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ORIGINAL RESEARCH

Heat waves reduce variability in milkweed development, simplify arthropod communities, and suppress herbivory

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Abstract
The frequency and intensity of heat waves are on the rise due to climate change. Heat waves are temporally discrete, and thus occur at different stages of plant development. Yet, compared with mean temperature, little is known about how the timing of extreme heat events interacts with the timing of plant development. In this study, we varied the timing of experimental heat waves applied to common milkweed (*Asclepias syriaca*) to determine how heat waves timing impacts plant developmental timing and subsequent plant–arthropod interactions. We found that heat waves delay and synchronize plant development, and that these effects are particularly strong for early season heat waves. Heat wave-exposed plants also supported fewer species of arthropods and experienced less chewing herbivory than ambient-temperature controls. Our study reveals that the relationship between extreme event timing and plant developmental timing will shape how increasing prevalence of extreme heat events impacts plant–arthropod communities.

Keywords *Asclepias syriaca* · Climate change · Extreme climate event · Herbivory · Phenology · Temporal ecology

Introduction

Shifting organismal phenology is a hallmark of climate change. A large body of ecological research confirms that increases in the mean temperature experienced by plants can alter the mean timing of plant development, with consequences for species interactions (Wolkovich et al. 2014). Mean developmental timing is, however, only one component of phenology. Another important component of phenology is the variability of developmental timing among individuals in a population (Cope et al. 2022). In any given population, individuals inevitably vary in the timing of developmental stages, such as emergence, budbreak, and flowering; this variability can stem from, for example, individuals' genotype (Barker et al. 2018), microsite conditions (Jackson 1966), or maternal effects (Donohue 2009). Within-population timing variability has been linked to pollination success (Schmitt 1983; English-Loeb and Karban 1992; Ollerton and Lack 1998), plant-associated community diversity (Johnson and Agrawal 2005; Johnson et al. 2006), and herbivore pressure (Ekholm et al. 2020).

Compared with mean developmental timing, less is known about how variability in developmental timing among individuals will respond to climate change. Preliminary studies of tree flowering phenology indicate that higher mean temperatures in spring can lead to greater developmental asynchrony among (Rivest et al. 2021) and within (Bogdziewicz et al. 2020) populations, by spreading out developmental events across a longer growing season and thus reducing the chance that individuals' development overlaps. Due to the time-sensitivity and reproductive implications of pollination, flowering phenology is likely under greater selection for synchrony than other developmental stages. Therefore, vegetative developmental timing may or may not follow the same pattern.

Although research at the intersection of climate change and organismal development has focused on elevated mean temperatures, temperature extremes are also increasing over time. Extreme climate events like heat waves are becoming both

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more frequent and more intense (Fischer and Knutti 2015), with sometimes disastrous ecological consequences (Maxwell et al. 2019). For example, heat waves can negatively impact survival and fecundity of both plants (Orsenigo et al. 2015; Jagadish et al. 2021) and plant-associated insects (Sentis et al. 2013; Hemberger et al. 2023; Melone et al. 2024). The temporally discrete nature of extreme climate events means that they only directly affect plants at one particular point of their development (Cinto Mejía and Wetzel 2023), and may have differential effects depending on the event timing due to developmental changes in stress tolerance (Cope et al. 2023; Grossman 2023). Impacts of heat waves and their timing on developmental timing and developmental variability are currently unknown.

Understanding the sources of developmental variability within plant populations is critical to understanding intraspecific diversity and its wide-ranging effects. Population-level trait diversity in plants is responsible for supporting plant-associated community diversity and ecosystem functioning (Westerband et al. 2021). Plants go through drastic trait changes over the course of development (Barton and Koricheva 2010; Cope et al. 2019; Henn and Damschen 2021), and thus, the developmental composition of a population is likely to be a major source of trait variability (Cope et al. 2022). Alteration of plant developmental variability is an under-studied mechanism by which climate change and extreme climate events may impact the structure and function of terrestrial ecosystems (Cope et al. 2023).

