RESEARCH ARTICLE

Effects of phenological mismatch under warming are modified by community context

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Abstract

Climate change is altering the relative timing of species interactions by shifting when species first appear in communities and modifying the duration organisms spend in each developmental stage. However, community contexts, such as intraspecific competition and alternative resource species, can prolong shortened windows of availability and may mitigate the effects of phenological shifts on species interactions. Using a combination of laboratory experiments and dynamic simulations, we quantified how the effects of phenological shifts in *Drosophila*–parasitoid interactions differed with concurrent changes in temperature, intraspecific competition, and the presence of alternative host species. Our study confirmed that warming shortens the window of host susceptibility. However, the presence of alternative host species sustained interaction persistence across a broader range of phenological shifts than pairwise interactions by increasing the degree of temporal overlap with suitable development stages between hosts and parasitoids. Irrespective of phenological shifts, parasitism rates declined under warming due to reduced parasitoid performance, which limited the ability of community context to manage temporally mismatched interactions. These results demonstrate that the ongoing decline in insect diversity may exacerbate the effects of phenological shifts in ecological communities under future global warming temperatures.

KEYWORDS
climate change, functional redundancy, host-parasitoid interactions, phenological shifts, population dynamics, resource competition

1 | INTRODUCTION

The activities of interacting species are often organized in time. Any shift in the timing of ontogenetic or phenological events modifies the outcome of species interactions, which affect population and community dynamics (Cushing, 1990; Miller-Rushing et al., 2010; Yang & Rudolf, 2010). Evidence is mounting that the timing of previously reliable environmental cues (e.g., temperature, precipitation, snowmelt, etc.) that species use to initiate key life-history events are being altered by climate change (Forrest, 2016; Körner & Basler,

2010; McNamara et al., 2011). For example, since 1896, spring temperatures have increased by about 1.12°C in the contiguous United States of America, and snowmelt has advanced by 14.6 days in parts of Greenland over ten years prior to 2007 (Høye et al., 2007; NCEI, 2016). Furthermore, differential responses across species within the same community indicate that the temporal coordination of species interactions is changing, which raises concerns that interacting species are becoming temporally "mismatched" (Both et al., 2009; Farzan & Yang, 2018; Kharouba et al., 2018; Renner & Zohner, 2018; Simmonds et al., 2020; Visser & Both, 2005).

In antagonistic interactions, a phenological mismatch usually benefits the fitness of one species while the other is harmed (Renner & Zohner, 2018; Stenseth & Mysterud, 2002). However, most phenological studies have ignored community contexts beyond pairwise interactions, which does not reflect the reality that consumers typically use multiple resource taxa and that natural levels of resource competition can show high spatial and temporal variation (Nakazawa & Doi, 2012; Revilla et al., 2014; Samplonius et al., 2021). Here, we define community context as the biotic conditions in which interactions occur and specifically use alternative host species' presence and resource competition levels to represent variation in the community context (Chamberlain et al., 2014; Song et al., 2020). Global declines in insect diversity and abundance make these two aspects of community context particularly imperative to study (Forister et al., 2019; Salcido et al., 2020). Such community contexts can increase temporal overlap with the appropriate life stages of interacting species, which may help promote interaction persistence in the face of shifting phenologies (Olliff-Yang et al., 2020; Timberlake et al., 2019; Yachi & Loreau, 1999). Though, it is uncertain how these processes will behave under future temperatures predicted by climate change and whether more diverse (e.g., functionally redundant) communities could help buffer adverse effects of warming on ecological communities. Therefore, there is a pressing need for studies that integrate relative interaction timing with concurrent shifts in temperature and community context.

We need to understand the intricacies of how unequal shifts in emergence phenologies disrupt the timing of species interactions to understand how climate change can decouple species interactions (Johansson et al., 2015; Kerby et al., 2012; Rudolf, 2018; Samplonius et al., 2016; Yang & Rudolf, 2010). For many interactions, the outcome depends on the developmental stages of interacting individuals. For instance, predators tend to attack specific developmental stages of their prey, and pollinators require plants to be in a particular flowering phase (Stacconi et al., 2015). Thus, the effects of phenological shifts on species interactions depend on how much the outcome of an interaction varies across developmental stages (i.e., the extent traits of individuals change during development) and how long individuals remain available to interact (i.e., the window of vulnerability; Johansson et al., 2015; Memmott et al., 2007; Miller & Rudolf, 2011).

Besides contributing to shifts in phenologies, warmer temperatures also modify growth rates, which alter the amount of time organisms spend within each developmental stage (Kingsolver et al., 2011). In ectothermic organisms, increased temperatures that do not exceed a species' optimal temperature will accelerate development rates, constricting the window of time spent in each ontogenetic stage. This ultimately narrows and shifts the window of vulnerability for predator-prey interactions (but see Tuda & Shimada, 1995) and can magnify size differences in competitive interactions (Benrey & Denno, 1997; Rudolf & Singh, 2013). For example, faster development rates of prey in warmer temperatures decrease the amount of time spent in each developmental stage and can result in natural enemies missing their window of opportunity to attack, even if

the relative appearances within a community remains unchanged (Klapwijk et al., 2010; Ren et al., 2020). Thus, environmental conditions that change the temporal availability of interacting species are likely to modify how the strength of species interactions scales with phenological shifts. However, few studies have quantified these effects.

Community contexts that alter growth rates and species' temporal availability are rarely considered a modifying factor in climate-driven phenological studies. Yet, levels of intraspecific competition (i.e., resource limitation or host density) and the presence of alternative resource species can affect growth rates and temporal availability at a similar magnitude to changes attributed to global warming (Benrey & Denno, 1997; Wolf et al., 2017). Development rates often slow down when levels of resource competition are high, extending the time for which prey species remain vulnerable to attack (Barker & Podger, 1970; Benrey & Denno, 1997). Similarly, the presence of alternative resource species with asynchronous growth rates or phenologies can help prolong the total period during which resources remain available (Stevens & Carson, 2001; Wolf et al., 2017). By promoting phenological and developmental diversity, alternative host species and densities may mitigate the effects of phenological shifts. To what extent is unclear.

Insects and their parasitoids are an excellent system for studying the effects of climate change on species interactions (Hance et al., 2007; Jeffs & Lewis, 2013). Certain parasitoid life-history traits, such as (1) age-related vulnerability of host to successful parasitism, (2) high thermal sensitivity given the parasitoids' obligate ties to host thermal performance, and (3) high host specificity, make them particularly prone to desynchronization with host species (Abarca & Spahn, 2021; Hance et al., 2007). Furthermore, the duration of host vulnerability and degree of phenological synchrony have been suggested to influence local stability within host-parasitoid systems (Tuda & Shimada, 1995). For example, stable host–parasitoid interactions require that some hosts survive, so some degree of asynchrony may be adaptive (Godfray et al., 1994). Thus, shifts away from the optimal temporal relationship can significantly affect their long-term persistence (Tuda & Shimada, 1995).

