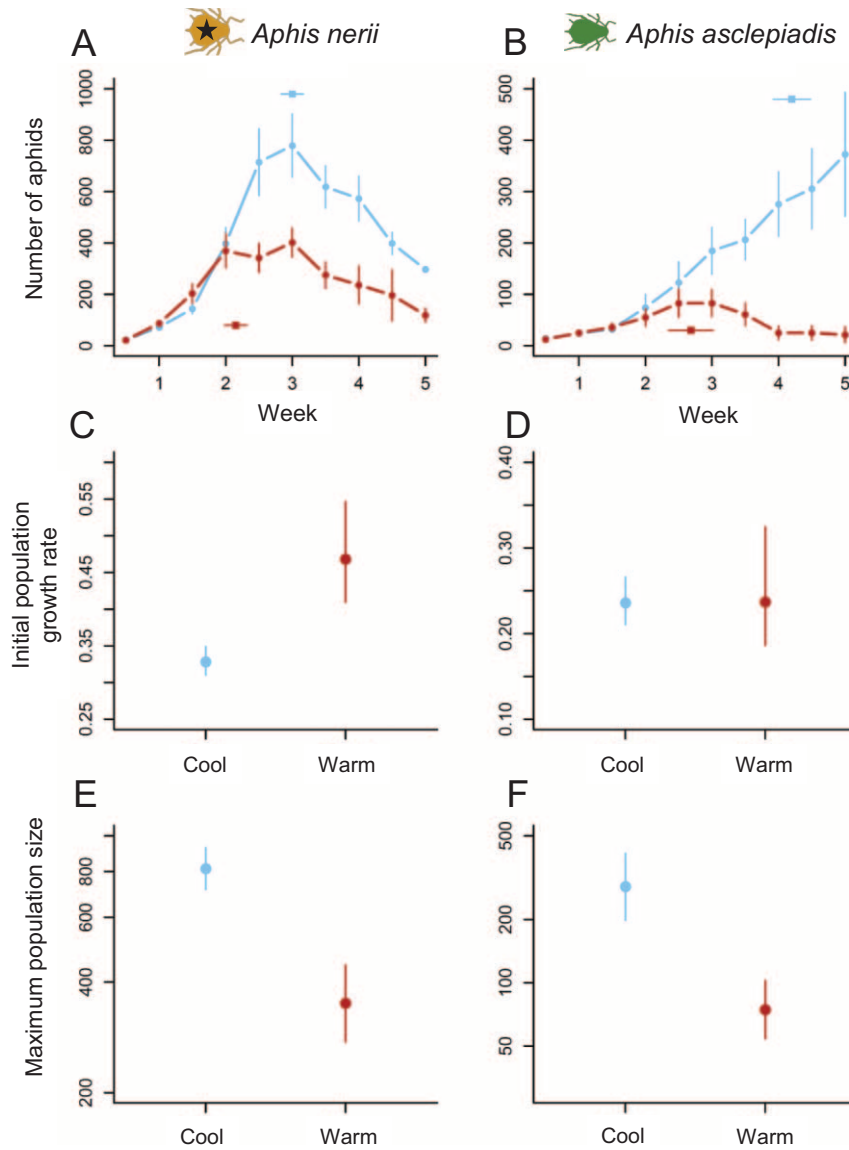


Figure 1: Impact of temperature on aphid populations. *A, B*, Aphid abundances throughout the experiment when species were grown with no interspecific competition (circles with vertical error bars) and the mean date at which populations peaked within each treatment (squares with horizontal error bars). *C, D*, Population growth rates in the absence of density dependence, estimated as the slope at the inflection point in a four-parameter logistic model (see Methods). *E, F*, Maximum population size reached in each treatment. Cool treatments are shown in light blue, and warm treatments are shown in dark red. The black star on *Aphis nerii* indicates that this species is the superior competitor. Data points are mean values \pm 1 SE. Note the smaller scale for *Aphis asclepiadis* and the log scale for maximum population sizes.

