

LETTER

Warming of experimental plant–pollinator communities advances phenologies, alters traits, reduces interactions and depresses reproduction

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Abstract

Climate change may disrupt plant–pollinator mutualisms by generating phenological asynchronies and by altering traits that shape interaction costs and benefits. Our knowledge is limited to studies that manipulate only one partner or focus on either phenological or trait-based mismatches. We assembled communities of three annual plants and a solitary bee prior to flowering and emergence to test how springtime warming affects phenologies, traits, interactions and reproductive output. Warming advanced community-level flowering onset, peak and end but did not alter bee emergence. Warmed plant communities produced fewer and smaller flowers with less, more-concentrated nectar, reducing attractiveness, and warmed bees were more generalized in their foraging, reducing their effectiveness. Plant–bee interactions were less frequent, shorter and peaked earlier under warming. As a result, warmed plants produced fewer, lighter seeds, indicating pollinator-mediated fitness costs. Climate change will perturb plant–pollinator mutualisms, causing wide-ranging effects on partner species and diminishing the ecosystem service they provide.

KEYWORDS

annual plants, bees, climate change, flowering, foraging, nectar, pollination, seed set, solitary bees, specialization

INTRODUCTION

Climate change is restructuring ecological communities, both by directly affecting the traits of species and by reshaping interactions between species (Scheffers et al., 2016). Shifts in the timing of life history events can expose species to novel abiotic conditions, with concomitant effects on morphological and behavioural traits, and alter temporal overlap with other species (Kharouba et al., 2018; Parmesan & Yohe, 2003). Although climate change-induced phenological shifts are well documented, the likelihood of interacting species experiencing opposing or differential phenological shifts is still little-understood (de la Torre Cerro & Holloway, 2021). For some mutualisms, phenological synchrony is critical; partner species,

which may differ greatly in life history, trophic level and interdependency, must coincide at particular developmental stages for the interaction to occur (de Manincor et al., 2020; Rafferty et al., 2015). In the context of plant–pollinator mutualisms, flowering phenology shapes community structure and composition (de Manincor et al., 2020) because it influences pollinator foraging behaviour and ultimately pollinator population dynamics (Ogilvie et al., 2017; Ogilvie & Forrest, 2017). In turn, pollinator phenology shapes plant gene flow and reproductive success, and structures plant–pollinator interactions (Duchenne et al., 2020; Memmott et al., 2007). Plant and pollinator phenologies may respond differently to climate change due to reliance on different cues or differing sensitivities to the same cues (Renner & Zohner, 2018).

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In addition to altering phenology, climate change can reshape plant–pollinator mutualisms by affecting partner traits, including morphological, physiological or behavioural traits (Gérard et al., 2020), many of which are sensitive to temperature (Scaven & Rafferty, 2013). Trait-matching is especially important in plant–pollinator interactions, where flower and pollinator morphological traits shape the accessibility of nectar and pollen rewards for pollinators and the effectiveness of pollen transfer for plants (Peralta et al., 2020; Rowe et al., 2020). Warming can reduce flower size and number (Descamps, Jambrek, et al., 2021; Hoover et al., 2012; Saavedra et al., 2003) and alter nectar production and composition (Descamps et al., 2018; Descamps, Quinet, & Jacquemart, 2021; Takkis et al., 2018). In response to reduced floral resource availability, pollinators with labile preferences are expected to shift from specialization to generalization, reflecting optimal foraging (Waser, 1986). Given female bees collect pollen for offspring provisioning whereas males do not (Danforth et al., 2019a, 2019b), floral trait alterations may yield sex-specific differences in foraging behaviour. Moreover, warming can disrupt pollinator development (Slominski & Burkle, 2019) and interact with body size to influence activity patterns (Gérard et al., 2022; Willmer & Stone, 2004). Ultimately, changes in these traits shape interaction networks, fitness and population dynamics of both plants and pollinators (Peralta et al., 2020; Scaven & Rafferty, 2013).

To our knowledge, studies investigating the effects of experimental warming on plant–pollinator interactions have been restricted to direct manipulation of only one partner (Descamps, Jambrek, et al., 2021; Gallagher & Campbell, 2020; Moss & Evans, 2022; Russell & McFrederick, 2021; Schenk et al., 2018; Slominski & Burkle, 2021), limiting our ability to detect emergent effects on the mutualism. To advance an understanding of how climate change will affect mutualisms, it is crucial to conduct experiments that subject both partners to the same stresses and capture multiple mechanisms of disruption. Here, we created experimental communities to test how simultaneous springtime warming, initiated just prior to emergence and flowering, affects plant–pollinator mutualisms. We consider both phenological and trait-based mechanisms of disruption and document the consequences of warming for interactions and reproductive output for plants and bees. We used as our model a solitary bee species that serves as a pollinator in both natural and agricultural communities (Sgolastra et al., 2012) and has life history traits that are shared by a large percentage of bees (Michener, 2007). We also used three annual plants, for which the fitness consequences of phenological mismatches are unknown despite their greater phenological sensitivity than perennials to climate change (Fitter & Fitter, 2002; Stuble et al., 2021).

We tested how simultaneous warming affects plant and pollinator (i) phenology (flowering onset, peak and duration; bee emergence and lifespan); (ii) traits (nectar

production and flower size; bee foraging specialization); (iii) interactions (bee visitation and handling rates) and (iv) reproductive output (seed set and mass; bee offspring production). We predicted that, under warming, (i) flowering onset and bee emergence would advance differently; (ii) plants would be stressed, reducing flower abundance, size and nectar production; bees would exhibit more labile preferences, reducing flower-visit specialization; (iii) interaction and handling rates would be reduced due to heat stress and increased incidence of short visits to flowers offering little reward and (iv) plant and bee reproductive output would be lower, reflecting reduced interaction rates. In providing the first test of how simultaneous warming affects pollination mutualisms, our findings offer insight into the functioning of plant–pollinator communities under climate change.