Although long-term phenological studies are vital to make more accurate predictions of the effects of phenological shifts on natural communities, these data are lacking and difficult to acquire. However, the combination of experimental and dynamic models offers a powerful alternative to extending single-generation experiments to multigenerational studies. Here, we employ laboratory experiments and dynamic simulations to examine how warming and community context modify the effects of phenological shifts on the strength and dynamics of host–parasitoid interactions. Parasitoids are essential in determining host population dynamics and are commonly used as biological control agents. Studies have shown that climate change reduces parasitoid performance (e.g., low thermal tolerance relative to the host) and shifts the relative timing of host-parasitoid interactions (Dyer et al., 2013; Jeffs & Lewis, 2013; Klapwijk et al., 2010; Moore et al., 2021; Thierry et al., 2022). Parasitoid species further vary in thermal sensitivity, generation times, and the developmental stages

they can successfully parasitize (Fleury et al., 2009; Hance et al., 2007).

Using a native *Drosophila*–parasitoid system from seasonal tropical forests of North Queensland, Australia (Jeffs et al., 2021), we experimentally delayed the emergence phenology of parasitoids relative to their hosts. We then assessed how resource competition and the presence of an alternative host species modified the effect of delayed emergence on host-parasitoid interactions in ambient (24°C) and predicted warming temperatures (28°C) (IPCC, 2018). Most phenological studies have focused on how increased temperature acts as the environmental cue that drives shifts in emergence phenology among interacting species (Klapwijk et al., 2010; Zettlemoyer et al., 2019). However, elevated temperatures persist throughout the growing season in tropical rainforests of Queensland (Alford et al., 2007). Thus, the temperature is not only the cue; it is also the context in which mismatched ecological interactions must proceed. Therefore, we decoupled the effects of temperature and phenology to quantify the impact of different phenological shifts in current ambient and predicted warming temperatures (Rudolf & Singh, 2013). This approach allowed us to detect direct physiological effects of elevated temperatures on host and parasitoid species, independently from shifts in phenology.

Additionally, we applied parameters derived from the single-generation experiment to simulate host-parasitoid population dynamics over 100 generations under our experimental conditions to examine their impact on long-term persistence. Combining the experiments with the dynamic model allowed us to assess (1) how temperature alters the effects of phenological shifts on rates of host survival (HS) and parasitism (PR), (2) to what extent does resource limitation, (3) the presence of an alternative host species modify effects of phenological shifts under warming, and (4) how resource competition, alternative host species, and temperature interact to affect long-term persistence of host-parasitoid interactions. Under elevated temperatures, we predict that parasitism rates (PRs) will decline more rapidly with each subsequent phenological delay. However, resource-limitation among hosts or an alternative host species will lessen the extent of the decline. Combining experimental and modeling approaches helped identify which conditions were favorable over a single generation but detrimental to host–parasitoid interactions' long-term persistence. The results represent an important step toward understanding how warming and community context interact to modify the effects of phenological shifts on the strength and dynamics of species interactions, which is critical for predicting how ecological communities will respond to climate change.

2 | MATERIALS AND METHODS

2.1 | Study system

Two species of *Drosophila*, *D. sulfurigaster* and *D. birchii*, were collected from the Australian rainforest in March 2018 and maintained at the Czech Academy of Sciences (CAS) as a collection of

isofemale lines (shipping to the Czech Republic was under permit no. PWS2016-AU-002018 from Australian Government, Department of the Environment). These species coexist across elevational gradients that span 900m at Kirrama (S18°12.676′ E145°47.530′), and Paluma (S19°00.386′ E146°12.732′) mountain ranges in Queensland and a shared suite of parasitoid wasp species attack them (Jeffs et al., 2021). These two species are commonly found in the same banana bait traps across their elevational range and likely share natural food sources like other Drosophilids (Valadao et al., 2019). *D. birchii* is a rainforest specialist found in higher abundances in mid- and high-elevation sites. It takes, on average, three more days (12 days) to complete development than the larger *D. sulfurigaster* (9 days). Individuals used in this experiment were collected as eggs from mass-bred population cages, which originated from eight isofemale lines from each fly species, respectively. We used mass-bred populations to limit the possible effects of unnaturally low genetic variation in iso-female lines, commonly used in laboratory studies.

We used two hymenopteran parasitoid species, collected from the same tropical Australian locations, Kirrama, elevation 900m: *Asobara* sp. (Braconidae: Alysiinae; strain KHB, reference voucher no. USNMENT01557097, reference sequence BOLD process ID: DROP043-21), and *Ganaspis* sp. (Figitidae: Eucolinae; strain 69B, reference voucher no. USNMENT01557100, USNMENT01557297 reference sequence BOLD process ID:DROP164-21; Lue et al., 2021). These species await description by taxonomists but are precisely identified above so that this study can be linked to species names once available. Both parasitoid species specialize in larval stages, especially second instar, and are known to attack *D. birchii* and *D. sulfurigaster* successfully. At 24°C, *Ganaspis* sp. completes its development from egg to emerging adult in 29 days $\pm$ 1.4SD, while *Asobara* sp. develops in 17 days $\pm$ 1.96 SD. All parasitoids were maintained on *D. melanogaster*, so no parasitoid used in this experiment had prior exposure to *D. sulfurigaster* or *D. birchii*; thus, no acquired oviposition preference.