Temperature did alter the impact of priority on population persistence. While all *A. nerii* populations persisted (fig. 3C), many *A. asclepiadis* populations declined to extinction, with extinction rates impacted by both temperature ($\chi^2 = 17.65$, $df = 1$, $P < .001$) and arrival order ($\chi^2 = 17.84$, $df = 2$, $P < .001$; fig. 3D). Planned post hoc contrasts (see Methods) revealed an interactive effect of arrival order and temperature on *A. asclepiadis* extinction; in the warm treatment, persistence declined by 80% in late-

versus early-arrival treatments, whereas in the cool treatment it declined by only 22% ($P = .003$; table A1; fig. 3D).

Hypothesis 4: The Impact of Temperature on Dispersal

For *A. nerii* grown alone, both the proportion of winged individuals and per capita dispersal had negative coefficients for the squared effect of time (both $P < .001$; all winged and

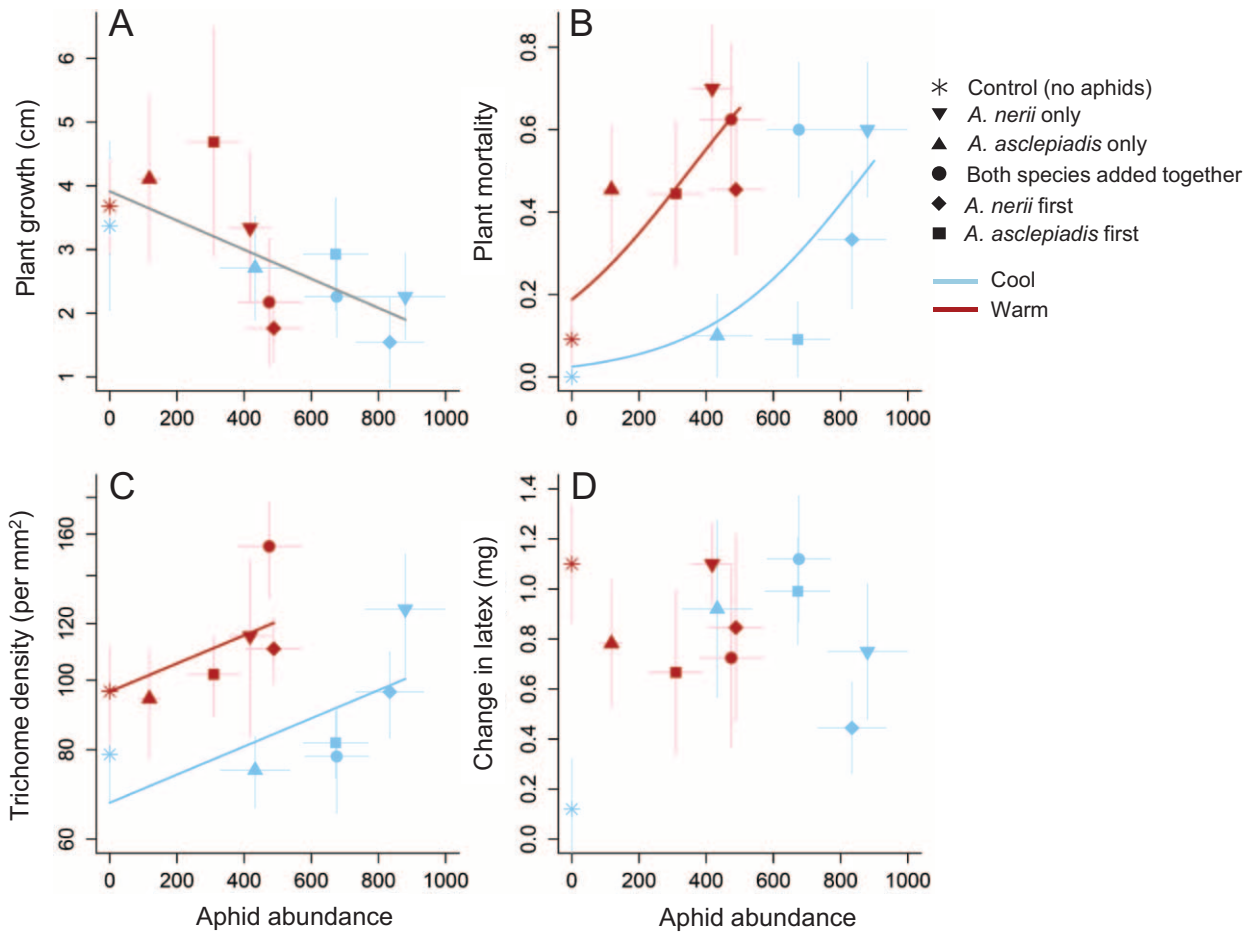


Figure 2: Impact of temperature and aphids on milkweed plants. *A*, Plant growth (change in height between the first and twenty-first day of the experiment). *B*, Plant mortality (the proportion of plants that died before the end of the experiment). *C*, Trichome density at 3 weeks. *D*, Change in latex production (difference in exudation between the first and twenty-first day of the experiment). Cool treatments are shown in light blue, and warm treatments are shown in dark red. Aphid abundance in all panels is the mean of the maximum number of aphids reached per plant in a treatment (both aphid species combined when both species were present). The gray line of best fit in *A* indicates that only aphid abundance had a significant effect on plant growth. No significant trends were found for latex (*D*). Data points are mean values for each treatment \pm 1 SE. Note the log scale for trichomes (*C*).