We examined the effect of extreme climate events on plant developmental variability and arthropod community patterns using a temporally explicit, variability-conscious approach. We conducted experimental heat waves with three different seasonal timings to address the question of how extreme heat events interact with plant developmental timing to influence the population-level mean and coefficient of variation for both plant traits and arthropod community metrics. Based on available results from studies of elevated mean temperatures, we predicted that heat waves would increase developmental variability among plants. We predicted that this increase in developmental variability would then lead to higher trait diversity and greater plant-associated arthropod richness in populations where plants experienced a heat wave. We also predicted that heat wave effects would depend on the timing of the event, because physiological heat sensitivity varies with ontogeny (Cope et al. 2023; Cinto Mejía and Wetzel 2023); specifically, we predicted that plants would be more susceptible to heat wave effects earlier in the season (Jentsch et al. 2007; Jagadish et al. 2021).

Methods

We constructed an experimental common garden of common milkweed (*Asclepias syriaca*) at Michigan State University's Kellogg Biological Station (South Gull Lake, MI, USA) using rhizome from a natural population at the University of Michigan Biological Station (Pellston, MI, USA). The common garden consisted of 6 randomized complete block plots, each containing 40 milkweed individuals with the same genetic composition (4 treatments × 10 genets). Individual rhizome pieces were 20 cm long, planted 15 cm deep, with 2 m spacing between individuals and blocks. Planting occurred in October 2020, plants overwintered underground, and the experiment began in May 2021.

Our four treatment groups included an ambient-temperature control group and experimental heat waves at three different time points: May 25–28, June 14–17, and July 6–9. Heat wave timing affected the proportion of plants that experienced the heat before they emerged aboveground vs. after ($F_{2,15} = 9.77$, $p = 0.002$; Fig. S1B). During the May heat wave treatment, 93% of plants were pre-emergence, compared with 67% in June and 44% in July. Treatment groups did not differ significantly in emergence timing ($X^2_3 = 4.5$, $p = 0.21$; Fig. S1A).

Each heat wave treatment consisted of one 60-h experimental heat wave applied simultaneously to individual plants using portable in-field heating chambers constructed with greenhouse film and 300 W infrared heaters (Fig. S5). Adding infrared heaters to the passive heating provided by greenhouse film allows for nighttime heating, which is typical of heat wave events (De Boeck et al. 2010). The 60-h duration was chosen based on similarity to past heat events at the field site (Robertson 2020). Heaters were turned on from a common electrical switch at night and when the sun was obscured by cloud cover. Temperature inside the chambers was monitored using HOBO pendant loggers (Onset Computer Corp., MA). Heat wave treatments increased daily minimum air temperatures by 1.8–2.5 °C, mean air temperatures by 2.5–3.8 °C, and maximum air temperatures by 3.6–6.1 °C (Table S1). Heat waves also increased in-soil temperatures by 0.3–3.5 °C, increased soil surface temperatures by 0.9–12.8 °C, and decreased soil moisture by 0.4–6.6 °C (Table S1).

Because we were interested in plant-mediated effects on arthropods, rather than direct effects of heat waves on arthropods, we visually sampled arthropod communities after heat waves were completed. Starting at the end of the final heat wave treatment, we surveyed plant emergence, developmental stage (number of internodes), chewing damage (proportion of leaves with damage), and per-plant arthropod species richness three times per week for the remainder of the growing season (July–October). Additionally, 2 weeks after the final heat wave treatment, we collected the youngest fully expanded leaf on each plant to measure trichome density and specific leaf area (SLA). We determined the average trichome density across both sides of each leaf using a Leica S9i microscope at 145× and the ImageJ cell counter tool (Schneider et al. 2012). We obtained SLA by dividing leaf area by leaf dry weight.

Statistical analyses were conducted using linear and generalized linear models and mixed models in R (Bates et al. 2014; R Core Team 2023). We tested the effects of heat waves on emergence date of individual plants using a linear mixed model with a random intercept for plot. We tested the effects of heat wave timing on the plot-level proportion of plants emerged using a linear model. For all other response variables, we tested the effects of heat waves on the within-plot mean as well as the within-plot variability calculated at each sampling date. We used the coefficient of variation (CV) as a standardized measure of dispersion in these traits among individuals. Sampling date was included as a random intercept in models of response variables that had multiple sampling dates represented per plot. A logit transformation was used for proportion variables, with an adjustment factor of 0.025, and a negative binomial generalized linear mixed model was used for arthropod richness. We used type III ANOVA for hypothesis testing and Tukey tests for post hoc comparisons (Fox and Weisberg 2018; Lemth 2023; R Core Team 2023).