2.2 | Experimental design

We reared *Drosophila* larvae in ambient (22.9°C $\pm$ 0.47SD with 69% $\pm$ 4.34 SD relative humidity) and predicted warming (27.4°C $\pm$ 1.15 SD with 60% $\pm$ 10.1 SD relative humidity) temperatures for the 24 and 28°C treatments, respectively. Our predicted warming temperatures are based on climate change models that predict a 1.9–3.9°C increase in temperatures by 2070 in Australia if no reduction in greenhouse gasses occurs (IPCC, 2018). All rearing happened in a 12-h light/12-h dark photoperiod. We manipulated levels of intraspecific competition among *Drosophila* larvae by providing 2 or 20 ml of the fly medium. We used a published egg wash protocol to add 100 *Drosophila* eggs to all vials resulting in densities of 50 individuals/ml using an egg wash protocol for the high competition and five individuals/ml for the low competition treatments (Nouhaud et al., 2018). We decided to manipulate the volume of food instead of the abundance of larvae to avoid any frequency-dependent
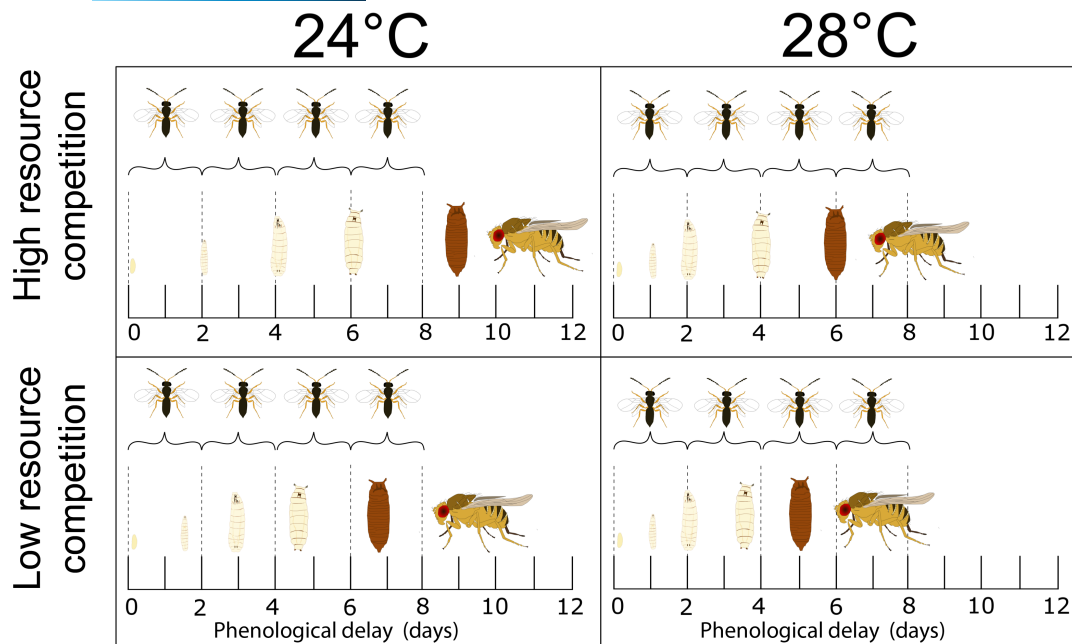
FIGURE 1 A schematic representation of the experimental design. Differences in development rates and developmental stages in the control treatments (without parasitoids) are presented as Drosophila transitioning from larvae (beige), through pupae (brown), to adult flies. To mimic a phenological delay in emergence times between Drosophila and parasitoid wasps, parasitoids from a single species were introduced to vials in 2-day intervals, as shown by the dotted lines. We replicated this design with *Drosophila sulfurigaster* and *Drosophila birchii* alone and the two Drosophila species together for the alternative host species treatment, and across the two parasitoid species – *Asobara* sp. and *Ganaspis* sp.[Colour figure can be viewed at wileyonlinelibrary.com]

parasitism effects. We selected the high competition treatment to represent a scenario with extreme resource limitations. Thus, we established four temperature/competition treatments that varied host development rates: (1) slowest development (24°C with 2 ml food); (2) slow development (24°C with 20 ml food); (3) fast development (28°C with 2 ml food); and (4) fastest development (28°C with 20 ml of food). We repeated this process for both *Drosophila* species in isolation and together for alternative host species treatments. The 100 total eggs were composed of equal proportions of the two species (e.g., 50 eggs *D. sulfurigaster* and 50 eggs *D. birchii*). We incorporated interspecific competition between host species, which naturally occurs in multispecies communities, within each vial in the combined treatment.

We manipulated four phenological relationships between host and parasitoids in 2-day intervals. Adult parasitoids either "emerged" (e.g., manually introduced) at the same time as their host (i.e., day 0) or 2, 4, or 6 days later. At each parasitoid emergence time, three mated female and three male parasitoids of a single parasitoid species were added to vials with *Drosophila* larvae using an aspirator. After 48 h, we removed the parasitoids from the vials. We maintained the vials under the same temperature and light conditions described above. The removal of parasitoids allowed a more precise measurement of the vulnerability window and largely prevented the complete mortality of all *Drosophila*. The optimal phenological relationship is unknown in this system, but the developmental stage that maximizes reproductive output differs among parasitoid species. To measure development times, emerged individuals were recorded

daily and stored in 95% ethanol (Figure 1). Collection stopped after 4 days of no emerging adult hosts and parasitoids. We replicated all treatments across both wasp species. Each treatment consisted of at least five replicates initiated over 5 days and represented blocks in our statistical analyses.

All experiments were set up in 2.8 cm (diameter) × 9 cm (height) glass vials, with a 4 ml base layer of 1.5% agar gel to reduce desiccation of the fly medium. The agal layer also served as a potential refuge from parasitoid attacks. Control treatments consisted of ten unexposed vials for each host species combination (*D. birchii*, *D. sulfurigaster*, *D. sulfurigaster+birchii*). We used the control vials to calculate the average and standard deviation in development time (egg-to-adult) and HS in the absence of parasitoids across treatments.

2.3 | Response variables

We counted the total number of adult *Drosophila* (d_i) and the number of adult parasitoids (p_i) that emerged from each vial. The proportion of HS was estimated using HS = d_i/T, where T is the average abundance of flies reared in control treatments. In cases where HS > 1 (cases where more flies came out in the presence of parasitoids, compared to control treatments without parasitoid), we set HS = 1. PR was estimated using PR = pi/T. In cases where PR > 1 (cases where more parasitoids emerged than flies in control treatment), we set PR = 1. Both estimates accounted for differences in the number

of *Drosophila* that a given temperature and competition treatment supported in the absence of parasitoids.

2.4 | Statistical analysis

All statistical analyses were performed using R statistical software v. 3.6.0 (R Core Team, 2021). We used generalized linear mixed models (GLMMs) to analyze the mean and variance in host development time, HS, and PR as response variables. We applied a mixed model approach with block as a random intercept. We included an observation level random effect to meet overdispersion and heteroscedasticity model assumptions for HS and PRs. The response variables in the alternative host species treatment of *D. sulfurigaster*+birchii refer to the sum of the two host species.