dispersal $df = 1$), indicating that both measures had non-linear responses and that both reached maxima prior to the end of the experiment (fig. 4A, 4C). There was also a time by temperature interaction for both responses (proportion of winged individuals $P = .011$; per capita dispersal $P < .001$); in warmed conditions, both responses increased more rapidly and plateaued sooner, resulting in overall higher mean levels of dispersal in the second half of the experiment (fig. 4A, 4C).

For *A. asclepiadis* grown alone, the proportion of winged individuals and dispersal increased over time (both $P < .001$; fig. 4B, 4D). Temperature altered the trend for *A. asclepiadis* winged individuals, as toward the end of the experiment the proportion of winged individuals increased, but only in cool conditions (temperature \times time squared; $P <$

.001; fig. 4B). There was also a rise in *A. asclepiadis* dispersal rate in the second half of the experiment, as indicated by a positive coefficient for the squared effect of time ($P < .001$; fig. 4D), but temperature did not alter this effect.

Discussion

Our study demonstrates that temperature can strengthen priority effects among competing herbivores by changing how these herbivores impact their plant resource. We predicted that temperature would alter competitive dynamics in this system through four distinct pathways, and found support for all four of our hypotheses. Higher temperatures caused populations of both species to peak earlier and reach lower maximum sizes (fig. 1), as predicted if warming causes

