

RESEARCH ARTICLE

Temperature influences pollinators' choice of floral partners independently of community composition

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Funding information

DEVCOM Army Research Laboratory, Grant/Award Number: W911NF1910231; Division of Biological Infrastructure, Grant/Award Number: DBI-2305867; Division of Environmental Biology, Grant/Award Number: DEB-1834487 and DEB-2129759; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: DGE-2140004

Handling Editor: Kate Pereira Maia

Abstract

1. Climate change can impact species interactions by changing the spatial and/or temporal overlap of interaction partners, but interspecific interactions can also vary when partners remain co-located in space and time. Understanding the effects of climate-driven environmental variation, such as rising temperatures, is particularly important for interactions that underlie key ecosystem functions like pollination. However, very little is known about how temperature variation may impact plant-pollinator interaction patterns in the absence of shifts in species presence or abundance, in part because environmental variation across multiple days or sites is often confounded with changing community composition.
2. In this study, we examined the effects of temperature variation on pollinators' choice of floral partners within near-static ecological communities by sampling interactions at multiple temperatures within individual days—a method that allowed us to disentangle the effects of temperature variation and species turnover on patterns of plant-pollinator interactions. The substantial temperature variation both within and across days in each growing season also enabled us to largely disentangle temperature variation from time-of-day effects. With this sampling protocol, we show that temperature can influence pollinator floral choice independently of changes in species composition.
3. We found differences in the choice of floral resources across pollinator taxa as temperature varied during individual days and further found that bumble bees, but not sweat bees, exhibited this pattern when analyzed independently. We also confirmed that our observed trends were not driven by variation in the number of interactions recorded, the relative abundance of pollinators, or in the overall attractiveness of flowers at different temperatures.
4. We propose that thermal niche partitioning in this system could be driven by physiological and behavioral factors including energetics and competition for specific floral resources at different temperatures. These insights into thermal variation in pollinators' floral choice contribute to wider understanding of the

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fine-scale mechanisms through which climate change may impact ecological networks, community resilience, and ecosystem functioning.

KEYWORDS

dietary preference, energetics, floral choice, plant–pollinator interactions, pollination ecology, temperature, thermal niche

1 | INTRODUCTION

The structure and function of ecological communities are influenced by the environments in which they exist. Climatic factors like temperature and precipitation, along with human impacts like land use change, are key factors driving the abundance and distribution of organisms (Devoto et al., 2009; Ganuza et al., 2022). With changes to these conditions, organisms may shift their geographical distributions or alter the timing of key life history events (e.g. emergence from overwintering, flowering, and reproduction), potentially reducing the times and spaces over which interacting species co-occur. These spatiotemporal mismatches can thus result in the reduction or loss of interactions that underlie important ecological functions and maintain biodiversity (Burkle et al., 2013; Hegland et al., 2009). Furthermore, even if organisms continue to co-exist in space and time, variation in abiotic resources and stressors (e.g. water, heat) can trigger physiological and behavioural changes that could result in altered interaction patterns both in tandem with and independently of changes to the abundance or distribution of the species involved (Espíndola et al., 2011; Scaven & Rafferty, 2013).

Understanding the effects of temperature variation on plant–pollinator interaction patterns is of urgent importance in an era of unprecedented climate change. Animal pollination is a key component of reproduction for around 85% of flowering plants (Ollerton et al., 2011), and these plant–pollinator interactions involve multiple dynamic components that are likely to respond to rising temperatures even without major shifts in species' ranges or phenologies. The quantity and composition of nectar—a major incentive for pollinator visitation—is expected to shift with abiotic conditions like temperature and water availability (McCombs et al., 2022; Russell & McFrederick, 2022). Temperature differences can also alter the energetic balance that determines when pollinators are able to forage and the caloric reward that they seek from nectar (Heinrich, 1975; McCallum et al., 2013). Thus, it is reasonable to expect plant–pollinator interactions to vary to some extent in response to local environmental conditions.

Previous work has found evidence that local temperature may affect the rates of interaction occurrence and patterns of specialization between plants and insect pollinators (Classen et al., 2020; Richman et al., 2020). However, study designs like transplant experiments and elevational comparisons are not well suited for disentangling the ways that temperature can affect plant–pollinator interactions independently of the potentially confounding influence of species turnover. Specifically, elevational gradients provide

predictable thermal variation over which researchers can observe interactions at different temperatures, but often exhibit high rates of species turnover. Transplant experiments involve directly changing species composition to observe how these species respond to different environmental conditions. While understanding such joint influences of thermal and biological variation can provide key information for how plant and pollinator co-occurrence may be affected by climate change, it is also important to determine whether pollinators' foraging preferences themselves may change under novel temperature regimes.

We examined how populations of insect pollinators altered their choice of floral partners in response to naturally occurring temperature variation. We used a sampling approach in which we surveyed plant–pollinator interactions at repeated intervals within distinct sampling days at six sites in the Rocky Mountains of Colorado, USA, where temperature can vary by 30°C within a single day. This approach held plant community composition constant within each sampling day and greatly limited variation in pollinator community composition, thus allowing us to isolate the effect of temperature variation on floral choice among populations of insect pollinators. We hypothesized that differences in plant resource production and pollinator metabolic needs across temperatures would lead to changes in the frequency of visits that distinct pollinator taxa made to available flowers. We thus predicted that we would find an effect of temperature on pollinators' choice of available floral partners in these relatively static communities, though we expected that these effects would be highly dependent on the taxonomic identities of the plant and pollinator involved in each interaction. Our findings provide novel insight into the ways that interacting populations respond to temperature variation and lay the groundwork for future work predicting how global environmental change may alter the structure and function of plant–pollinator communities.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted this study near the Rocky Mountain Biological Laboratory (38°57.50' N, 106°59.30' W, 2900-m above sea level) in the Gunnison National Forest (Gunnison County, Colorado, United States). This subalpine ecosystem is categorized by open wildflower meadows surrounded by aspen and conifer forests in a near-natural condition. Importantly, there is a conspicuous absence of European

honey bees (*Apis mellifera*) and a very limited number of non-native floral species (e.g. *Linaria vulgaris*, *Taraxacum officinale* and *Tragopogon dubius*) present in the area. The floral growing season and pollinator foraging season generally occurs from late May until the end of August, which is the majority of the snow-free season. During this summer growing season, temperatures range from approximately 0°C to over 30°C, with average daytime temperatures of 21°C (Prather et al., 2023).