We modeled host development times using data from control vials only (i.e., no parasitoids). We modeled temperature, competition, host species combination, and potential interactions between the three factors as fixed effects. Log-transformed development time data improved model fit and helped meet assumptions of normality. We modeled HS and PRs as a function of the same cofactors using a binomial GLMM with a logit link function. All statistical models included a three-way interaction between temperature, resource competition, and phenological delay. We also explored other potential interactions for which no a priori hypotheses were made by comparing models that incorporated interactions with either host or parasitoid species and included all nested two-way interactions. We selected the model which minimized AICc using the *bblme* package in R (Bolker & R Development Core Team, 2020). We used the *DHARMa* (Hartig, 2019) package to test whether assumptions of normality, non-constant error variance, and overdispersion were violated. *DHARMa* simulates mixed models' scaled (quantile) residuals and provides built-in tests to inspect model assumptions. We performed post-hoc multiple comparisons using Wald chi-squared tests in the *emmeans* package (Lenth, 2019) and adjusted *p*-values using the Tukey method when necessary. All figures and coefficient tables were generated using the *ggplot2* and *sjPlot* R packages, respectively (Lüdecke, 2021; Wickham, 2011).

2.5 | Dynamic model and simulations

We used *Drosophila* host (H), and parasitoid wasp (W) emergence counts to parameterize a stage-structured modification of the Nicholson–Bailey host–parasitoid model. A detailed explanation for model derivation, parameter estimation, and simulation protocols can be found in the supplementary file (pp. 36–40). What follows is an abbreviated description.

For a single generation, starting with $H_0 = 100$ eggs, the number of surviving uninfected "H_8" and infected "I_8" hosts at day 8, are given by:

$$H_8 = H_0 e^{-8M-2p}, \quad (1)$$

$$I_8 = H_0 e^{-8M-d}(1 - e^{-2p}), \quad (2)$$

respectively, where $e^x=\exp(x)$ is the exponential function (e≈2.71828). Day 8 was the last day that a wasp could have infected any given host. Based on the biology of our system, we assumed that a single infected host gives rise to at most a single adult parasitoid. "M" is the common mortality rate per day suffered by infected and non-infected hosts. "p" is the attack rate per day exerted by the three female wasps in the experiments. Parasitoid handling turns hosts into the infected state or kills them instantly with rate "d" (i.e., injuries) resulting in a loss of hosts and parasitoids. The "$8M$" and "$2p$" factors indicate that attacks occur in a 2-day window over an 8-day period before emergence.

Daily mortality consists of an intrinsic rate "m" and a resource competition effect

$$M = m + a\left(\frac{H_0}{R}\right), \quad (3)$$

where the strength of competition is proportional to initial egg numbers H_0, inversely proportional to the initial supply of food R, and "a" represents a competition coefficient.

Equations (1–3) only consider intra-specific competition. Interspecific competition requires additional parameters, which cannot be independently estimated due to experimental limitations. Thus, we consider single hybrid host populations (*D. sulfurigaster*+*birchii*) for two-host experiments for parameter estimation.

2.5.1 | Parameter estimation and single-generation simulations

To estimate "m", "a", "p", and "d," we set H_8 and I_8 to the number of emerging flies and wasps, respectively, on and after day 8. Next, we calculate empirical mortality using the formula

$$\mu = \frac{\ln(H_0/H_8)}{8}, \quad (4)$$

that is, daily rate of geometric decline (8 days). This was done for all combinations of food level ($R = 20, 40$ ml), temperature (24C, 28C), and attack windows (no parasitoid, days 0–2, 3–4, 5–6, 7–8). The rates "m" and "a" were solved from a system of equations using (3) with $M = \mu$, at low ($R = 20$ ml) and high ($R = 2$ ml) competition levels, in the absence of parasitoids ($W = 0$). Next, for the given competition level and wasp attack window, we solved the "p" that causes difference in mortality between conditions with ($W = 3$) and without wasps ($W = 0$). Experiment replication allowed estimation of expected values and variances for "m", "a", and "p". Finally, we used the discrepancy between I_8 and prediction by Equation (2) to estimate handling mortality "d".

Single generation experiments are simulated by running a day-by-day version of Equations (1 and 2) from day 1 to 8, including environmental and demographic stochasticity effects. Simulated H_8 and

I_8 are compared with corresponding observed numbers of emerged flies and wasps in each combination of species, temperature, food level, and attack window, respectively.

2.5.2 | Multiple-generation simulations

We projected fly and wasp populations for 100 generations using parameters from single generation simulations. Starting at generation 0 with $H_0 = 100$ fly eggs and $W = 3$ female wasps, the number of eggs and females in generation 1 and beyond were updated by

$$H_0 = R_F H_8, \quad (5)$$

$$W = 0.5 S_W I_8, \quad (6)$$

where H_8 and I_8 follow the stochastic implementation of Equations (1 and 2) previously described in section (a). R_F is the host net reproductive ratio, and S_W is the parasitoid wasp adult survival rate. The 0.5 assumes a 50:50 female:adult sex ratio for the parasitoid. We took care to substitute "p" by "$pW/3$" because "p" was estimated for $W = 3$ females, but now W changes across generations.

We do not have reliable information (from experiments or the literature) about possible ranges of variation for R_F and S_W for our experimental species. We acknowledge this uncertainty and thus consider a broad range in our simulations to minimize bias. We set 10 different values for each. For $R_F = 1, 2, ..., 10$. Values equal to 1 or lower always lead to host extinction; thus, $R_F = 1$ is a meaningful lower bound. The upper bound $R_F = 10$ is more than enough to sustain 100% of hosts populations in the absence of wasps across many treatment combinations. For $S_W = 0.1, 0.2, ..., 1$. The $S_W = 1$ upper bound for wasp survival is an ideal condition not found even under laboratory conditions.

With 100 replicates for each $10 \times 10 = 100$ R_F and S_W combination, and 120 combinations of temperature (24, 20°C), food level (20, 2 ml), host species (D. birchii, D. sulfurigaster, D. sulfurigaster+birchii), wasp species (Asobara sp., Ganaspis sp.), and phenological delay (no wasp, day 0, 2, 4, 6), the total number of simulated time series was 1,200,000. The simulations were executed in Matlab 2017a. The end of the Supplemental Information file shows a representative subset of simulations (pp. 41--44). We calculated the number of generations host and parasitoid populations persisted before going extinct and statistically compared which factors promoted the probability of host–parasitoid persistence.

We recognize that natural variation in phenology, climate, and community contexts is difficult to capture using dynamic models. Still, this model does generate testable hypotheses that future studies can test with added variation in dynamic models or the documentation of these factors in nature over long periods. More detailed methods used for fitting with data (SI pp. 5--8), simulating host–parasitoid interactions across generations (SI pp. 3–5 and 39–40) and statistical analyses are described in Section 2.