MATERIAL AND METHODS

Study system

In greenhouses in Riverside, CA, USA (33.9806°N, 117.3755°W), we created two temperature treatments in two separate rooms: one targeting ambient temperatures and one targeting warming of 4°C. The ambient treatment simulated the mean high and low temperatures in Riverside in spring using monthly climate normals from 1981 to 2010 (NOAA). We programmed the warmed room to heat to +4°C above the ambient treatment on a 12:12 h day: night cycle. This magnitude of warming falls within projections of the Coupled Model Intercomparison Project (Fan et al., 2020).

Focal pollinator species

Osmia lignaria (Hymenoptera, Megachilidae) is a solitary, polylectic, univoltine bee native to much of North America, including southern California. Females lay eggs in spring, larvae undergo a summer diapause before pupating, and adults develop in autumn, remaining inside cocoons during winter diapause (Bosch & Kemp, 2001; Sgolastra et al., 2010). Temperature regulates development (Sgolastra et al., 2011), and emergence phenology is sensitive to temperature (Slominski & Burkle, 2019).

We obtained dormant adult bees from a supplier (Mountain West Mason Bees) in December 2020. The bees were kept in diapause at approximately 4°C and 70% relative humidity until used in our experiment in April 2021. In total, bees wintered for 165 days.

Focal plant species

Collinsia heterophylla (Plantaginaceae), *Nemophila menziesii* (Boraginaceae) and *Phacelia campanularia*

(Boraginaceae) are annual spring-blooming forbs native to Southern California. All three species are visited by *O. lignaria* (Boyle et al., 2020; Wood, 2010), and, although each species (or congener) is self-compatible, autonomous self-pollination yields few seeds and floral morphology and development (herkogamy, dichogamy and/or gynodioecy) promote out-crossing (Armbruster et al., 2002; Cruden, 1972; Gillett, 1961).

We obtained seeds from a local supplier (Theodore Payne Foundation). In February 2021, 360 seeds of each species were planted under ambient greenhouse conditions. Seedlings ($n = 260$ per species) were transferred to 1.9 L pots in March 2021. Plants were numbered and watered ad libitum to isolate temperature effects from water limitation. Plants were monitored every 1–5 days until treatment, and we recorded the onset of floral bud formation to the nearest day.

Experimental design

Each temperature treatment was replicated in 5 mesh arenas (4.6 m³; BugDorm) placed in either the ambient or warmed greenhouses. Four arenas per treatment were used to create communities containing potted plants of each species and *O. lignaria* (hereafter “foraging arenas”); one arena per treatment was used to create communities containing only potted plants of each species for floral trait measurements (hereafter “trait arenas”). We suspended data loggers (Onset HOBO) in each arena and greenhouse to measure temperature and relative humidity at 10-min intervals. Temperature treatments began on 14 April 2021, once bees (prior to emergence, as adults in cocoons) and plants (prior to flowering, but with floral buds) were placed in arenas.

One of our goals was to test whether springtime warming, imposed on all species in our communities at a common time point, altered phenological synchrony. We, therefore, standardized the developmental stages of all species before treatment. After wintering, cocoons were weighed to separate the sexes (0.136 ± 0.018 g [mean \pm SD] for females, 0.079 ± 0.009 g for males). Forty cocoons were assigned to each treatment, 10 per foraging arena, 4 females and 6 males to match the recommended sex ratio (hereafter the first cohort; Bosch & Kemp, 2001). Each cocoon was placed inside a paper straw liner inside a wooden nest block, with the open end of the straw enclosed with a microcentrifuge tube to retain bees upon emergence. Bee emergence was checked twice in the morning and twice in the afternoon. To each treatment, we assigned 205 plants, 40 per foraging arena, comprising 15 *P. campanularia*, 15 *C. heterophylla* and 10 *N. menziesii*. All plants had at least one floral bud but had not started flowering, indicating they were at the same developmental stage, and we assigned plants such that the variation in date of floral bud formation was equivalent among arenas. In each arena, potted plants

were arranged in five trays of eight plants each, with 2–3 plants per species per tray. Each foraging arena included a moist clay-soil mixture for nest cell construction and a south-facing empty nest block with 32 paper tube-lined holes.

Inside each trait arena, we placed 45 plants, 15 per species, arranged in trays similarly to plants in foraging arenas, except species were not intermixed. These plants experienced the same conditions as those in foraging arenas but enabled us to measure how treatments affected floral traits without interfering with visitation or attractiveness.

Data collection

We recorded the date of the first bloom and the number of flowers per plant daily for the first 12 days, after which we recorded the number of flowers per plant once per week until all plants ceased flowering.

Emergence for the first cohort of bees was recorded daily for 2 weeks, after which we removed straws from which no bees emerged. To standardize bee density, we emerged the second cohort of cocoons under controlled conditions (21°C) so that each foraging arena had four females and six males. Upon emergence, we used oil-based paint pens to mark each bee's thorax with unique colours, and bees were immediately released in the foraging arena. We noted mating, nesting activity and death.

Twice per week (AM and PM), we selected two individuals per species from each trait arena for floral measurements. On 1–2 flowers with dehiscent anthers per plant, we measured nectar volume and concentration and flower size. Flowers were sampled only once, and we avoided consecutive sampling of plants. In total, 386 flowers were measured ($N = 201$ in ambient, $N = 185$ in warmed). To measure volume, we extracted nectar with microcapillary tubes (Drummond) and used digital calipers to measure the length of the nectar column. To measure concentration, we displaced nectar onto handheld refractometers (Bellingham + Stanley) and recorded % Brix (i.e. g sucrose per 100 g solution). Three measures were taken to estimate flower size, depending on morphology: for zygomorphic flowers of *C. heterophylla* we measured corolla length, keel width and banner height from corolla base; for actinomorphic flowers of *N. menziesii* and *P. campanularia* we measured two widths perpendicular to each other and height from corolla base.