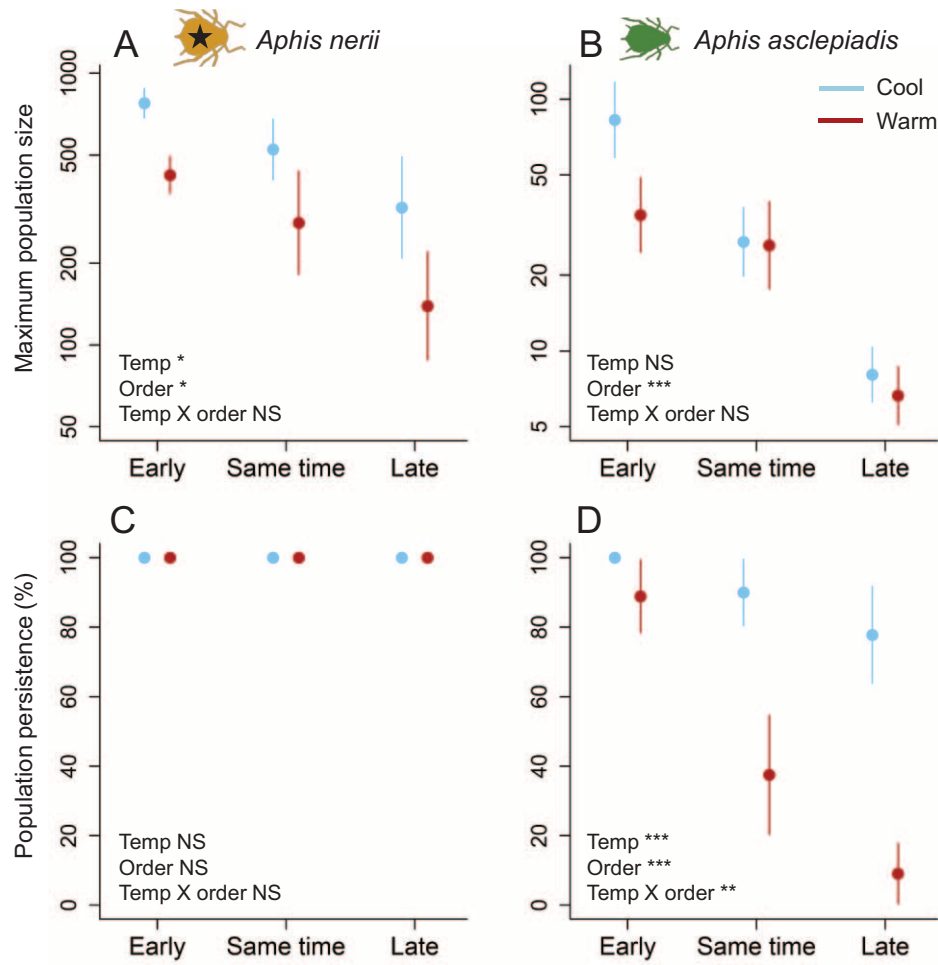


Figure 3: Impact of temperature and arrival order on aphid populations. Maximum population size (A, B) and proportion of aphid populations that persisted until the plant died (C, D) for each species when grown in competition with the other species. Each species was added 2 weeks before its competitor (early), at the same time as its competitor (same time), or 2 weeks after its competitor (late). Model results shown represent P values from linear models (for temperature and arrival order effects) or planned post hoc comparisons (for the interaction between temperature and arrival order), with significance indicated as one asterisk for $P < .05$, two asterisks for $P < .01$, three asterisks for $P < .001$, and NS for not significant (see Methods). Cool treatments are shown in light blue, and warm treatments are shown in dark red. The black star on *Aphis nerii* indicates that this species is the superior competitor. Data points are mean values \pm 1 SE. Note the log scale for maximum population size (A, B).

herbivores to exert stronger top-down pressure that lowers their carrying capacities. Our plant responses show a greater per capita impact of aphids at higher temperatures on both resource quantity (plant mortality) and quality (trichomes; fig. 2). This decline in resources at higher temperatures was associated with a stronger effect of arrival order on the population persistence of the weaker competitor (*Aphis asclepiadis*), with early arrival increasing persistence much more at high temperatures than at low temperatures (80% vs. 22%; fig. 3D). Warming also increased the dispersal rate of *Aphis nerii* but not *A. asclepiadis*, indicating that the temperature could alter the relative dispersal rates of these two species and thus their arrival order at a local site (fig. 4). Taken to-

gether, these results demonstrate that even in a simple three-species system, temperature can simultaneously disrupt multiple processes that span spatial and temporal scales and together determine local and regional coexistence.

The most pronounced effect of temperature and arrival timing on herbivore dynamics was the increased extinction rate of *A. asclepiadis* when it arrived late in warmer conditions (fig. 3D). The greater disadvantage of late arrival for *A. asclepiadis* compared to *A. nerii* indicates that when competition is asymmetric, the inferior competitor may rely more on arriving first. This supports classic priority effects research showing that a competitively inferior species of fly was able to persist only when it arrived before its competitor (Shor-