3 | RESULTS

3.1 | Host development times and survival across temperatures and community contexts without parasitoids

In the absence of parasitoids, warming and competition levels altered mean host development times by as much as 47% (up to 4 days; Figures S1 and S2). On average, the shortening of developmental time due to warming was more pronounced (Mean = −2 ± 0.2 days) than its extension due to increased competition (Mean = +1.2 ± 0.2 days); and the changes were consistent in direction for all species combinations (Table S1 and S2). Variance in development times, measured as the standard deviation, varied significantly across species, but these values depended on an interaction between temperature and resource levels (Figure S2; Tables S3 and S4). On average, the D. sulfurigaster+birchii combination had a 158% greater variance in emergence times than D. birchii and 52% greater variance than D. sulfurigaster alone. Survival rates were always the highest in 24°C and low competition treatments across all host species combinations, but species responses to warming and competition varied (Figure S3; Tables S5 and S6). For example, D. birchii survival (post hoc odds ratio [OR] = 7.54, $p < 0.001$) declined by 47% under warming temperatures, compared to a 15% decline in D. sulfurigaster (OR = 2.17, $p = 0.002$; Figure S3). Although D. sulfurigaster regularly achieved higher survival rates relative to D. birchii, D. birchii survival was not significantly reduced when reared with D. sulfurigaster in any high competition treatment (Figure S4; Tables S7 and S8; $p > 0.05$).

3.2 | Effects of phenological shifts across temperatures

The effect of parasitoids on average HS depended on the relative emergence time of parasitoids and their interaction with warming (Figure 2a; Figure S5b; Tables S9 and S10; note that warming alone did not alter average HS). In both temperatures, the probability of HS was at or near zero when host and parasitoids emerged simultaneously. HS increased significantly through the first 4 days of delay, followed by a plateau between delays of 4 and 6 days (Figure 2a; $p > 0.05$). During the first 4 days of phenological delays, faster development in elevated temperatures magnified differences in HS across delays. In ambient temperatures, the largest rise in odds of HS occurred between a 2- and 4-day delay (OR = 22.36, $p < 0.001$), compared with 0- and 2-day delay (OR = 31.11, $p < 0.001$) under warming (Figure 2a). Interestingly, HS rates rarely exceeded 80% of those attained in trials without parasitoids. Parasitoids continued to inflict mortality on hosts even with late phenological delays.

PRs declined as phenological delay increased ($p < 0.05$ for all phenological delays). Warming significantly reduced the odds of parasitism (OR = 10.9, $p < 0.001$), but this decline in parasitism was not

FIGURE 2 The association between phenological delay, temperature, and resource competition with average host survival and parasitism rates. The predicted probabilities of (a) host survival (Table S9) and (b) parasitism rates (Table S11) are displayed as a function of phenological delay from independent mixed-effects logistic regressions. The bar plots represent the estimated marginal means, averaged over all host and parasitoid species combinations with 95% confidence intervals. Colored circles indicate the observed means of (a) host survival and (b) parasitism rates for each host-parasitoid combination separately. All effects were tested using Tukey's HSD test for multiple comparisons and are provided in the text. All effects were tested using Tukey's HSD test for multple comparisions, and signficant differences (*p* < 0.05) are indicated with asterisks [Colour figure can be viewed at wileyonlinelibrary.com]
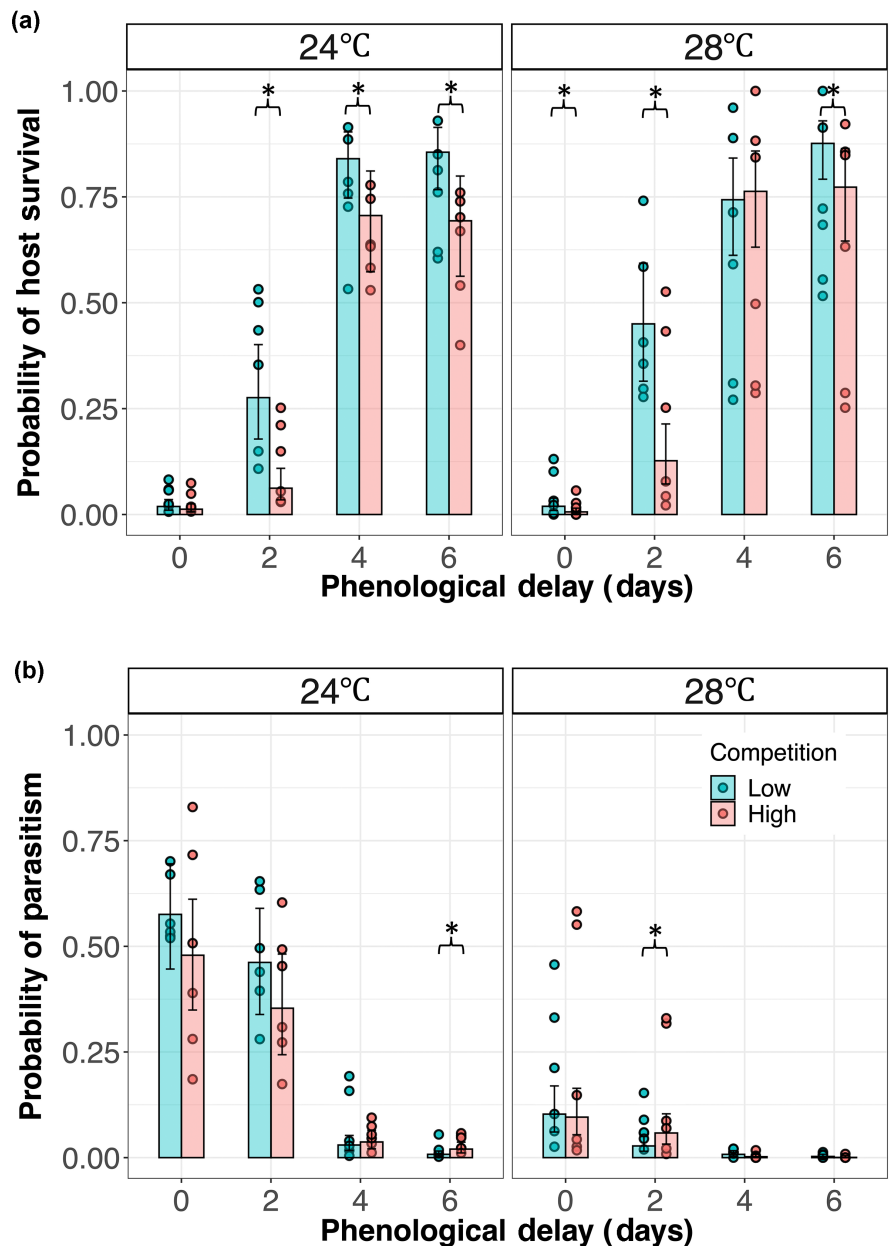
coupled with increased HS. When emergence phenologies matched, HS was at or near 0% in both temperature treatments. Rates of parasitism ultimately exceeded 52% (95% CI: 42, 64%) in ambient temperature, compared with a maximum of 10% (95% CI: 6, 15%) under warming. Consequently, even though hosts were developing faster in elevated temperatures, the chance of parasitism was already less than 5% with just a 2-day delay, and differences in PRs across phenological delays diminished (Figures 2b; Figure S5a; Tables S11 and S12). In both temperatures, the largest decline in average parasitism occurred between delays of 2 and 4 days (24°C OR = 0.05, *p* < 0.001; 28°C OR = 0.09, *p* < 0.001). Averaged over both temperatures, *Asobara* sp. PRs were 35% and 11% higher during the 0- and 2-day windows of delay, respectively. In contrast, *Ganaspis* sp. rates of parasitism significantly outpaced *Asobara* sp. by 2% on the fourth day of delay. These results suggest that warming reduced the effects