Throughout this study, we refer to 'plant-pollinator interactions' because pollination is the ecological function motivating our research. However, accurately categorizing pollen transfer and pollination success is a labour-intensive process that generally requires some assessment of pollen deposition on stigmas and/or seed production following a single insect visitation event (Ne'eman et al., 2010). In order to perform this study at the scale of entire plant-pollinator networks, we opted to use floral visitation as a proxy for pollination. While visitation is by no means a perfect proxy for pollination (King et al., 2013), it provides a baseline understanding of the broad-scale processes that underlie the transfer of pollen by insect visitors.

All fieldwork was conducted under USFS Special Use Permit GUN1120. Our work did not require any ethics approvals.

2.2 | Data collection

We conducted our research at four meadows in the summer of 2021 and at six meadows, including all four from the previous year, in the summer of 2022 (Supporting Information S1). At each meadow, we established three 1-m × 10-m transects in which we conducted weekly surveys over the 6–9 weeks during which flowers were blooming. In order to observe pollinators foraging at multiple temperatures within the same plant community, we conducted three sampling rounds on each study day, beginning at 10:00 AM, 12:00 PM and 2:00 PM, unless precluded by inclement weather. At each meadow, we also installed a data logger (HOBO Pendant, UA-001-08) covered by a radiation shield 10-cm above the ground to passively record site-specific temperature at 30-min intervals.

For each of our three daily sampling rounds, we observed plant-pollinator interactions for 45 min of active sampling evenly distributed across the three transects. We separated each of these three transects into five 1-m × 2-m segments in which we surveyed the species identity and floral abundance of every plant rooted inside the segment available for interaction with an insect visitor. We defined these insect visitors, or possible pollinators, broadly as any flying insect that touched the reproductive parts (stigmas or anthers) of a flower regardless of whether pollen was visible on its body. If any insect touched the reproductive organs of a flower rooted within our transects during our active sampling time, we immediately collected it for subsequent laboratory identification to species level, with the exception of bumblebees (Apidae: *Bombus* spp.), which we were able to identify to species in the field using a local field guide.

Collection of insects at this scale has been shown not to significantly affect insect population densities within or across seasons (Gezon et al., 2015).

2.3 | Data analysis

We conducted all analyses in the statistical software R (R Core Team, 2023). All data and a fully replicable Rmarkdown of the analyses are available on Zenodo (<https://doi.org/10.5281/zenodo.17049963>; Arrowsmith et al., 2025).

2.3.1 | Pollinator community composition between sampling rounds

We performed matrix regression to verify that pollinator community composition remained constant across sampling rounds on the each day. We calculated beta diversity of insects between each sampling round using *vegan* (Oksanen et al., 2025) and adapted the *MRM* function from *ecodist* (Goslee & Urban, 2007) to include a permutation control by site/date in order to isolate the specific effect of these variables during unique site/date pairs.

2.3.2 | Temperature variation

This study relied upon our sites experiencing variation in temperature throughout the course of individual days. To test whether we captured this temperature variation during our sampling periods, we used a linear mixed effects model (Bates et al., 2015) with average temperature during each sampling round as our response variable, sampling date and round as fixed effects, and site as a random intercept. We then assessed the overall effect of round using analysis of variance (ANOVA) and contrasts between rounds using the *emmeans* package (Lenth, 2024) using a pairwise contrast and a Tukey adjustment for multiple comparisons. We also performed ANOVAs for each site/year combination to examine temperature variation within and among rounds at individual sites.

2.3.3 | Choice of floral partner

We isolated the effect of temperature from that of plant community composition using a mixed conditional logistic regression from the *mclogit* package (Elff, 2022). This type of multinomial statistical model can be used to find patterns in the selection of a resource from among a set of available choices ('choice set'), such as the selection of a habitat patch from the landscape available to a free ranging animal (Duchesne et al., 2010). In our case, this model assessed whether pollinators' choices of floral partners within the choice set of plants available at a given site and date changed in relation to the temperature variation that naturally occurred

across rounds. We included temperature as a main effect via both linear and quadratic terms because we expected that pollinators' responses to temperature could be non-linear. We also included a factor with three levels defining sampling round as a fixed effect, since floral resources can fluctuate over the course of a day in response to pollinator foraging (Inouye, 1978) and intrinsic daily cycles (Herrera, 1990; Polatto et al., 2014). A significant effect of sampling round would thus indicate that some portion of our observed trends could be driven by changing resource availability, despite the constancy in the flowers present. We performed post hoc analysis on the relationship between sampling rounds in our model using the *emmeans* package (Lenth, 2024) using a pairwise contrast and a Tukey adjustment for multiple comparisons. In all models, we included the taxonomic identity of the plant and insect involved in each interaction as random slopes and intercepts, under the assumption that taxa would exhibit different mean interaction occurrence and respond differently to temperature moving from that mean.

We conducted the above analysis at three different biologically relevant groupings. First, we analysed all insects that were identified to the species or morpho-species level in order to obtain the broadest possible understanding of how temperature influenced pollinator foraging choice. Then, we isolated the two most commonly observed insect genera—bumble bees (Apidae: *Bombus* spp.) and sweat bees (Halicitidae: *Lasioglossum* spp.)—and conducted the same analysis for these two genera separately in order to understand how our broad-scale trends might vary within finer level taxonomic groupings. We used these finer scale models to visualize how these two genera visited key floral partners across temperatures using the *ggeffects* package (Lüdtke, 2018).