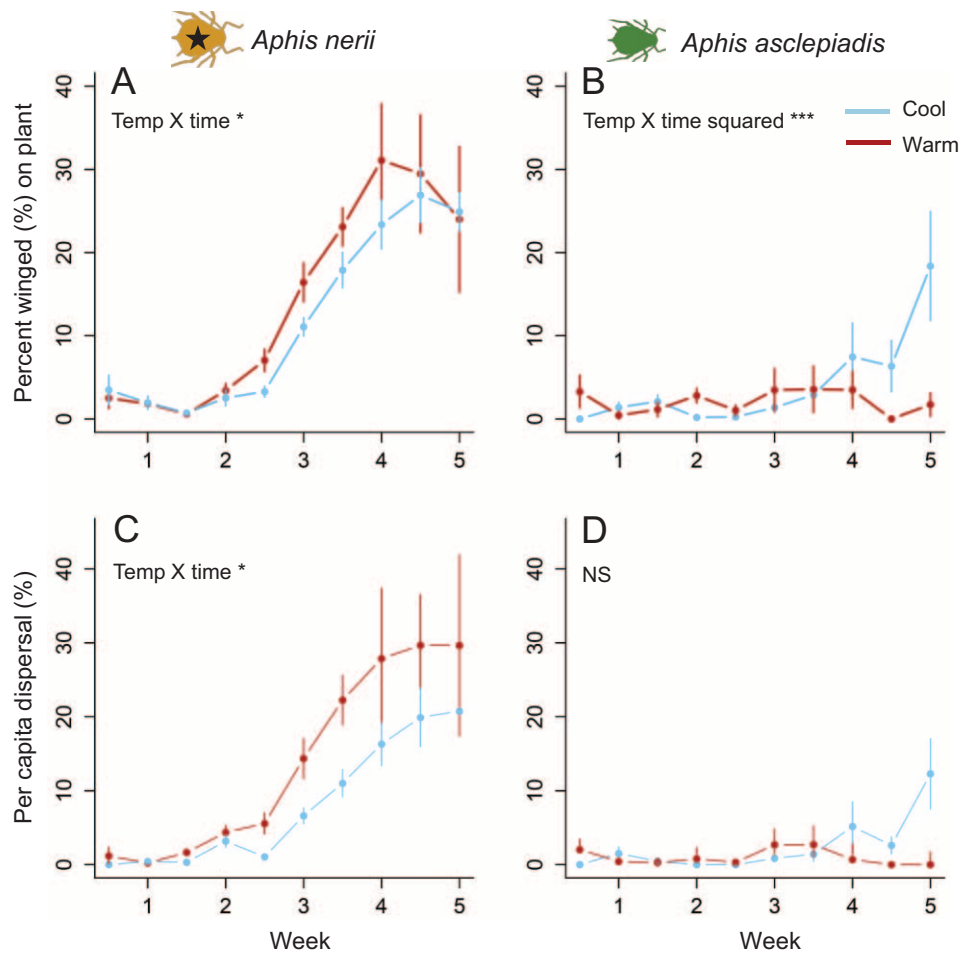


Figure 4: Impact of temperature on aphid dispersal. A, B, Proportion of aphids with wings at each survey. C, D, Proportion of individuals of each species newly dispersed to sticky cards since the previous survey. Significance of the temperature effect is indicated as one asterisk for $P < .05$, two asterisks for $P < .01$, three asterisks for $P < .001$, and NS for not significant. Cool treatments are shown in light blue, and warm treatments are shown in dark red. The black star on *Aphis nerii* indicates that this species is the superior competitor. Data points are mean values ± 1 SE.

rocks and Bingley 1994) and more recent work demonstrating how native plants can be suppressed to local extinction when exotic grasses germinate earlier in the growing season and deplete shared resources (Wainwright et al. 2012). These pronounced priority effects that shape community assembly are most likely to occur whenever ecologically similar species compete strongly for a shared and limited resource (Fukami 2015), as was the case in our study and in many documented cases of priority effects (Alford and Wilbur 1985; Peay et al. 2012; Vannette and Fukami 2014; Cleland et al. 2015). In addition, the stronger growth response of the dominant competitor to warming that we observed (fig. 1C, 1D) may be common to other systems if fast-growing species tend to have higher optimal temperatures (Frazier et al. 2006) or are able to respond more rapidly to increased temperatures (Walker et al. 2006). Whenever warm-

ing intensifies competitive asymmetries, the weaker competitor could become increasingly dependent on priority effects to persist. A formal examination of the link between temperature responsiveness and competitive rank across ecosystems would provide valuable predictive insights into how these dynamics will play out as the climate warms.