We recorded plant–bee interactions (flower visits) for 15 min at a time per arena, twice per day (AM and PM), on three non-consecutive days per week. Interactions were recorded for 23 days over an 8-week period, at which point all bees had died. Individual bees were followed until they were no longer visible (e.g., entered a nest) or ceased visiting flowers. During each observation, we recorded: bee identity, plant identity, number of visits to flowers, handling time (amount

of time a bee spent on one plant) and reward collected (pollen, nectar, or both).

We harvested at least two non-dehiscent fruits per plant per foraging arena. For each plant, we selected two sampling dates for which harvested fruits were processed for seed mass and number. After fruits dried at 60°C for 24 h, seeds and undeveloped ovules were counted under a microscope. Seed set was estimated as number of seeds/number of initial ovules. Seeds were weighed to the nearest 0.0001 g.

We removed nest blocks from foraging arenas 1 week after the last bee was observed, and stored them at ≈21°C for 107 days. Cocoons were wintered at ≈4°C and 70% RH for 165 days starting October 1st, 2021. Cocoons were weighed 14 March 2022, inserted into separate paper straws in a nest block and emerged at ≈20°C in a mesh cage. We checked straws daily, recording emergence and sex.

Statistical analyses

All analyses were performed in R version 4.1.1 (R Core Team 2021). Model assumptions were checked using the R package DHARMA (Hartig, 2022).

To evaluate the effects of warming on flowering onset, we performed Cox proportional hazard regression mixed-effect models (R package *coxme*; Therneau, 2020) for the community and each species. Day of individual plant flowering onset was the response variable, temperature treatment was the predictor, and arena identity was a random effect. To evaluate differences in other aspects of flowering phenology (peak, duration), we fitted zero-inflated GLMMs with Poisson error distribution and log-link function (R package *glmmTMB*; Brooks et al., 2017). We used the number of open flowers for the community and each species on any observation day as responses, and temperature treatment, day of year, day of year² (to check for non-linear effects) and their interaction as predictors. Day of year and day of year² were scaled and centered around the mean, and individual plant identity nested within arena identity was a random effect in all models.

For the first cohort of bees, we performed Cox proportional hazard regression mixed-effect models to estimate differences in day of bee emergence between temperature treatments for both sexes and males and females, including arena identity as a random effect. To evaluate how bee density changed through time, we fitted zero-inflated GLMMs with Poisson error distribution and log-link function (R package *glmmTMB*; Brooks et al., 2017) using the number of bees alive at each observation period as the response, temperature treatment, day of year and their interaction as predictors and arena identity as a random effect.

To evaluate differences in nectar volume and concentration, for each species we fitted LMMs using (log+1

transformed) volume (R packages *lme4*, *lmerTest*; Bates et al., 2015, Kuznetsova et al., 2017) and beta regressions with logit-link (R package *glmmTMB*; Brooks et al., 2017) using concentration, respectively, as responses, temperature treatment as the predictor, and individual plant identity as a random effect. To evaluate differences in flower dimensions for each species, we performed PERMANOVAs using Bray–Curtis distance matrices and 1000 permutations (R package *vegan*; Oksanen et al., 2020). To visualize differences in multivariate space, we performed principal component analyses on flower size measurements (R package *ade4*; Dray & Dufour, 2007) and drew biplots (R package *factoextra*; Kassambara & Mundt, 2020).

To evaluate differences in bee foraging specialization between treatments, we used the function *H2fun* (R package *bipartite*; Dormann et al., 2008) to calculate two-dimensional Shannon entropy, or H2' index (Blüthgen et al., 2006). The H2' index ranges from 0 to 1; larger values indicate greater selectivity. For the plant–bee interactions in each treatment, we built three networks: one considering both sexes, and two networks considering only one sex to account for behavioural differences. Each network comprised a matrix with rows of individual bees per observation period and columns of the three plant species. Values corresponded to the number of visits between a bee and one of the plant species. To test for between-treatment differences in H2' values we used a null model approach. We first calculated the difference (delta) between the empirical H2' values. We then calculated the difference between the H2' values for 10,000 simulated networks obtained by re-sampling visits from a matrix pooling all values, keeping the number of visits in each treatment constant. Finally, we calculated the probability of drawing a value greater than delta in the simulated distribution, which corresponds to a *p*-value for a one-tailed test (using the function *1-ecdf(delta)*, where *ecdf* is the empirical cumulative distribution function).

We divided the number of flowers visited by bees and the time spent on flowers collecting rewards in each foraging arena during each observation period by the observation duration to obtain flower visitation rates (flowers visited per min) and flower handling time (time spent on flowers per min). To evaluate differences in flower visitation rate and flower handling time, we fitted GLMMs with Gamma error distribution and log-link function. We fitted separate models using either visitation rate or handling time by both sexes and by male and female bees to the community, and by both sexes to each species as responses. We used temperature treatment, day of year, day of year², and their interactions as predictors. Day of year and day of year² were scaled and centered around the mean, and arena identity was a random effect.

To evaluate differences in seed set and mass, we fitted models for each species. We fitted GLMMs with

binomial distribution and logit-link using seed set as the response and temperature treatment as the predictor, and LMMs using log-transformed seed mass as the response and temperature treatment as the predictor. Individual plant identity nested within arena identity was a random effect. To evaluate if seed set was related to flower visitation rate, we fitted a GLMM with binomial distribution and logit-link on a subset of plants for which we tracked individual visits by bees throughout their activity period ($N = 121$ in ambient, $N = 113$ in warmed). We used seed set as the response, temperature treatment, visitation rate, and their interaction as predictors (no multicollinearity was detected, variance inflation factor was <1.6 for all predictors), and individual plant identity nested within arena identity as a random effect.