Results

Overall, heat waves delayed and synchronized plant development. The mean number of internodes per plant averaged across the growing season, an indicator of developmental progression, was lower in plants that experienced a heat wave relative to control plants ($X^2_3 = 22.8$, $p < 0.001$; Fig. 1A). May heat waves reduced internode number by 18%, June heat waves by 16%, and July heat waves by 15%. Among-plant developmental variation at any given sampling date (coefficient of variation in internode number) was also impacted by heat wave treatments ($X^2_3 = 13.4$, $p = 0.004$; Fig. 1B). May heat waves reduced developmental variability by 15% and June heat waves reduced developmental variability by 17%.

In contrast to developmental variation, the heat wave treatments had no effect on the traits we measured. Heat waves did not impact trichome density ($F_{3,20} = 1.2$, $p = 0.34$; Fig. S2A) or specific leaf area ($F_{3,20} = 0.68$, $p = 0.57$; Fig. S3A). Heat waves also had no effect on among-plant variability in trichome density ($F_{3,18} = 1.7$, $p = 0.19$; Fig. S2B) or specific leaf area ($F_{3,18} = 0.55$, $p = 0.65$; Fig. S3B).

Heat waves had no effects on mean arthropod richness ($X^2_3 = 4.6$, $p = 0.21$; Fig. 2A). In contrast, among-plant variability in arthropod richness was greater in some heat wave treatment groups relative to controls ($X^2_3 = 17.8$, $p < 0.001$; Fig. 2B). May and July heat waves both increased variability in arthropod richness by 14%. The three most common

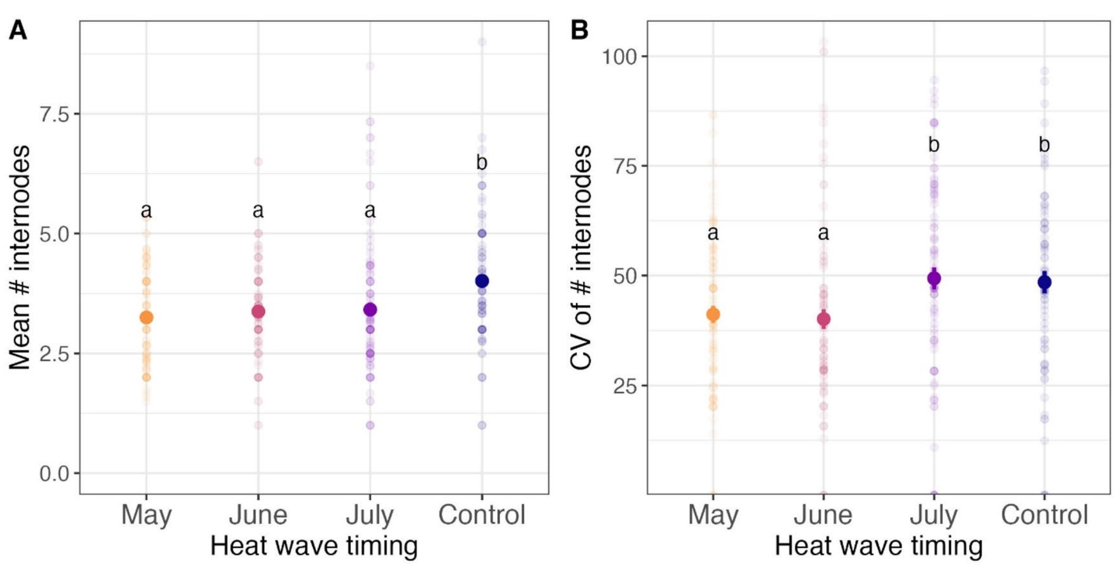

Fig. 1 Heat wave effects on the mean (**A**) and variability (**B**) of plant development. Plant development is estimated as the number of internodes on each plant. Points and whiskers represent means and SEs of each treatment group. Mean and CV were calculated among individuals within experimental plots for each survey