Higher temperatures increase herbivore vital rates more than producer vital rates across a range of taxa (Dell et al. 2011), which has been shown both theoretically (Gilbert et al. 2014) and empirically (O'Connor et al. 2009) to result in increased top-down pressure on primary producers. We predicted that this different temperature response of plants and insects would exacerbate the impact of aphids on milkweed plants and result in more pronounced priority effects at higher temperatures (O'Connor et al. 2011; Fukami 2015). Indeed, we found that warming strengthened the im-

fact of aphids on plant mortality and trichomes (fig. 2). The high levels of mortality experienced by plants with aphids but not control plants demonstrates the strong top-down pressure that herbivores can exert on their plant resources (fig. 2B). The compounding effect that warming had on aphid-induced declines in plant longevity was likely a major driver of the lower population sizes and increased intensity of priority effects that we observed in warmed treatments (figs. 1, 3). Likewise, trichome density increased at higher temperatures for plants with aphids but not control plants, indicating that warming can amplify the induction of defenses (fig. 2C). This greater induction of defenses may be a general indirect response to warming that results from greater impacts of herbivores on their hosts (Underwood 2000). When considered together, the temperature dependence of plant-herbivore interactions and the well-known impact of early-season herbivory on late-season herbivore performance in a variety of systems, including maize (Erb et al. 2011) and *Brassica* (Li et al. 2014), suggest that the strengthening of priority effects at higher temperatures via stronger niche preemption and niche modification could be widespread. This could have broad implications for herbivore coexistence under climate change if warming increases the ability of early-season herbivores to impede the establishment and persistence of later-season competitors (Jamieson et al. 2012).

Priority effects frequently occur in metacommunities where limited dispersal leads to species arriving at different times, yet most studies of priority effects do not explicitly consider dispersal dynamics (Grainger and Gilbert 2016). Temperature can have direct and indirect effects on dispersal rates that could alter arrival times and scale up to impact metacommunity dynamics (Gilbert and O'Connor 2013; Travis et al. 2013). Species likely to have temperature-dependent dispersal rates include those that disperse in a life stage whose length or timing is altered by warming (e.g., marine plankton; O'Connor et al. 2007), that require a critical temperature threshold for flight (e.g., winged insects; Battisti et al. 2006), that undergo shifts in body size as temperatures change (e.g., reptiles; Kingsolver and Huey 2008), or that have physiological dispersal responses to changes in local environmental conditions (e.g., wing-dimorphic insects; Zera and Denno 1997). We predicted that warming would increase aphid dispersal rates due to declining resources (Dixon 1977) and used a direct measure of short-distance dispersal as well as the production of winged individuals as a proxy for long-distance dispersal potential to test this prediction (fig. 4). These two measures of dispersal responded nearly identically to temperature, with warming increasing the propensity for short-distance dispersal and the production of winged individuals in *A. nerii* only (fig. 4). The dispersal responses of *A. nerii* were likely driven by declining resources (Dixon 1977; Müller et al. 2001) and not crowding, as warmed plants had higher

dispersal but lower densities (figs. 1, 4). The observation that the *A. asclepiadis* dispersal rate did not increase with warming (fig. 4), despite lower resource quantity and quality in warmed conditions (fig. 2B, 2C), demonstrates the species-specific nature of dispersal responses to temperature (Travis et al. 2013) and indicates that warming could shift relative arrival times on individual plants. Modeling or empirical work that tests how the effects of warming on local interactions and dispersal scale up to determine regional coexistence across a landscape of habitat patches will be essential to fully understand the impact of temperature on coexistence across spatial scales.

At a broader spatial scale, increasing temperatures are likely to advance both the spring emergence date of *A. asclepiadis* and the date at which temperatures are high enough to allow *A. nerii* to disperse northward (Bale et al. 2002). Likewise, the range limits of all three species may advance northward as the climate warms (Parmesan and Yohe 2003). For example, a shift in the winter range of *A. nerii* could be particularly rapid if warmer winter temperatures permit overwintering farther north within milkweed's current range. In this and other systems, northward range shifts or advancing phenologies that allow a dominant competitor to arrive earlier in the growing season could reduce or eliminate seasonal priority effects that are essential for the persistence of weaker competitors (Wainwright et al. 2012). Indeed, because shifts in phenologies (emergence date, migration date) and winter and summer ranges are unlikely to be completely synchronized across competing species, seasonal arrival orders could be disrupted in many systems, with resulting breakdowns in the advantages associated with early arrival (Yang and Rudolf 2010; Cook et al. 2012).