We did not analyse bee nesting success because there were too few nests in both treatments ($N = 1$ in ambient, $N = 4$ in warmed).

RESULTS

Temperature treatments

Mean day and night temperatures in the ambient treatment were $31.4 \pm 0.06^\circ\text{C}$ and $17.3 \pm 0.02^\circ\text{C}$, respectively. Monthly averages ranged from $21.7 \pm 0.09^\circ\text{C}$ in April to $27.2 \pm 0.09^\circ\text{C}$ in June (Table S1). Mean day and night temperatures in the warmed treatment were $35.4 \pm 0.06^\circ\text{C}$ and $19.3 \pm 0.03^\circ\text{C}$, respectively, with monthly averages from $26.1 \pm 0.11^\circ\text{C}$ in April to $28.7 \pm 0.09^\circ\text{C}$ in June (Table S1). Relative humidity was $67.3 \pm 0.10\%$ and $59.2 \pm 0.11\%$ in the ambient and warmed treatments, respectively (Table S1).

Phenology

Flowering onset was advanced under warming at the community level (0.40 ± 0.12 [estimated coefficient, mean \pm SE], $z = 3.45$, $p = 5.7e^{-04}$), occurring 9.3 ± 0.53 days after the beginning of the experiment in the ambient treatment and after 7.2 ± 0.39 days in the warmed treatment. Flowering onset occurred earlier in the warming treatment for *C. heterophylla* (0.78 ± 0.21 , $z = 3.73$, $p = 1.9e^{-04}$) and marginally earlier for *P. campanularia* (0.36 ± 0.19 , $z = 1.93$, $p = 0.05$), but not for *N. menziesii* (0.36 ± 0.24 , $z = 1.51$, $p = 0.13$; Figure 1). The estimated flowering peak occurred 7.4 days earlier under warming for the entire community (Figure 2). The estimated peak occurred 8.4 days earlier for *C. heterophylla* and 4.2 days earlier for both *N. menziesii* and *P. campanularia* under warming (Figure S1, Table S2). Flowering periods were shorter for warmed communities (Figure 2) and species (Table S2). Overall, communities across both treatments had similar numbers of open flowers over time,

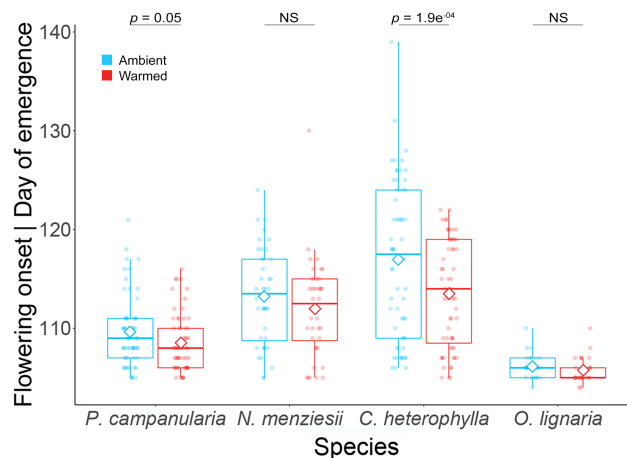


FIGURE 1 Day of year of flowering onset for *Phacelia campanularia*, *Nemophila menziesii* and *Collinsia heterophylla* and emergence for *Osmia lignaria* under ambient (blue) and warmed (red) treatments. Diamonds indicate mean values.

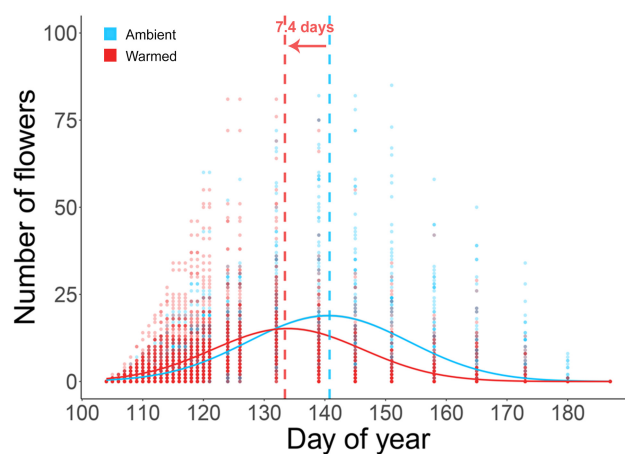


FIGURE 2 Number of open flowers per plant over time for all plant species (community) under ambient (blue) and warmed (red) treatments. Dashed lines indicate estimated flowering peaks, which occurred 7.4 days earlier under warming. Nine data points greater than 100 were omitted to enhance visibility of the rest of the data.

with warmed *C. heterophylla* and *N. menziesii* producing fewer flowers and warmed *P. campanularia* producing more flowers over their entire flowering periods (Figure S1, Table S2).

Bees emerged 2.14 ± 0.22 days and 1.76 ± 0.24 days after the beginning of the experiment in the ambient and warmed treatments, respectively (0.05 ± 0.26 , $z = 0.20$, $p = 0.84$; Figure 1). Males emerged 1.94 ± 0.34 days and 1.29 ± 0.21 days post ambient and warmed treatment, respectively (0.25 ± 0.34 , $z = 0.72$, $p = 0.47$). Females emerged 2.38 ± 0.27 days and 2.42 ± 0.43 days post ambient and warmed treatment, respectively (-0.32 ± 0.41 , $z = -0.81$, $p = 0.42$). Between treatments, bee density did not differ (0.54 ± 0.82 , $z = 0.66$, $p = 0.51$), and decreased comparably over time (-0.01 ± 0.01 , $z = -0.92$, $p = 0.36$).