of phenological shifts on PRs due to significant declines in parasitoid performance and, to a lesser extent, accelerated host development rates.

3.3 | Modifying effects of competition across phenological shifts and temperature

The effects of temperature and relative emergence time on HS did not vary with levels of resource competition (Figure 2a; Table S10). Alongside shifts in relative emergence time, resource competition had the strongest effect on HS (Table S9), where hosts had a 22% (95% CI: 16, 30%) chance of survival at high levels of resource competition, compared to 42% (95% CI: 33, 51%) at low levels of competition (OR = 0.40, *p* < 0.001). Importantly, the relationship between

phenological shift and survival varied significantly across competition treatments. For example, delaying parasitoid emergence by 2 days (relative to 0-day delay) increased survival by 9% (OR = 11.1; $p < 0.001$) in high competition compared with an 34% (OR = 28.6; $p < 0.001$) increase at low competition levels.

In contrast, the effects of temperature and phenological shifts on PRs depended on levels of resource competition (Table S11). Under warming, PRs became significantly greater in high competition treatments at the 2-day delay (OR = 2.17, $p = 0.032$), compared to the 6-day delay in ambient temperatures (OR = 2.61, $p = 0.01$). Notably, competition could not increase parasitoid recruitment with delays longer than 2 days at 28°C. Thus, even though competition slowed development rates, including in higher temperatures, host species did not remain susceptible to parasitism across a broader range of phenological delays under warming. Together, these results highlight that shifts in resource competition primarily determined HS, while temperature changes drove differences in PRs.

3.4 | Effect of alternative host species across phenological shifts and temperature

The effects of phenological delay on HS varied across host species combinations and its interaction with temperature (Figures S6 and S7; Table S9). Differences in HS among species increased with additional phenological delay and accelerated under warming. In elevated temperatures, with a 4-day delay, the probability of *D. birchii* survival was 74% (OR = 0.008, $p < 0.001$) and 45% (OR = 0.14, $p < 0.001$) less than *D. sulfurigaster* and *D. sulfurigaster+birchii* respectively. During the equivalent 4-day delay, differences in HS among species were insignificant in ambient temperatures. On average, single-species treatments with *D. sulfurigaster* and *D. birchii* had the highest and lowest probabilities of HS, respectively, while the treatment with both species present showed an intermediate probability of survival (Table 1; Figure S6).

In contrast, PRs differed across single and multiple host species combinations, with average PRs being highest with both host species present. While average HS rates differed among host species combinations ($p < 0.05$), average PRs showed no

TABLE 1 The estimated marginal mean probabilities of host survival and parasitism rates. These marginal means are averaged across phenological delays, temperatures, levels of resource competition, and wasp species. Letters in brackets denote significant differences in probabilities in multiple pairwise comparisons ($p < 0.05$)

| Species	Host Surv. Prob. (95% CI)	Parasitism Prob. (95% CI)
Drosophila birchii	0.17 (0.12, 0.24)[A]	0.04 (0.03, 0.07)[A, B]
Drosophila sulfurigaster	0.53 (0.43, 0.63)[B]	0.03 (0.02, 0.05)[A]
D. sulfurigaster + birchii	0.29 (0.22, 0.38)[C]	0.05 (0.03, 0.07)[B]

significant differences. Thus, the average development time, HS, and PRs of the *D. sulfurigaster+birchii* combination were comparable to the pooled mean values of the two host species in isolation. Interestingly, each species in isolation showed significant differences in survival across temperatures at each relative delay, but when an alternative host species was present, HS rates did not differ across temperatures at any relative delay (Table S13; $p > 0.05$). This is likely due to opposing responses to phenological delay, temperatures, and resource competition between *D. birchii* and *D. sulfurigaster*. These results suggest that within a single generation, the presence of alternative host species dampened differences in the probability of HS and PRs across both temperatures and levels of resource competition, but not throughout phenological shifts.

3.5 | Simulation results: Changes in host-parasitoid persistence with phenological shifts, warming, and community context

The effects of phenological delays on host–parasitoid persistence varied significantly with warming (Table S14). Under warming, a delay of 2 days resulted in the highest probability of host-parasitoid persistence (odds ratio [OR] = 0.49, $p = 0.0013$), compared to a 4-day delay in ambient temperatures (OR = 2093.8, $p < 0.001$). The persistence of host-parasitoid interactions was significantly reduced if parasitoids were perfectly synchronized with their hosts or the shifts in relative emergence times became too delayed (Figure 3). Interestingly, the chances of parasitoid persistence were greater than average during a single delay window (2-day delay; OR = 742.95; $p < 0.001$) under simulated warming, while ambient temperatures indicated two windows of delay (2-day delay; OR = 4.38; $p < 0.001$ and 4-day delay; OR = 19.92; $p < 0.001$) with increased probabilities of parasitoid persistence. This supports predictions that accelerated development rates under our warming conditions narrowed the window of vulnerability in host–parasitoid interactions. Moreover, warming reduced the average probability of host–parasitoid persistence irrespective of phenological relationships (OR = 83.5, $p < 0.001$; Figures S8–S10).