2.3.4 | Pollinator activity and plant attractiveness

A number of variables could influence the pollinator visitation patterns that we recorded in the field independently of temperature variation. For instance, differences in the number and composition of pollinators observed during a sampling round could alter competitive dynamics, and daily patterns of floral resource production and utilization could yield different overall numbers of interactions to particular flowers. In order to ensure that our observed relationships between temperature and interaction occurrence were not confounded by any such trends in pollinator activity or floral resource production, we performed three sets of supporting analyses. For all three analyses, we built generalized linear mixed-effects models (GLMMs) using the *glmmTMB* package (Brooks et al., 2017), calculated type-II ANOVA tables using the *car* package (Fox & Weisberg, 2019) and calculated pairwise contrasts for relationships in which the factor of sampling round was significant using the *emmeans* package (Lenth, 2024) using a pairwise contrast and a Tukey adjustment for multiple comparisons.

First, we tested whether temperature or sampling round influenced the total number of plant–pollinator interactions that we

observed, which could illustrate broad-scale variation in the foraging activity of pollinators or overall availability of floral resources. We used a negative binomial error distribution with the total number of observed interactions during each round as our response, temperature (linear and quadratic) and sampling round (factor) as fixed effects, and date and site as random intercepts.

Second, we tested whether temperature or sampling round influenced the relative abundance of pollinator taxa observed during our sampling periods, which could yield different competitive landscapes and likelihoods of pollinator observation. We modelled our response as a proportion of the total interactions belonging to a particular insect taxon during each sampling round and used a binomial error distribution. As above, we included fixed effects defining temperature (linear and quadratic) and sampling round. Since this model was specific to the identity of pollinators present, we included insect species as a random slope with temperature as well as site, date and insect species as random intercepts.

Third, we tested whether temperature or sampling round influenced the relative abundance of visits received by particular plant species. We expected that such variation could occur if particular floral species produced different amounts of floral resources at particular temperatures or times of day, or if pollinator foraging earlier in the day depleted resources for visitors later in the day. While our mixed conditional logistic regressions accounted for the overall composition of the floral community, it could not account for the raw amount of nectar or pollen available at these flowers, since we did not empirically collect that data due to logistical constraints in the field. We modelled our response variable as a proportion of the total interactions received by a particular plant species during each round, using a binomial error distribution and fixed effects as above. Our random effects were also as above, but with a random slope and intercept of plant identity replacing the random effects of insect species.

3 | RESULTS

3.1 | Sampling information

We conducted 186 sampling rounds across 2 years during which we observed a total of 1296 plant–pollinator interactions between 47 insect taxa that we could identify to the species level and 64 floral species (Supporting Information S1). The most commonly observed insect pollinators were in the genus *Bombus* ($n = 656$, 50.6% of total insects observed) and the genus *Lasioglossum* ($n = 171$, 13.2% of total insects observed). The number of interactions that we observed during each sampling round ranged substantially, from a single interaction involving an insect that we could identify to species to 31 interactions. The total number of interactions observed during a single sampling round also varied across the season and peaked around early July. On average, we observed about 7 ± 6.2 (mean $\pm$ SD) total interactions between 3.5 ± 2.1 pollinator taxa and 2.2 ± 1.1 plant species per sampling

round. We found no significant effect of sampling round on the composition of the pollinator communities within individual site/dates ($\beta = -0.031$, $p = 0.824$; Table S2a).

Recorded temperatures during our sampling periods ranged from 15.04°C to 38.27°C. Temperature significantly varied with date ($\chi^2 = 25.439$, $df=2$, $p < 0.001$) and sampling round ($\chi^2 = 18.470$, $df=2$, $p < 0.001$; Table S2b), with temperatures generally increasing over the season (Figure 1a) and over the course of individual days (Figure 1b). We identified significant differences in temperature between round 1–round 2 ($t_{176} = -3.613$, $p = 0.001$) and round 1–round 3 ($t_{176} = -4.240$, $p < 0.001$), but not between rounds 2 and 3 ($t_{176} = -0.733$, $p = 0.744$; Table S2c). When we analysed each site/year combination separately (Table S2d), we found significant relationships between temperature and sampling round at only two site/year combinations—Ohio Pass High ($F_2 = 4.598$, $p = 0.026$) and Ohio Pass Low ($F_2 = 4.173$, $p = 0.035$), both of which were only sampled in 2022. We also saw substantial overlap in the interquartile ranges for temperature variation across all site/years (Figure 1b), including a lack of linear increase among the means for the three rounds at multiple sites.

3.2 | Choice of floral partner

Quadratic temperature ($z = -2.441$, $p = 0.015$) significantly influenced pollinators' floral choice when we tested across all taxonomic groups (Figure 2a; Table S2e). We also found that pollinators' floral choice was affected by sampling round, suggesting an effect of changing resource availability across rounds despite constancy in floral composition. Specifically, we found that pollinators' floral choice significantly differed between the second and third sampling rounds ($t_{6786} = 2.408$, $p = 0.043$; Table S2f) and marginally differed between the first and second sampling rounds ($t_{6786} = -2.150$, $p = 0.080$). The first and third sampling rounds did not exhibit different floral choice across all pollinators ($t_{6786} = -0.078$, $p = 0.997$). We found linear ($z = 2.380$, $p = 0.017$) and quadratic ($z = -3.381$, $p < 0.001$) effects of temperature on floral choice when we isolated just the *Bombus* genus, though we did not see a significant effect of sampling round for this taxon (Tables S2g,h). Neither temperature nor sampling round influenced floral choice for our next most commonly recorded insect genus, *Lasioglossum* (Tables S2i,j).