Traits

Nectar volume was lower under warming (Figure 3a–c, Table S3), decreasing by 62.7% in *C. heterophylla*, 60.4% in *N. menziesii*, and 75.8% in *P. campanularia*. Nectar was more-concentrated under warming (Figure 3d–f, Table S4), increasing by 21.5% in *C. heterophylla*, 6.1% in *N. menziesii*, and 124.5% in *P. campanularia*. Flower size was affected by temperature in *C. heterophylla* ($p = 0.005$) and

P. campanularia ($p = 0.002$), but not in *N. menziesii* ($p = 0.1$, Table S5, Figure S2b). Flowers of *C. heterophylla* had narrower wings and shorter banner petals (5.6% and 4.4% decrease, respectively) under warming (Table S5, Figure S2a). Flowers of *P. campanularia* had shallower corollas (17.5% decrease) under warming (Table S5, Figure S2c).

Bees were more specialized in their foraging patterns in the ambient treatment when both sexes were considered ($H2'_{\text{ambient}} = 0.62$ vs. $H2'_{\text{warmed}} = 0.50$; $p = 0.03$) and

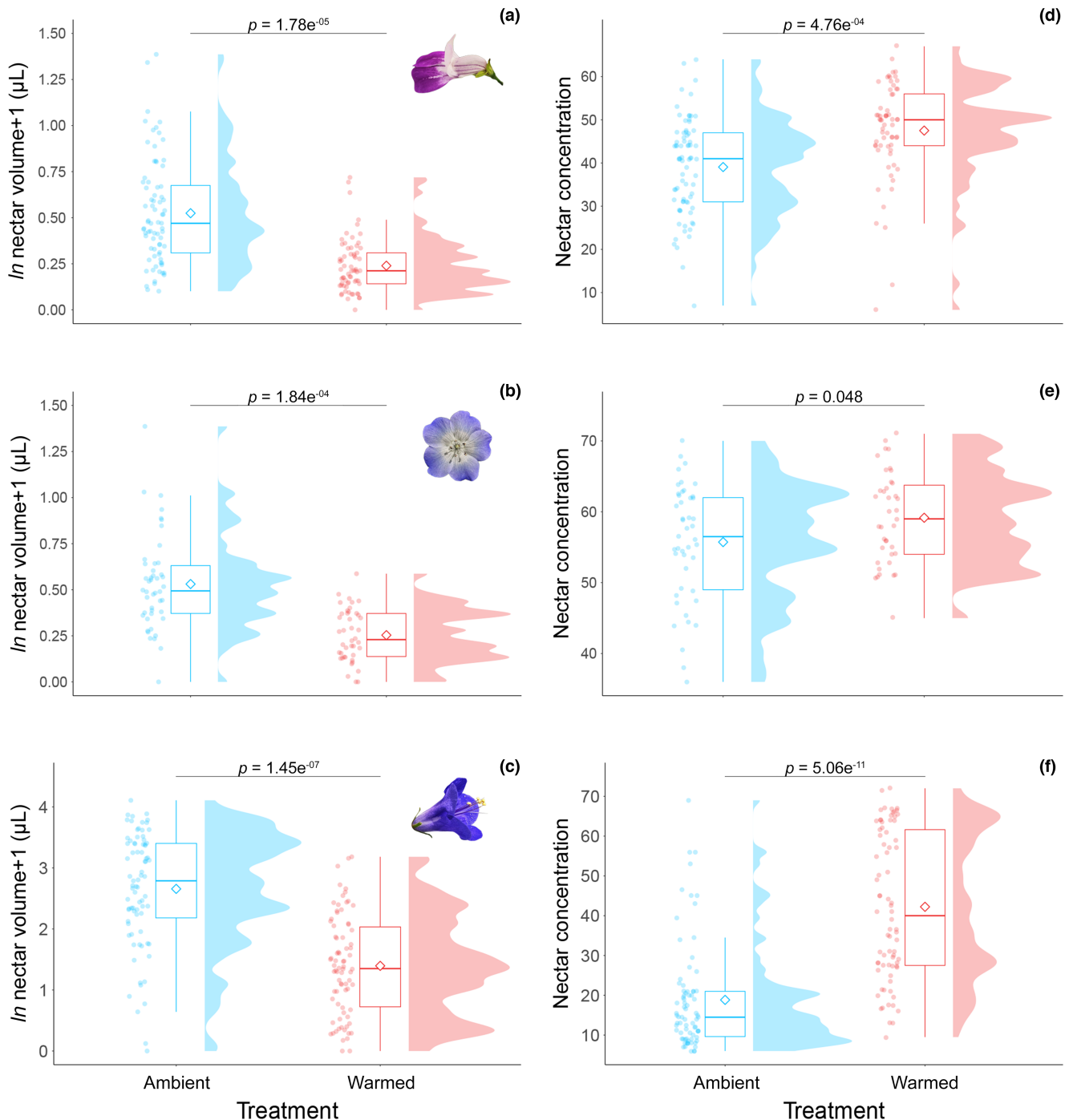


FIGURE 3 Raw data, boxplots, and density of data points for (a–c) nectar volume (μL) and (d–f) nectar concentration (% Brix) for (a, d) *Collinsia heterophylla*, (b, e) *Nemophila menziesii* and (c, f) *Phacelia campanularia*. Diamonds indicate mean values.

when only females were considered ($H2'_{\text{ambient}} = 0.53$ vs. $H2'_{\text{warmed}} = 0.43$; $p = 0.04$). There was no difference in specialization for males ($H2'_{\text{ambient}} = 0.74$ vs. $H2'_{\text{warmed}} = 0.59$; $p = 0.18$).