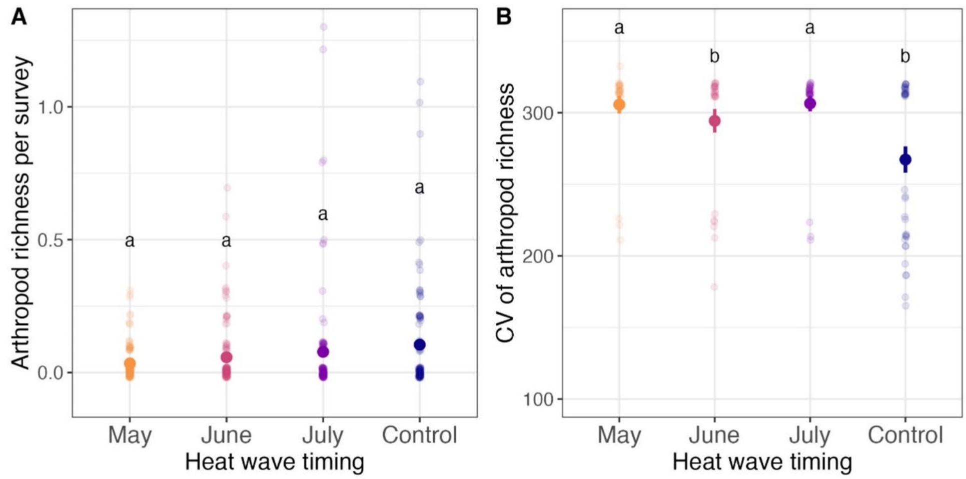

Fig. 2 Heat wave effects on mean (**A**) and variability (**B**) of arthropod richness on experimental plants. Points and whiskers represent means and SEs of each treatment group. Mean and CV were calculated among individuals within experimental plots for each survey

arthropod species observed were *Liriomyza asclepiadis* (Diptera: Agromyzidae), *Myzocallis asclepiadis* (Hemiptera: Aphidae), and *Tetraopes tetropthalmus* (Coleoptera: Cerambycidae), together making up 66.4% of surveyed arthropods (Table S2). Of 125 total arthropod observations, only 7 were made in the first survey after heat wave treatments, indicating that at least 94% of arthropods colonized plants post-heat wave; arthropod richness and herbivory were highest in August (Fig. S4).

Heat wave-exposed plants experienced less chewing damage than control plants ($X^2_3 = 34.8$, $p < 0.001$; Fig. 3A). May heat waves reduced chewing damage by 54%, June heat waves by 39%, and July heat waves by 41%. Among-plant variability in chewing damage was also impacted by heat wave treatments ($X^2_3 = 27.5$, $p < 0.001$; Fig. 3B). Specifically, July heat waves increased variability in chewing damage by 32%.

Discussion

In our study, heat waves led to plant populations that were less developmentally diverse and supported fewer plant-associated arthropods. Heat waves in general delayed plant development and led to higher synchronization of development among milkweed individuals (Fig. 1). Development was generally more delayed and more synchronized by heat waves that occurred earlier in the growing season, meaning