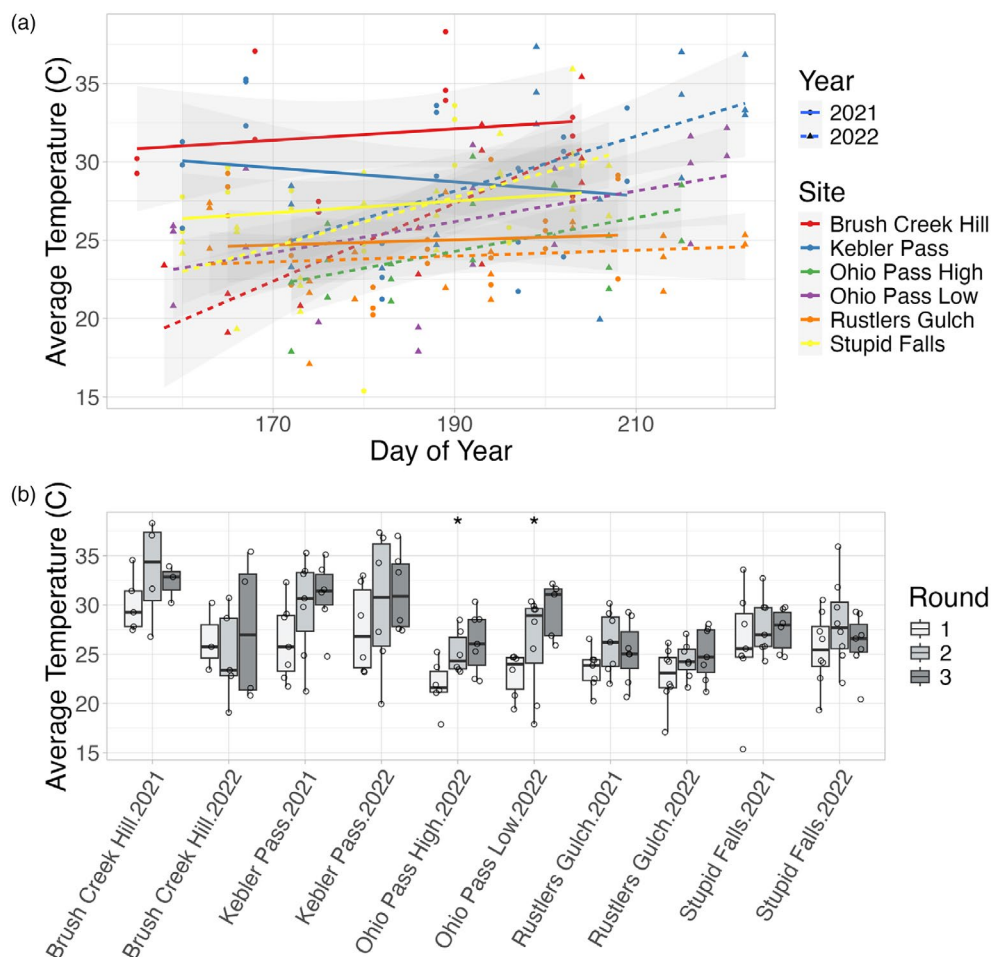


FIGURE 1 Observed relationship between temperature and (a) date, (b) sampling round. Asterisks indicate sites for which temperature and round were significantly correlated at a significance level of $\alpha < 0.05$.