Plant–bee interactions

We recorded 2702 interactions between plants and bees ($N = 1904$ in ambient, $N = 798$ in warmed). Flower visitation rate was lower in the warmed arenas (0.38 ± 0.04 visits per min) compared with the ambient arenas (0.91 ± 0.08 visits per min) when considering the entire community (Figure 4a), and each species (Figure S3, Table S6). Visitation rate peaked 6.7 days earlier under warming at the community level (Figure 4a). Peak visitation rate advanced for *C. heterophylla* and was delayed for *N. menziesii* under warming, while no differences were detected for *P. campanularia* (Figure S3, Table S6). Female but not male bees had lower visitation

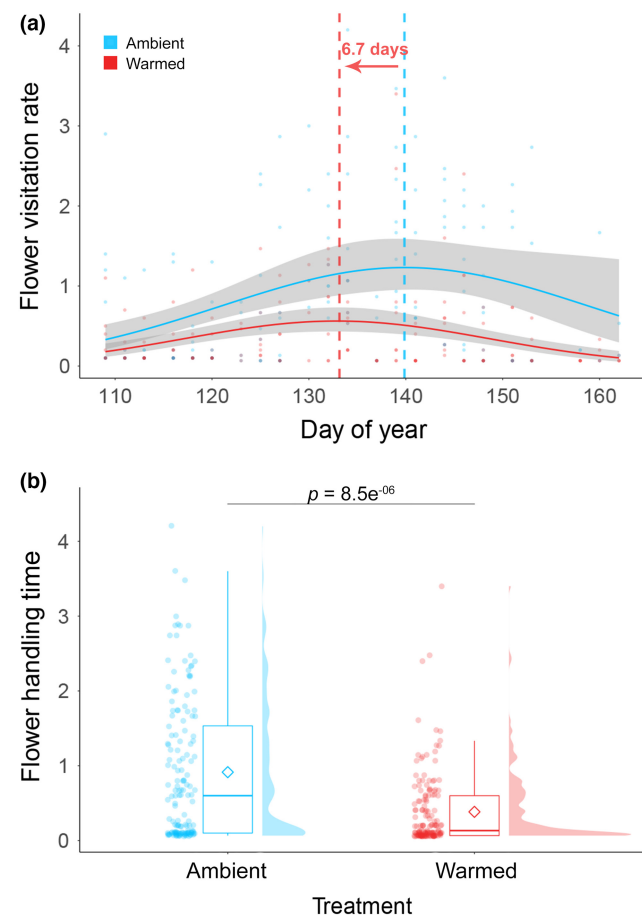


FIGURE 4 (a) Flower visitation rate (number of visits per foraging arena per min) and (b) flower handling time (seconds spent on flowers collecting floral resources per foraging arena per min) by all bees to all plant species under ambient (blue) and warmed (red) treatments. Dashed lines in panel (a) indicate the estimated peak for flower visitation rates, which occurred 6.7 days earlier under warming, and shaded areas represent 95% confidence intervals. Diamonds in panel (b) indicate mean values.

rates under warming (Table S6). Male and female bees showed different visitation rate patterns in the ambient treatment, with male bee visits peaking earlier and female bee visits peaking later in the season, while they showed similar patterns under warming (Figure S4, Table S6). Warmed bees spent less time foraging on flowers of each plant species (Figure S5, Table S7) and at the community level, making visits that were less than half the duration of visits by bees in ambient conditions (0.38 ± 0.04 vs. 0.91 ± 0.08 s per min; Figure 4b). Female bees spent less time foraging on flowers in the warmed arenas, while no differences were observed for male bees (Figure S6, Table S7).

Reproductive output

Seed set was lower under warming in all species (Figure 5a–c, Table S8). Seed set decreased by 25.3% in *C. heterophylla*, 7.1% in *N. menziesii*, and 8.2% in *P. campanularia* under warming. Seed mass decreased by 23.8% in *C. heterophylla* under warming (Figure 5d), while no differences were observed in *N. menziesii* or *P. campanularia* (Figure 5e,f, Table S9). Overall, seed set was positively correlated with the visitation rate, and we found a correlation between the visitation rate and treatment (Table S10). Seed set was high, independently from the visitation rate in the ambient treatment, whereas more visits were needed to reach the maximum seed set under warming (Figure 6).

All cocoons developed into adults and emerged in the spring of 2022. The nest from the ambient treatment contained one cocoon (0.088 g), from which a male emerged within 5 days. Nests from the warmed treatment contained 11 cocoons. Seven cocoons developed into males (0.053 ± 0.005 g), emerging within 2–6 days, and four into females (0.106 ± 0.008 g), emerging within 9–10 days.

DISCUSSION

Our results demonstrate that warming can perturb an ecologically and economically critical mutualism, causing wide-ranging effects on partner species and potentially diminishing the ecosystem service they provide. Specifically, we show that warming had varied effects on both the phenologies and traits of the plants and pollinators evaluated, generating emergent effects on their interactions and plant fitness. At the community level, warming advanced flowering onset, but bee emergence was less responsive. Because emergence tended to precede flowering in both warmed and ambient communities, earlier flowering onset reduced the phenological mismatch between these initial phenophases. However, warmed plant communities produced fewer floral resources. Given nectar is critical for bee