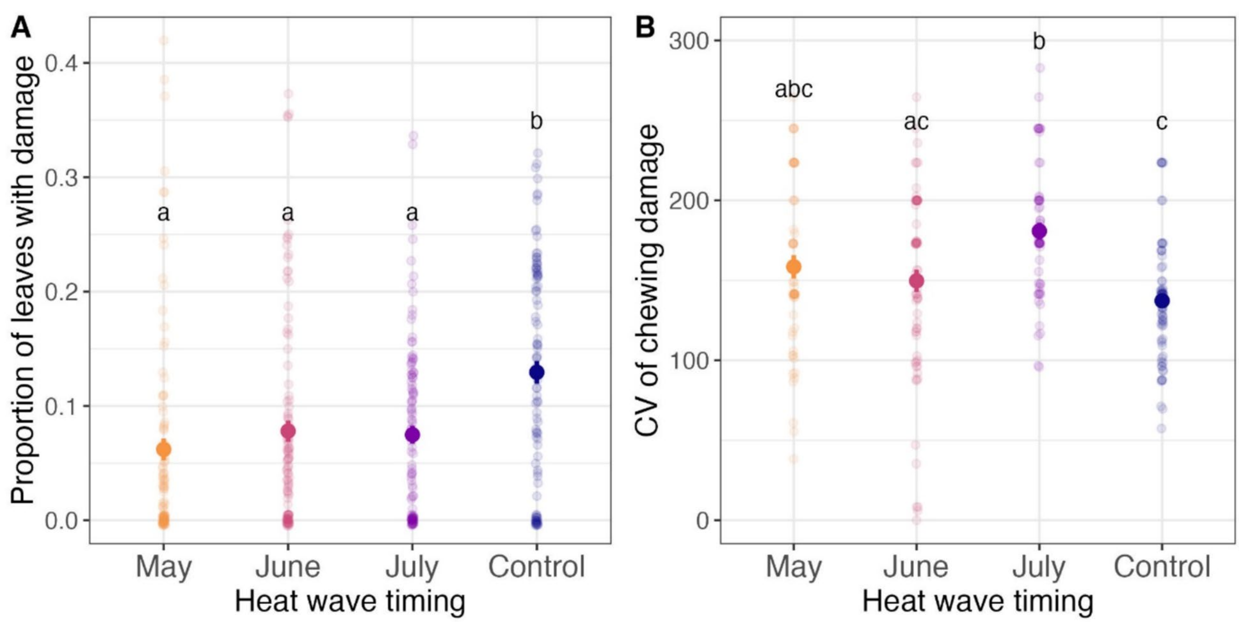

Fig. 3 Heat wave effects on mean (**A**) and variability (**B**) of chewing herbivore damage. Points and whiskers represent means and SEs of each treatment group. Mean and CV were calculated among individuals within experimental plots for each survey

that the effects of heat waves depended on the timing of the event. Heat wave exposure also had cascading effects on plant–insect interactions, leading to fewer species of arthropods and less chewing herbivory on heat wave-exposed plants (Figs. 2, 3).

Pre-existing adaptation for gradual seasonal warming may explain why studies of increased mean temperatures tend to find accelerated plant development (Wolkovich et al. 2014); in contrast, the lack of adaptation for acclimation to extreme heat may explain our finding of delayed development. Rapid increases in temperature at the onset of a heat wave may outpace plants' ability to physiologically acclimate to warming, and thus may cause more stress than gradual mean temperature increases (Fig. 2A, Grossman 2023). Temperate plants in general are well adapted to acclimate to gradual warming over the course of a season, but less well adapted to rapid temperature changes (Grossman 2023).

Heat wave events, particularly in May or June, reduced developmental variability among milkweed plants over the rest of the season (Fig. 2B). Notably, this effect is opposite from our prediction based on prior studies of mean warming, where elevated mean temperatures increased developmental variability in plant populations (Bogdziewicz et al. 2020; Rivest et al. 2021). This result points to the potential for climate change to both expand and contract developmental variability among plants depending on the degree of gradual warming vs. extreme heat events.

There are at least two possible explanations for why heat waves lead to developmental synchrony, while mean warming leads to developmental asynchrony. First, heat waves and mean warming may impact developmental variability differently because of their different relationships with growing season length. Warmer mean temperatures extend the growing season, spreading out plant development over a longer period of time and leading to greater asynchrony (Bogdziewicz et al. 2020; Rivest et al. 2021). Heat waves, on the other hand, may homogenize plant development by delaying development for all individuals and thus reducing the effective length of the growing season. Second, heat waves and mean temperature may represent qualitatively different phenological cues. Warmer mean temperatures may still fall within normal seasonal tolerances for plants, and may be recognized as phenological cues alongside other standard cues, such as moisture and day length, leading to typical within-population variability in phenology (Wolkovich et al. 2014; Grossman 2023). On the other hand, heat waves may be experienced as an acute stress cue (Jagadish et al. 2021), potentially overriding within-population variability in other phenological processes.

Heat wave-exposed plants supported fewer arthropod species and experienced less chewing herbivory, indicating a negative effect of heat waves on plant-associated arthropod communities (Figs. 2A, 3A). Mean warming studies generally find the opposite pattern, where elevated mean temperature benefits herbivores by increasing their metabolic rates (Jamieson et al. 2012). Heat waves have been associated with both increased metabolic rates and increased mortality, depending on the thermal tolerances of the arthropod species involved (Harvey et al. 2020). Our study, however, did not test direct impacts of heat waves on arthropods; most individual herbivores colonized plants after the heat wave treatment and did not experience the heat wave directly, so they were not subject to any potential temperature-related accelerated development, nor were they subject to direct heat stress.