Our simulations indicated that high levels of resource competition among hosts did not increase the number of relative emergence times that supported parasitoid persistence in either ambient or elevated temperatures. Instead, the chances of parasitoids persisting for extended generations were significantly greater when competition levels were low, and this was consistent across all phenological delays, except a 0-day delay (OR = 1.8, $p = 0.19$). When averaged across all phenological shifts and temperatures, the presence of alternative host species increased the odds of persistence by factors of 17.98 (*D. sulfurigaster*) and 2.73 (*D. birchii*), respectively (Figure 3). This suggests that while our single-generation experiment identified intermediate levels of survival and PRs when additional host species were present, those differences in survival and PRs had meaningful, positive effects on host–parasitoid coexistence across multiple

FIGURE 3 The Observed association between phenological delay, temperature, and resource competition with the persistence of *Drosophila*-parasitoid interactions in the dynamic simulation. Each point (*n* = 9599) overlaid on the boxplot represents the proportion of replicated simulations (*n* = 100) in which host-parasitoid interactions persisted for at least ten generations. Many proportions are at or near zero; thus, some points are not visible. We, therefore, restricted the *y*-axis to show all values less than 0.3. All levels of host net reproductive rate (2–10) and adult parasitoid survival rate (0.1–1) are included [Colour figure can be viewed at wileyonlinelibrary.com]
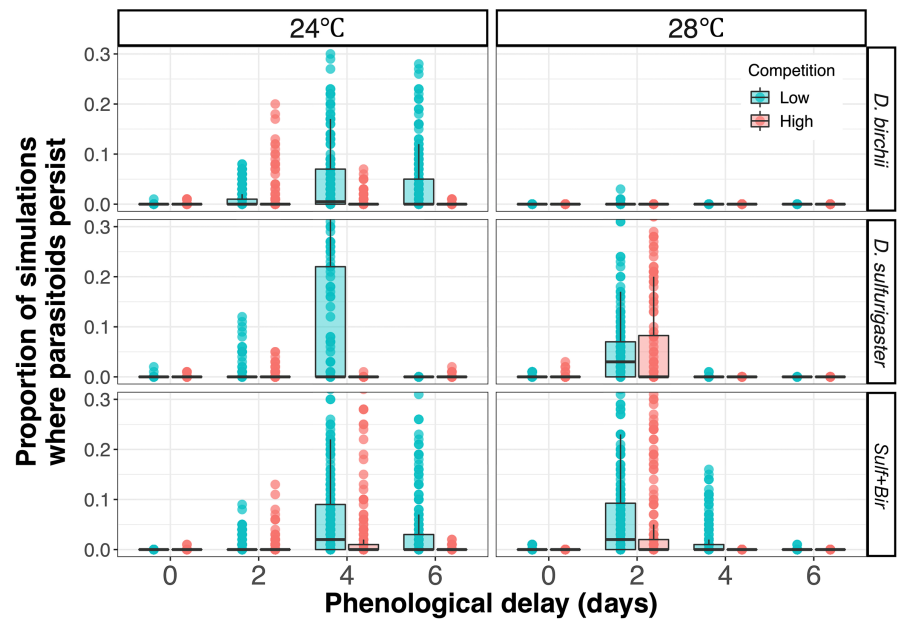
generations (additional evidence on model performance is provided in Supplemental Information; Figure S11, Tables S15 and S16).

4 | DISCUSSION

Although studies recognize that climate change is altering phenological relationships among interacting species, the consequences for species interactions in different community contexts remain unclear (Forrest & Miller-Rushing, 2010). Here, we show that delays in the emergence of parasitoids, relative to their insect hosts, significantly alter the strength and persistence of host–parasitoid interactions. Notably, the magnitude of these effects varied across temperatures and the community context in which the interaction occurred. Modifications in the outcome of the host–parasitoid interaction were due to both changes in host development times and declines in host and parasitoid performance under warming, irrespective of shifts in development rates. These findings demonstrate that modifying the effects of phenological shifts on host–parasitoid interactions via community contexts could help maintain the availability of prey when hosts and parasitoids become temporally mismatched. However, unless either parasitoid or host evolve or show adaptive plasticity in response to warming, these benefits may not be realized in predicted warmer environments due to significant declines in performances of host and especially parasitoids (Faillace et al., 2021). Thus, accounting for interactive effects between climate and community context is necessary to predict phenological shifts' immediate and long-term consequences on biotic communities.

4.1 | Effects of phenological shifts on outcomes of host–parasitoid interactions

Phenological shifts had the most substantial effect on the strength and persistence of the host-parasitoid interactions, and this effect persisted even after accounting for changes across temperatures, resource competition, and the presence of alternative host species. This is consistent with other host–parasitoid studies, which have highlighted the importance of windows of vulnerability and correct stages (ages) in determining the immediate and long-term effects of interactions (Benrey & Denno, 1997; Chi & Su, 2006; Stacconi et al., 2015; Tuda & Shimada, 1995). Thus, phenological shifts in specialized, strongly coevolved systems, such as these, are more likely to desynchronize host and parasitoid populations, leading to the destabilization of interactions (Rasmussen et al., 2014; Ren et al., 2020). However, our results highlight that the extent phenological shifts destabilize host–parasitoid interactions will likely vary across parasitoid species due to differences in parasitoid performance across host developmental stages. In diverse host-parasitoid systems, variation in age-dependent patterns of host exploitation across parasitoids can significantly impact the population stability and persistence of late-emerging parasitoids or early emerging hosts (Briggs & Latto, 1996; Sait et al., 1997).

4.2 | Phenological shifts in a community context perspective

Community context proved to be a significant modifying factor on the immediate and long-term consequences of phenological shifts in our study. While increasing intraspecific competition extended the duration of *Drosophila's* larval stage, our study indicates that it is not likely to promote host-parasitoid interaction persistence. Limited resources slowed host development and increased host mortality, reducing the recruitment potential for the next generation of parasitoids. Interestingly, the effects of interspecific competition among host species had a minimal impact on HS rates and parasitism. Other studies have found that, in addition to declines in individual survival, host populations experiencing intense competition may also be of

lower quality for parasitoids. This can reduce population growth to rates that cannot support long-term parasitoid persistence (Cuny et al., 2019; Jones et al., 2009). Furthermore, if parasitized hosts are more inclined to density-dependent mortality, as observed in some (Ives & Settle, 1996), but not in all host-parasitoid systems (Spataro & Bernstein, 2004; White et al., 2007), this effect is likely to be amplified. Overall, these results suggest that extending the temporal availability of hosts via competition is unlikely to dampen the impact of phenological shifts. However, more levels of competition would be required to identify any non-linear effects of resource competition on the stability of host-parasitoid interactions (Zhang et al., 2015). Phenological shifts towards later emergence times of parasitoids may reduce host-parasitoid persistence if parasitoids struggle to establish on high-density (e.g., low quality) host populations.