While both our plant and aphid results are consistent with theory describing the temperature dependence of trophic interactions, two aspects of our study system should be considered carefully when interpreting our results within this theoretical framework. First, temperature change may cause physiological plant responses not captured by our measured responses and not addressed by theory focused primarily on temperature-induced changes to growth and feeding rates. For example, increased physiological stress on plants precipitated by aphid feeding at higher temperatures could have contributed to plant declines with warming, independent of any temperature-induced changes to aphid growth or feeding rates (Jamieson et al. 2012). Likewise, the mechanisms through which aphids induce and respond to trichomes remain unresolved, and increased trichome density in warm conditions may have also impacted aphid performance (Levin 1973; Agrawal 2004a, 2005).

Second, even when the predicted asymmetries in plant and herbivore temperature sensitivities occur, the theory we consider can give rise to different outcomes when inter-

actions with other trophic levels or greater numbers of species are considered. For example, differences in plant versus herbivore growth rates may depend on the temperature sensitivity of plant nutrient resources, which can be driven by soil microbes and standing stocks of organic matter (O'Connor et al. 2011; Gilbert et al. 2014). In our experiment, we supplied a limited and controlled amount of soil nutrients to avoid confounding plant-herbivore dynamics, which may explain why plant growth did not respond to warming (fig. 2A; Walker et al. 2006). Field studies may benefit from explicit tracking of soil nutrient dynamics, as differences among biogeographical regions are expected (Melillo et al. 1993; Delgado-Baquerizo et al. 2013) and may lead to predictable differences in plant-herbivore responses to warming (O'Connor et al. 2011). Similarly, more complex communities could experience outcomes that differ from the responses to pairwise competition observed here—for example, as a result of higher-order interactions (Levine et al. 2017; Mayfield and Stouffer 2017). Nonetheless, priority effects are predicted to be especially pronounced in diverse communities (Fukami 2015) and have been shown to be a key determinant of community assembly in a variety of more speciose systems, including terrestrial plants (Fargione et al. 2003; Cleland et al. 2015), mycorrhizal fungi (Kennedy et al. 2009), nectar microbes (Vannette and Fukami 2014), and marine invertebrates (Petraitis and Latham 1999). Even in these more complex systems, early-arriving species can determine the success of late arrivers, suggesting that the outcomes observed in our simplified system may apply more broadly. Our results therefore suggest that in the many systems in which priority effects shape ecological communities, the negative outcomes associated with late arrival could be exacerbated by warming.

In this study, we demonstrated how even a few degrees change in temperature alters plant-herbivore interactions, the importance of arrival time, and dispersal, thus revealing novel links across space and time in the responses of ecological communities to climate change. Our study builds on the results of recent experiments that have demonstrated how temperature can alter the impact of arrival time on competitive outcomes in tadpoles (Rudolf and Singh 2013) and microbes (Clements et al. 2013; Tucker and Fukami 2014), by linking the known temperature dependencies of trophic interactions and dispersal to priority effects. In doing so, we show how predictable responses to warming across trophic levels and spatial scales can generate substantial shifts in competitive outcomes. Rudolf and Singh (2013) illustrated how higher temperatures alter size-mediated competitive interactions and strengthen the impact of hatching order in amphibians, which may be a general phenomenon because of the relationship between temperature and development time (Yang and Rudolf 2010). Our work

likewise suggests that the impact of temperature on resource-mediated competitive interactions that results in stronger priority effects may be a general response caused by the asymmetrical response of plants and herbivores to temperature. Although it is well understood that simply assessing individual species' responses to warming tells an incomplete story of how species will fare under climate change, the complex spatial and temporal dimensions of species interactions have yet to be well incorporated into our understanding of climate change impacts (Gilbert and O'Connor 2013; Wolkovich et al. 2014). Our study provides a starting point for incorporating spatial and temporal shifts in species interactions that are influenced by temperature and suggests a way forward for better understanding the impacts of climate change in patchy ecosystems.

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Oleander aphid (*Aphis nerii*) feeding on common milkweed (*Asclepias syriaca*). Photo credit: Adam Rego.