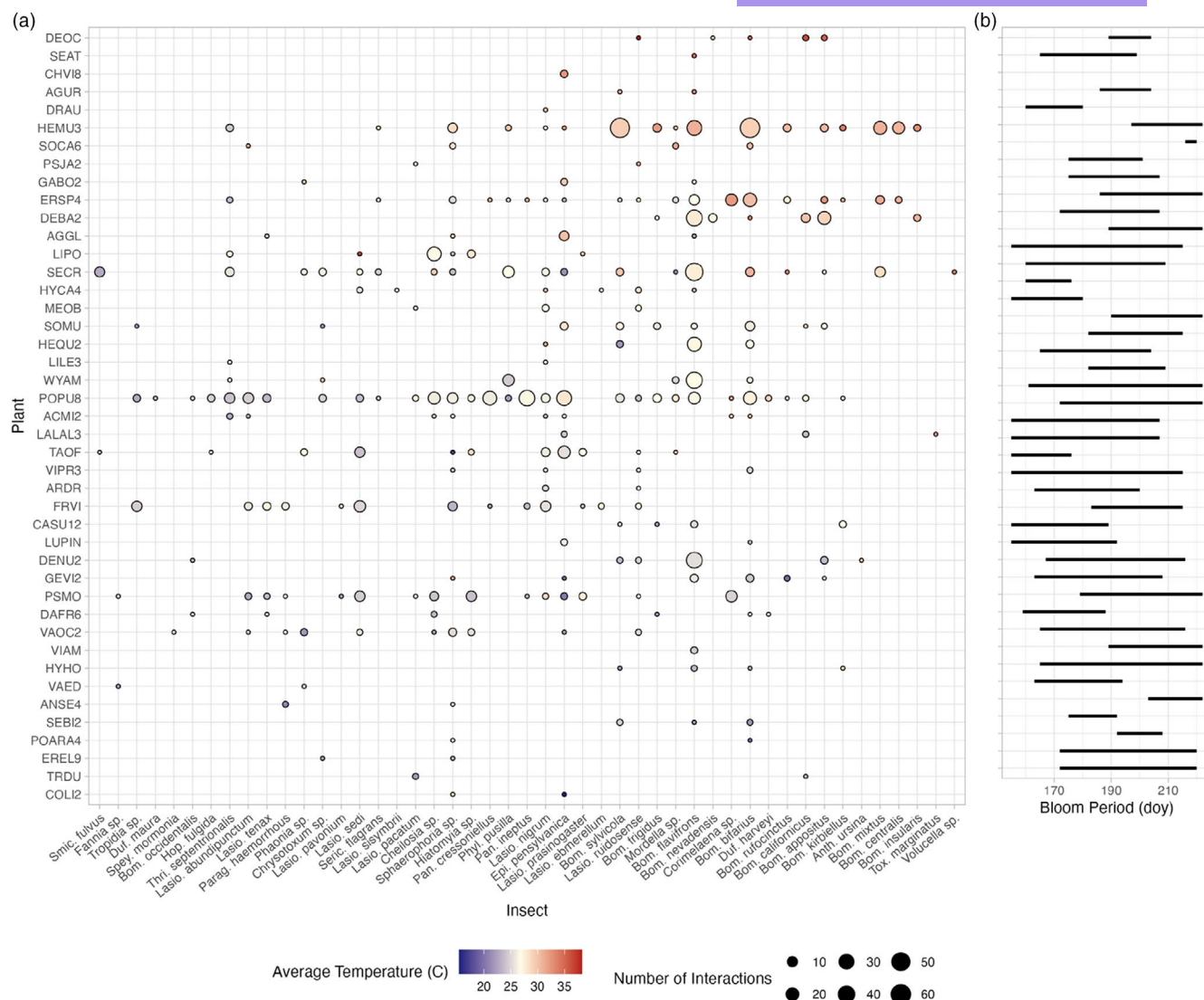


FIGURE 2 (a) Average temperatures at which we observed plant–pollinator interactions. Warmer colours indicate interactions that were observed at higher temperature on average and the size of points reflect the number of times that plant–pollinator pair was observed in our dataset. (b) Day of year of bloom times recorded across all sites and years.

Among *Bombus* species, we examined the floral choices predicted by our model for our two most common species—*Bombus flavifrons* ($n = 261$) and *Bombus bifarius* ($n = 145$)—and each species' most common floral partners—for *B. flavifrons*: *Senecio crassulus* ($n = 47$), *Wyethia amplexicaulis* ($n = 38$), *Delphinium barbeyi* ($n = 36$) and *Delphinium nuttallianum* ($n = 36$); for *B. bifarius*: *Heliomeris multiflora* ($n = 60$), *Erigeron speciosus* ($n = 23$) and *Potentilla pulcherrima* ($n = 21$). We also included interactions between *B. flavifrons* and *S. crassulus* ($n = 7$) and *B. bifarius* and *H. multiflora* ($n = 30$) in our assessment in order to increase the comparability of these two visualizations. We found distinct peaks indicating increased likelihood of floral choice at specific temperatures for both *Bombus* species. Optimal temperature for choice of the four modelled floral partners by *B. bifarius* spanned 5.93°C, with a distinct gap between the lowest-temperature floral partner (*P. pulcherrima*) and the other three species. Optimal temperature for choice of the five modelled floral partners by *B. flavifrons* spanned 7.04°C with two low-temperature partners (*D. nuttallianum* and *W. amplexicaulis*), one

mid-temperature partner (*D. barbeyi*) and two high-temperature partners (*S. crassulus* and *H. multiflora*) (Figure 3). We conducted similar visualizations for our two most common *Lasioglossum* species—*Lasioglossum sedi* ($n = 48$) and *Lasioglossum nigrum* ($n = 44$)—and each species' four most common floral partners—for *L. sedi*: *Fragaria virginiana* ($n = 15$), *Pseudocymopterus montanus* ($n = 11$), *T. officinale* ($n = 11$) and *P. pulcherrima* ($n = 4$); for *L. nigrum*: *F. virginiana* ($n = 11$), *P. pulcherrima* ($n = 7$), *T. officinale* ($n = 7$) and *S. crassulus* ($n = 4$). In contrast to the spread exhibited by our *Bombus* species, optimal temperature for *L. sedi* choice across the four floral partners fell within a range of 1.55°C, and for *L. nigrum* fell within a range of 0.86°C.

3.3 | Pollinator activity and plant attractiveness

We found no significant effect of temperature on the total number of plant–pollinator interactions that we recorded ($\chi^2 = 2.066$, $df = 2$,