The changes in arthropod communities observed here, therefore, represent indirect, plant-mediated effects of extreme heat events on arthropod communities, rather than a direct effect of heat, meaning that something about the host plants changed and led to reduced arthropod richness and chewing damage. Interestingly, trichome density and SLA—traits typically associated with defense against chewing herbivory—were unchanged in leaves produced post-heat wave. Previous work found that cardenolide defenses were reduced in milkweed leaves following a heat wave (Cope et al. 2023), but the potential for reduced defenses would not easily explain our observed reduction in herbivory.

Given the lack of heat wave effects on other plant traits, heat wave-induced changes in developmental timing emerge as a potential explanation for observed reductions in arthropod richness and consumption. Different stages of plant development offer different quantities, qualities, and types of food resources for herbivores and their natural enemies (Boege and Marquis 2005). Plant-associated arthropods frequently specialize on particular plant developmental stages, and plant development is a major contributor to variation in plant–insect interactions (Cope et al. 2022). Developmentally diverse plant populations, therefore, are expected to host most biodiversity in their associated arthropod communities. When heat waves delay and synchronize plant development, as observed here, they reduce an important component of intraspecific variation in plants and thus reduce niche breadth available for arthropods. Thus, at least locally, heat waves may have underappreciated negative impacts on arthropod communities even beyond the direct effects of heat stress. In a future with more frequent and severe heat waves, lower developmental niche breadth among plants may pose a threat to arthropod diversity.

In addition to reduced mean herbivory and arthropod richness relative to controls, heat wave treatments caused greater variability in herbivore metrics among individual plants. Higher herbivory variability after heat waves is consistent with our predictions based on the effects of mean warming, but unlike with mean warming, the increased variability in herbivore metrics associated with heat waves cannot be traced back to variability in developmental timing

(Bogdziewicz et al. 2020; Rivest et al. 2021). An alternate explanation for the observed increase in variability could be the very low richness in some heat wave-exposed populations—it was more common in heat wave-exposed populations to see just one or two plants with arthropods or herbivory present, whereas in control populations, it was more common to see arthropods and herbivory on most plants (Figs. 2, 3).

Event timing—when a heat wave occurred within the growing season (May, June, or July) or relative to plant emergence (before or after)—was an important determinant of some heat wave impacts. In general, plants had stronger responses to events that occurred earlier in the season (May or June, vs. July), consistent with a previous study where late-July heat waves had greater long-term impacts on milkweed-associated herbivores than late-August heat waves did (Cope et al. 2023). The early heat waves in the present study were early enough in the season to occur before most plants emerged, and yet they still had some of the strongest ecological impacts. These results indicate that dormant plants may be particularly vulnerable to heat wave effects, perhaps because they are already highly sensitive to phenological cues. Our study further underscores the importance of considering event timing explicitly in the studies of climate change and intraspecific variation (Cinto Mejía and Wetzel 2023).

Our results underscore the need to move beyond shifts in mean temperature and mean phenology in studies of climate change impacts. The experimental heat wave we conducted was within the range of recent temperature variability; future events are likely to be more intense and thus produce even more severe effects (Fischer and Knutti 2015; Maxwell et al. 2019). We found that heat waves had nearly opposite ecological effects to what is typically found with mean warming. Where gradual warming generally speeds up and de-synchronizes plant development, we found that heat waves can delay and synchronize it. Likewise, where gradual warming generally increases herbivory, we found that heat waves decrease it. Heat wave-induced reductions in developmental variability are also part of climate change impacts—not only on plants, but on the communities they support. A pressing question remains to be addressed: whether the opposite effects of gradual warming and heat waves could in some cases cancel each other out, in effect softening overall climate impacts in some plant–herbivore systems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-025-05733-0.

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Author contribution statement OLC and WCW designed the study. OLC implemented the experiment, collected and analyzed the data, and wrote the first draft of the manuscript. OLC and WCW revised the manuscript and gave final approval for publication.

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Availability of data and materials Data associated with this manuscript are available on the FigShare repository. Citation: Cope, Olivia; Wetzel, William (2025). Data associated with "Heat waves reduce variability in milkweed development, simplify arthropod communities, and suppress herbivory". figshare. Dataset. https://doi.org/10.6084/m9.figshare.29156051.v1.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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