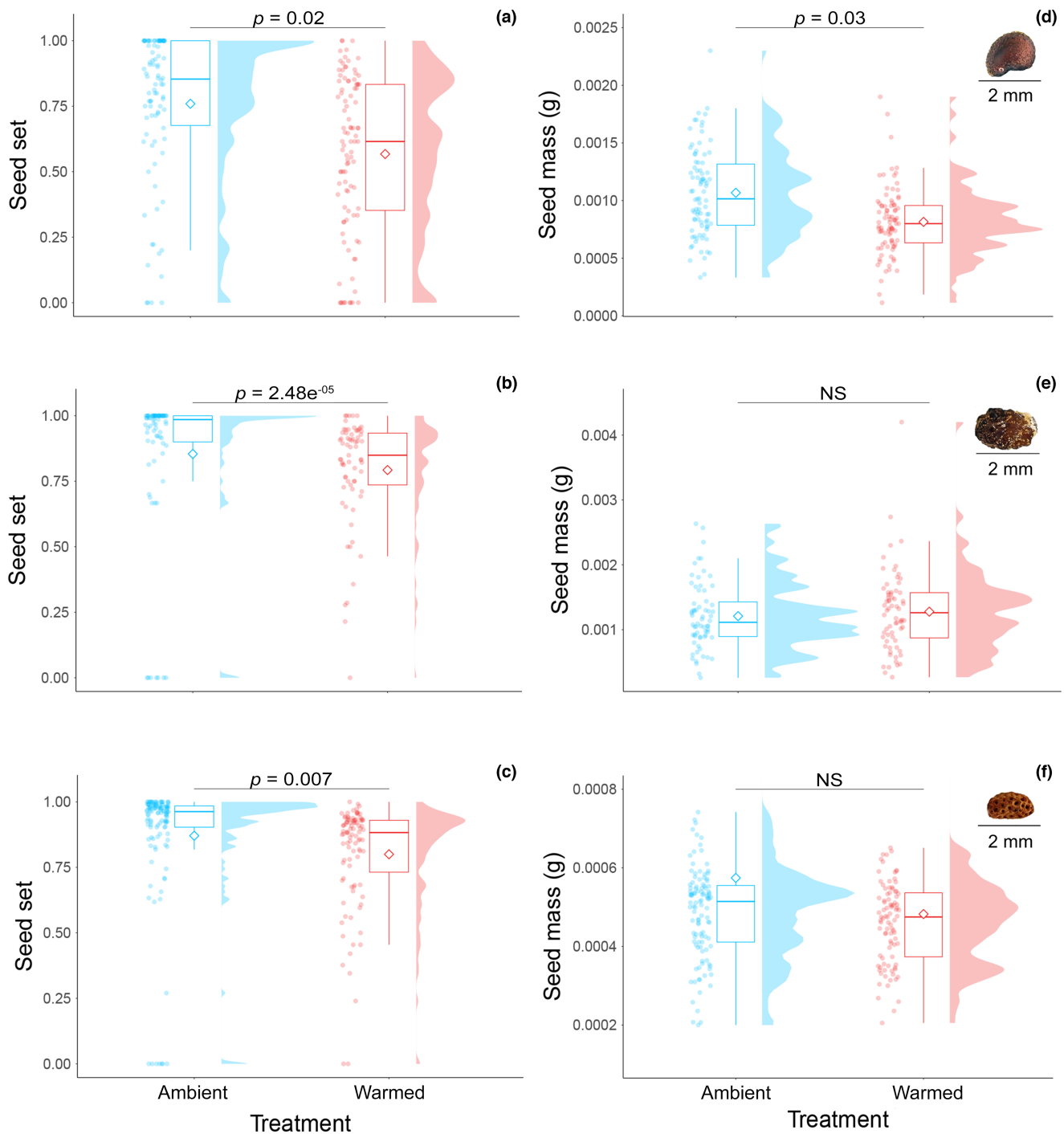


FIGURE 5 Raw data, boxplots, and density of data points for (a–c) seed set and (d–f) seed mass for *Collinsia heterophylla* (a, d), *Nemophila menziesii* (b, e), and *Phacelia campanularia* (c, f). Diamonds indicate mean values.

energetics (Nicolson, 2007), its scarcity likely limited foraging activity, reflected in the reduced interactions and handling time we documented. At the same time, limited floral resource availability was associated with more-generalized bee foraging patterns, reducing pollinator effectiveness and seed set. Thus, our results point to reciprocal negative effects of warming on mutualistic partners that emerge from how their individual species-level responses reshape their interactions.

Warming affected plant and bee phenology to different extents. Under warming, the phenology of the plant community was advanced: flowering started, peaked and ended earlier. However, each constituent plant species responded differently. For example, flowering onset in *N. menziesii* was unaffected by warming, and, whereas peak flower abundance was lower in warmed *C. heterophylla* and *N. menziesii*, warmed *P. campanularia* produced more flowers. Similar species-specific

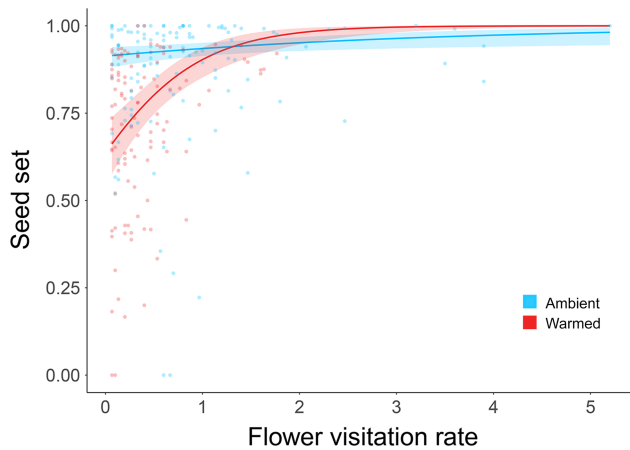


FIGURE 6 Interaction plot showing seed set in relation to flower visitation rate in the ambient (blue) and warmed (red) treatments. Shaded areas represent 95% confidence intervals.

responses of flowering phenology to warming have been described (Fitter & Fitter, 2002; Menzel et al., 2006; Rice et al., 2021) and likely reflect evolutionary history, including adaptations that shape phenological sensitivity to abiotic cues, and the degree of phenotypic plasticity (Arnold et al., 2019; Brunet & Larson-Rabin, 2012). Although warmed bees tended to emerge earlier, the effect was not significant. The timing of emergence in *O. lignaria* depends not only on temperature during the pre-emergence or incubation phase but also on the durations of the prepupal and diapause periods, both of which are sensitive to temperature (Sgolastra et al., 2011; Slominski & Burkle, 2019). Because longer diapause can correspond to a shorter incubation period (Bosch & Kemp, 2003), and the bees in our study experienced a relatively long diapause (165 days), they emerged soon after incubation in both treatments, narrowing the window for warming-induced advancement. Nevertheless, our results indicate that warming reduced the potential for phenological mismatch by advancing community-level flowering, shortening the interval between bee emergence and flowering onset.