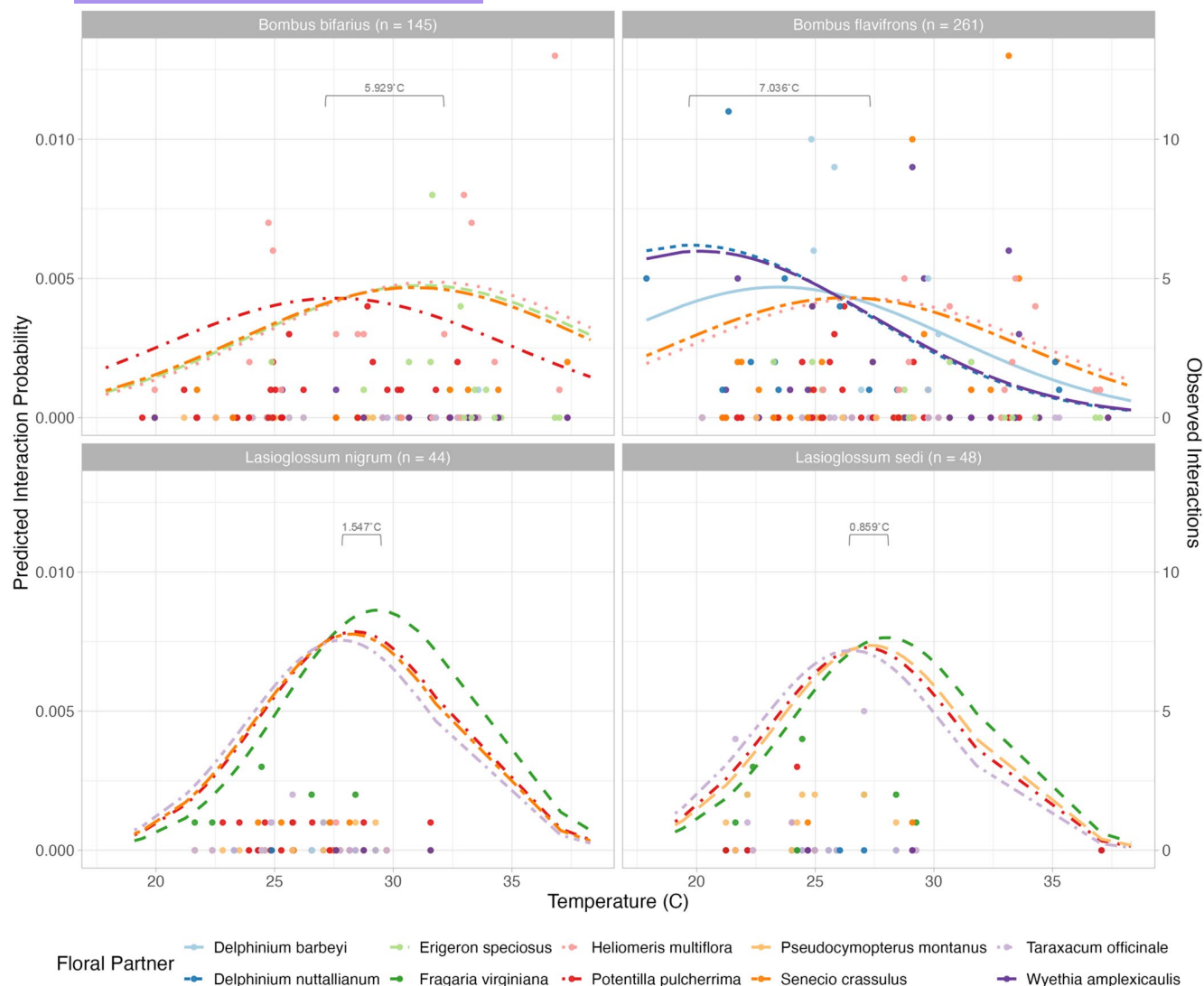


FIGURE 3 Predicted interaction probability curves (left axis, curves) and raw number of observed interactions (right axis, points) across temperatures for the two most common *Bombus* species and the two most common *Lasioglossum* species. Floral partners shown represent 70% of the total interactions for both *Bombus* and *Lasioglossum* and generally co-occur spatially and temporally.

$p = 0.356$; Figure 4A; Table S2k), the relative abundance of insects of different taxa observed across all floral partners ($\chi^2 = 4.023$, $df = 2$, $p = 0.134$; Figure 4C; Table S2m) or the relative abundance of visits to particular plants when pooled across all pollinators ($\chi^2 = 3.602$, $df = 2$, $p = 0.165$; Figure 4E; Table S2o). We found a significant effect of sampling round on the total number of interactions observed ($\chi^2 = 7.906$, $df = 2$, $p = 0.019$), and pairwise comparisons indicated a significant difference between round 2 and round 3 ($z = 2.726$, $p = 0.018$), but did not find a significant difference for the other pairwise comparisons of sampling round (Figure 4B; Table S2l). We found no significant effect of sampling round on either the relative abundance of insects observed foraging ($\chi^2 = 4.365$, $df = 2$, $p = 0.113$; Figure 4D; Table S2n) or relative abundance of visits to particular plants ($\chi^2 = 0.432$, $df = 2$, $p = 0.806$; Figure 4F; Table S2p). Statistical results from these tests can be found in Supporting Information S2 and DHARMA model diagnostics (Hartig, 2021) are available with our complete code on Zenodo.

4 | DISCUSSION

Global environmental change is likely to alter the structure, function and persistence of ecological communities. We examined one element of environmental change—temperature variation—and found that temperature influenced floral choice across pollinator taxa even in the absence of thermally mediated changes to community composition. Plant–pollinator interactions likely respond to a number of dynamic and potentially conflicting demands that may be more or less important at different temperatures. Co-occurring floral species may produce pollen and nectar at different quantities and with different chemical compositions, which could influence the nutritional value of a given floral visit and thus, the perceived value to a prospective floral visitor. For instance, *A. mellifera* appears to prioritize particular amino acids when collecting pollen (Cook et al., 2003; Wright et al., 2018) and an inability to meet particular nutritional needs from available pollen resources negatively impacts