Most phenological studies have examined the consequences of phenological shifts between pairs of interacting species, rarely considering broader community contexts. Recent theoretical (Nakazawa & Doi, 2012; Revilla et al., 2014; Takimoto & Sato, 2020) and experimental (Olliff-Yang et al., 2020; Timberlake et al., 2019) studies have pointed out this gap and suggest that the presence of alternative resource species should weaken the effects of phenological mismatches, especially if those resources have complementary phenologies. By combining experimental and theoretical approaches, our results helped fill these gaps. We showed that multispecies host communities were more likely to support the persistence of parasitoid populations across a broader range of phenological shifts, temperatures, and competition levels than pairwise interactions. Moreover, we found that the presence of an alternative host species diminishes differences in average HS and PRs across different biotic and abiotic factors. Similar to other studies, temporal complementarity between species (e.g., variation in growth rates) and a diversity of responses to environmental changes were major stabilizing mechanisms in our system (Craven et al., 2018; Sasaki et al., 2019; Zhang et al., 2013), although this is the first example using a host-parasitoid system. While most studies recognize that functional redundancy and trait diversity at any given time can positively affect community resilience to environmental changes, it is rarely considered that these community parameters continuously change during the development of individuals within the community. Future studies should explicitly consider that the degree of functional redundancy within a community will likely vary during the development of individuals within communities. Our results suggest that the presence of alternative host species serves as an essential buffer to phenological shifts in ecological communities, as it can provide complementary phenologies, increases functional redundancy and can dampen community responses to variation in biotic and abiotic environments (Yachi & Loreau, 1999; Yang, 2020).

4.2.1 | Complex effects of elevated temperatures on consequences of phenological shifts

We show that the effects of phenological shifts varied with warming, but to what extent differ between hosts and parasitoids.

Although growth rates of both host species increased with warming, the declines in PRs and increased HS across phenological shifts did not scale with differences in growth rates. Thus, besides variation in developmental rates among temperatures, community contexts, and species, other factors contribute to differences in effects of phenological shifts across treatments. For example, preference and the ability to locate prey of different developmental stages of higher quality could also modify outcomes of host-parasitoid interactions under warming (Augustin et al., 2021; Moiroux et al., 2015).

Our dynamic model revealed that host–parasitoid interactions were less likely to persist in predicted global warming temperatures. We also identified that some host and parasitoid species could not support interactions under warming, even when parasitoid survival, host fecundity, and phenological relationships were ideal (Figure 3; Figures S8–S10). This highlights that physiological changes in elevated temperatures, beyond shifts in development rates, can considerably modify the effect of phenological shifts on species interactions. For example, regardless of the developmental relationship, warming may compromise immune systems or the ability to heal from injuries (i.e., oviposition punctures; Abram et al., 2019; Catalán et al., 2012; Cavigliasso et al., 2021). Other studies have found that hosts are more able to successfully defend themselves against immature parasitoids in warmer temperatures (Thomas & Blanford, 2003; Wojda, 2017). Furthermore, parasitoids usually show lower thermal tolerances relative to their hosts (Agosta et al., 2018; Fellowes et al., 1999; Karban, 1998; Thierry et al., 2019; Zamani et al., 2007). Both of which support our current findings that the stability of host–parasitoid interactions is likely to decline with increasing mean temperatures.

Importantly, this simulation model does not account for evolutionary processes over generations that may help species readjust their phenological relationship to other species, community contexts, or environmental changes. Some evidence suggests that interacting species can evolve or adjust their phenological responses through adaptive phenotypic plasticity, thereby maintaining interactions' synchronization and limiting fitness costs (Kingsolver & Buckley, 2018). However, if phenological changes are too large for plasticity to counterpart, these plastic responses may not be able to prevent climate-driven phenological mismatches. Additionally, allowing dispersal and habitat heterogeneity could significantly change community dynamics (Davis et al., 1998; Holt & Hassell, 1993). Dispersal can mitigate the observed declines in performance and interaction persistence under elevated temperatures. At the same time, spatial variation in habitat structure provides refuges from attack and modifies the searching behavior of natural enemies. Both factors are predicted to promote population stability and persistence (Bukovinszky et al., 2007; Hassell et al., 1991; Sait et al., 1997), but to what extent will require further investigation. These discoveries have important implications for the persistence of key trophic interactions and top-down control, as such interruptions to top-down processes have been identified as key consequences of climate change in terrestrial and aquatic systems (Derocles et al., 2018; Shurin et al., 2012; Velthuis et al., 2017).

5 | CONCLUSION

Although long-term phenological observational studies are extremely valuable, experimental approaches combined with parameterized dynamic models can help disentangle the roles that environmental variation plays in altering the timing of species interactions in future climatic conditions. Our combined experimental and simulation study showed that the strength and persistence of species interactions are sensitive to phenological shifts among interacting species. However, the effects of phenological shifts depend on community complexity and host density. We found that the presence of another host species helps promote the long-term persistence of species interactions across a range of phenological relationships, temperatures, and levels of resource competition. The loss of biodiversity may thus reduce the persistence of species interactions. Therefore, biodiversity preservation should be a priority, given its essential role in maintaining species interactions in the face of ongoing phenological shifts, increased temperatures, and changes in other biotic environmental factors (Forister et al., 2019). Combining short-term experimental approaches with dynamic modeling techniques may be helpful in systems that lack long-term phenological data (Kharouba & Wolkovich, 2020; Rafferty et al., 2013). However, experimental studies often underestimate the effects of warming on phenology and consumer recruitment due to complex interactions among multiple biotic and abiotic drivers (Wolkovich et al., 2012). Incorporating community contexts into future phenological research will be essential to accurately predict the consequences of phenological shifts on entire ecological communities.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

Nicholas A. Pardikes and Jan Hrcek designed research; Nicholas A. Pardikes, Melanie Thierry, Chia-Hua Lue, Tomás A. Revilla, Daniel Souto-Vilarós performed research; Nicholas A. Pardikes, Jan Hrcek, Tomás A. Revilla, Melanie Thierry, Chia-Hua Lue, and Daniel Souto-Vilarós wrote the paper; Nicholas A. Pardikes and Tomás A. Revilla analyzed data.

DATA AVAILABILITY STATEMENT

All data and code used in this manuscript will be archived in Dryad and made available with the publication.

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