Greater synchrony in initial phenophases did not compensate for reduced resource availability. In addition to fewer flowers in two species, we observed reduced flower sizes and nectar production in warmed plants. Warming during floral tissue development can modify floral features and negatively affect floral resource production and quality (Descamps, Quinet, & Jacquemart, 2021; Russell & McFrederick, 2021; Takkis et al., 2018), with profound consequences for plant fitness (Borghini et al., 2019; Liu et al., 2012). Under warming, two of our study species produced smaller flowers, and all three species produced lower volumes of more-concentrated nectar. These warming-induced alterations in floral resources likely reduced the attractiveness for bees, modifying their foraging behaviour (Descamps, Jambrech, et al., 2021; Moss & Evans, 2022; Torchio, 1985). Indeed,

bees exhibited more labile preferences, reducing flower-visit specialization under warming. Whereas male bees visit flowers mainly to consume nectar (Danforth et al., 2019b), females tend to visit flowers that provide resources for offspring provisioning (Boyle et al., 2020; Danforth et al., 2019a; Ritchie et al., 2016). Despite being polylectic, female *O. lignaria* can show pollen preferences (Rust, 1990), which likely resulted in the more specialized behaviour observed under ambient temperatures. Conversely, increased generalization of warmed bees is expected under floral resource limitation and likely reflects optimal foraging (Emlen, 1966; MacArthur & Pianka 1966; Fontaine et al., 2008). These findings demonstrate the adverse impacts of warming on floral traits of annual wildflowers and associated changes in bee foraging behaviour.

Interactions were less frequent and shorter under warming. Visitation rates and handling time were especially reduced for warmed female bees, likely reflecting modifications in floral traits, but not for warmed males, likely because males spend minimal time foraging, searching instead for females (Danforth et al., 2019b). Corolla size and flower abundance can be positively correlated with pollinator visitation (Akter et al., 2017; Fowler et al., 2016; Knauer et al., 2021). Moreover, higher nectar sugar concentration can enhance flower visits (Cnaani et al., 2006; Fowler et al., 2016), and larger nectar volumes can increase the amount of time bees spend visiting flowers (Knauer et al., 2021; Thomson 1988). Reduced nectar volumes, corolla sizes, and flower abundances likely drove fewer flower visits and shorter foraging periods in warmed conditions, despite the potentially positive effect of increased nectar concentration. Additionally, flight is more energetically costly at higher temperatures, limiting bee foraging (Kenna et al., 2021). Because bee density did not vary by treatment, reduced interaction rates were a result of warming and not of bees having shorter lifespans. Weakened interaction strength can portend mutualism disruption (Burkle et al., 2013; Kiers et al., 2010), particularly in the absence of alternative partner species. Even if alternative partners are available, they are unlikely to be substitutable in terms of effectiveness (Brosi & Briggs, 2013) and the selection pressures they exert (Aigner, 2005).

Finally, warming negatively affected plant fitness; all three species produced fewer seeds per fruit and one species produced lighter seeds. Although seed set was positively correlated with the visitation rate, warmed plants needed to receive a higher number of visits to attain full seed set. Reduced reproductive output likely reflects reduced interaction rates and increased generalization in warmed communities. As warmed bees were more likely to visit flowers of multiple plant species, they probably facilitated heterospecific pollen transfer, reducing their per-visit effectiveness (Briggs et al., 2016). Differences in resource availability may also have contributed to differences in seed set; however, the fact that some fruits of

each species had full seed set regardless of temperature treatment suggests that plants could set full seed if adequately pollinated. Predominantly outcrossing annual plants like those in our communities are especially vulnerable to population declines from reduced pollination success and depressed seed set (Halley & Manasse, 1993).

Bee nesting activity was low in both treatments, suggesting nest initiation and cell construction may have been limited by a lack of fertilized eggs, rather than floral resource availability (Danforth et al., 2019a). Additionally, because males in our communities were not able to disperse after mating, they may have harassed females, interrupting their nesting and provisioning behaviour. Under warmer conditions, female solitary bees may produce more brood cells, as was the case in our warmed communities where 10 times as many brood cells were produced, but higher temperatures may also be linked to reduced bee lifespan, translating into reduced reproductive output (Wong & Forrest, 2021). Lastly, the bees we used may not have been adapted to our ambient conditions, which were likely warmer than those experienced in their source populations, potentially reducing male bee fertility and attractiveness (Martinet et al., 2021) and female nesting success (Pitts-Singer et al., 2014) across treatments.

To isolate key factors, we created controlled, simplified communities; however, we recognize that this does not allow for interactions with alternative partners that could modify the responses of our focal species. We also sought to isolate the effects of springtime warming on the emergence and flowering phenology by starting our temperature treatments at a common developmental point for both bees and plants. Warming bees or plants at earlier stages, for example as larvae or seedlings, or throughout their life cycles would likely produce different results. To guard against the loss of the essential ecosystem service of pollination in our managed and natural communities with continued climate change, we need experiments that anticipate future conditions and capture the complex responses of ecological communities.

CONCLUSIONS

Simultaneous warming of plants and pollinators resulted in reduced community functioning, manifested in altered phenologies and traits, lower interaction rates and depressed plant reproduction. Our work suggests that current levels of warming could already be perturbing plant–pollinator communities and illustrates that relatively subtle changes in the timing of flowering, flower and nectar production, and bee foraging behaviour can have significant negative consequences for pollination success. If the negative effects of warming are compounded through multiple generations of plants and pollinators, population declines are likely, resulting in less-resilient communities with profound consequences for ecosystems and the services they provide.

AUTHOR CONTRIBUTIONS

All authors designed the study and collected data, NdM and AF performed analyses, NdM and NER wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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