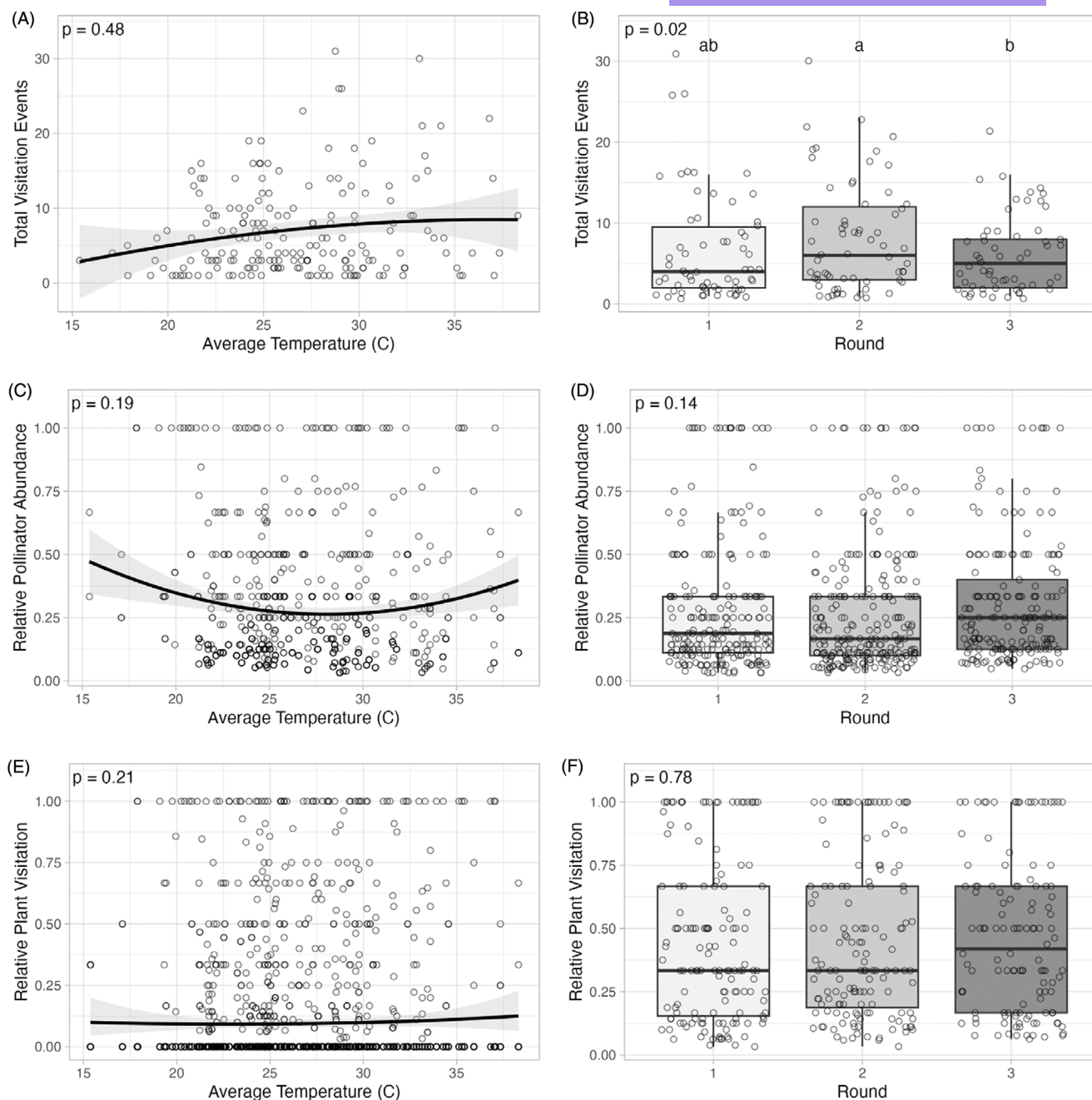


FIGURE 4 Effects of temperature and sampling round on (A, B) total number of plant–pollinator interactions observed, (C, D) relative abundance of insect taxa and (E, F) relative number of visits to plant species. For the relationship between round and the relative number of plant visits (F), only the non-zero values are reported for visual clarity, but reported p -value reflects all modelled data.

these bees' physiology and survival (Di Pasquale et al., 2016). No specific information is available about how the availability of particular amino acids or other macronutrients in the pollen produced by flowers in this system varies with temperature or about the specific nutritional needs of the insects that we recorded. However, we know that the quantity of pollen produced and the performance of pollen in terms of plant reproduction can vary with environmental variables (Delph et al., 1997; Rosbakh et al., 2018) so thermal variation in the nutritional quality of pollen is certainly feasible. Nectar also provides carbohydrates and other key nutrients to fuel flight,

and balancing the needs for these different nutrients, sugars and water could drive pollinator nectar foraging preference across temperatures (Hendriksma et al., 2014). Finally, in variable climates like the subalpine meadows in which our study took place, temperature regulation via floral warmth or cooling can also be a reward driving insect visitation patterns (Cooley, 1995; Herrera, 2025; Rands & Whitney, 2008; Sapir et al., 2006; Seymour et al., 2003) and we would expect that the value of a thermal reward to vary substantially across the wide range of temperatures that we recorded during our sampling periods.

In addition to the significant effect of temperature when all pollinator taxa were assessed together, we also found that temperature influenced the floral choice of bumble bees (*Bombus* spp.)—the most commonly observed insect genus in our system—when analysed alone, though we were unable to distinguish any significant differences in floral choice across temperatures for the next most commonly observed bee genus, *Lasioglossum*. We surveyed the two genera in tandem using the same methodologies and used local keys to identify species in both genera, precluding bias related to research methods in these contrasting responses. However, these bees represent contrasting phylogenetic, morphological and physiological traits that may provide some clues regarding our differing results. Both family identity and body size have been shown to influence bees' rates of heat transfer (Herrera, 2024) and *Bombus* spp. have substantially larger body sizes (9–22 mm) than do *Lasioglossum* spp. (5–11 mm; Michener, 2007). Body size is also associated with a number of important energetic and chemical balances. Larger insects have higher energetic needs (Chown & Gaston, 2010), while smaller insects generally experience higher rates of water loss (Kühnel et al., 2017). Thus, the small-bodied *Lasioglossum* spp. that were not responsive to temperature may instead exhibit foraging preferences according to humidity or nectar water availability. Additionally, bumblebees have modest thermoregulatory capabilities that smaller bodied bees lack, allowing them to survive cold temperatures and dissipate excess heat when flying at warmer ambient temperatures (Heinrich & Esch, 1994; Sepúlveda-Rodríguez et al., 2024). The maintenance of these thermoregulatory systems could therefore alter the energetic needs of *Bombus* spp. when foraging at different temperatures in ways that are not as prevalent among *Lasioglossum* spp.

Life history traits could also contribute to the contrasting responses to temperature that we found in our two focal genera. While individuals from both genera need to forage to fuel their own flight, bumblebees gather resources to support an entire colony and the foraging yield from a single individual or from multiple individuals foraging during a single time period can be augmented by sister workers foraging at other times and temperatures. These bees might therefore be able to more discriminately forage according to specific nutrient needs, while *Lasioglossum*, with individuals solely responsible for their own reproductive output, may be less able to respond to small changes in pollen or nectar quality (Seeley, 1986; Evans & Raine, 2014; Grüter & Hayes, 2022). Some *Lasioglossum* species exhibit primitive eusociality (Danforth, 2002) and further study of whether this life history trait correlates with thermal variation in foraging among *Lasioglossum* species could provide interesting insight into the role of sociality in the relationship between temperature and plant–pollinator interactions.

4.1 | Thermal patterns of pollinator preference are independent of community composition

Throughout this study, we were aware of the possibility that variation in pollinator abundance or plant resource availability could drive

foraging patterns independently of temperature. We accounted for this possible confounding effect in several different ways to ensure that our findings were truly driven by thermal variation. First, we structured our data collection to minimize variation in the plants and pollinators available to interact. Second, our main analyses are fundamentally invariant to changes in the total number of pollinators active during a given sampling period, since our multinomial model measured floral choice as the proportion of observed pollinator visitation events to particular floral species, not the absolute number of visits. Third, we statistically confirmed that the total number of interactions observed, relative abundance of pollinator taxa involved in interactions and relative abundance of plants receiving interactions did not vary with temperature. Thermal variation in the total number of interactions recorded could signify differences in the amount of nectar or pollen resources available across the floral landscape or in the ability of most insects to actively forage. Variation in the relative abundance of pollinator taxa visiting flowers could yield different amounts of competitive pressure within the pollinator community and variation in the relative abundance of visits received by specific plant species at different temperatures could indicate differing levels of floral rewards across our daily survey periods. The total number of interactions and their distribution across plant and pollinator taxa did not vary with temperature or time of day, with a single exception—a significant difference in the total number of interactions observed between round 2 and round 3 (Figure 4B). Notably, the lack of a significant effect of round on the relative number of visits to different plants (Figure 4F) allayed concerns that the pollen and nectar at particular flowers were being over-exploited by insect foragers even without changes to the presence or absence of the bloom itself (Keasar et al., 2008).

Instead, we propose that temperature may alter the relative, not absolute, attractiveness of floral resources to particular pollinator taxa. Floral resources are often quantified in terms of the volume and sucrose concentration of nectar or the mass and macronutrients (proteins, lipids and carbohydrates) of pollen. Many ecological frameworks effectively describe how individual elements of floral rewards like the volume of nectar (Valdovinos et al., 2013) or the protein:lipid content of pollen (Vaudo et al., 2016, 2024) influence pollinator foraging patterns, but are not clear about how insects perceive trade-offs between these different values. Our results suggest that temperature influences these trade-offs to make particular elements of floral rewards more attractive to specific taxa at different temperatures (Scriven et al., 2016; Smith & Amarasekare, 2018). Though our study design does not give us the ability to determine what element(s) of floral rewards are more attractive at different temperatures, it is likely that metabolic needs of pollinators and physiological responses of both guilds at different temperatures play important roles in this pattern (Bishop & Armbruster, 1999; McCallum et al., 2013; Stone, 1994).

Experimental work has shown that bumblebee metabolism and appetite decrease with an increase in ambient temperature from 26°C to 32°C (Kuo et al., 2023). In conjunction with other studies that have found bees exhibit trade-offs in preference between nectar temperature and sucrose concentration (Nicolson et al., 2013; Tan et al., 2014;

Whitney et al., 2008), we can surmise that insects in our system foraging at cooler temperatures may be more driven to find nectar with high sucrose concentration. Conversely at warmer temperatures, particularly above 30°C as we recorded for many of our survey rounds, insects may have less strict preferences and may even prefer more watery nectar if water stress is a higher priority than metabolic needs. Additionally, sucrose concentration is positively correlated with viscosity, so highly concentrated nectar may become too viscous for pollinators to efficiently drink (Kim et al., 2011; Shi et al., 2020). Since viscosity is also negatively correlated with temperature (cooler nectar is more viscous), we can begin to see the complex exchange of metabolic needs and physical ability to access nectar that could make a flower preferred at one temperature and disfavoured at another.

One recent study in this system reported higher nectar sugar concentration and volume for *E. speciosus* compared to *P. pulcherrima* (Bain et al., 2022). These were the second and third most visited flowers by *B. bifarius* in our dataset and our model predicted that *B. bifarius* interactions with *P. pulcherrima* should occur at lower temperatures than with *E. speciosus* (Figure 3). This contrast provides additional support for the idea that trade-offs between metabolic needs and physical ability to access nectar are at least partially responsible for the thermally variable plant–pollinator interaction patterns predicted by our models. These two plants, as well as many of the others that our model predicted would be visited by *B. flavifrons* and *B. bifarius* at different temperatures, co-occurred both spatially and temporally (Figure 2b; Supporting Information S1), precluding the possibility that this interaction preference was driven by variation in the geographical or phenological availability of resources and supporting our theory that some element of resource quantity, quality or accessibility drives this predicted trend. Little information is available to understand how temperature may influence other nutritional benefits derived from flowers, like macronutrients from pollen, but research linking bumblebee foraging to a similarly complex interplay of temperature, nectar sugar concentration and nectar microbiome (Russell & McFrederick, 2022) illustrates that variation in pollinator interaction patterns across temperatures is likely an effect of a wide range of biological processes.

4.2 | Implications of thermally mediated plant–pollinator interactions

Ultimately, our results show that for many insect pollinators including *Bombus* spp., foraging preferences are not static traits but rather respond to the dynamic environments in which these pollinators exist. Temperature-sensitivity in pollinator foraging patterns could support thermal patterns of niche partitioning within and across bumblebee species. Though limited information is available about intraspecific variation in bumblebee foraging patterns (but see Jin et al., 2024; Ye et al., 2024), *Bombus* at the population- or species-level tend to visit a variety of floral resources and most plants receive a variety of insect visitors when studied at the same scale (Waser et al., 1996). This generalization in plant–pollinator systems is expected to increase

the stability of pollination services over time and decrease the likelihood of coextinction in the event of partner loss (Bascompte & Scheffer, 2023; Kaiser-Bunbury et al., 2010; Zografou et al., 2020). However if temperature-specific preferences were shared across pollinators, competition should be maximized among pollinator species for floral resources and among plant species for pollinator visits, which could destabilize plant–pollinator networks (Johnson et al., 2022). Coexistence of these competing pollinators could be explained in part by thermal niche partitioning, in which different insects visit shared floral resources at different temperatures, though other drivers of niche partitioning like microclimatic variation or site-level variation in floral resources also surely contribute to the diversity of co-occurring pollinators. Our results help to contextualize these apparent conflicts by illustrating a scenario in which flowers receive continued visitation by insect pollinators across temperatures, with the identity of the insect visitor changing but the overall number of visits remaining somewhat consistent. Such a pattern should contribute to co-existence and the overall resilience of these communities (Cai et al., 2020) and preserve the species-level generalization that imparts resilience to these networks while allowing for more specialized interactions at the level of individual pollinator foraging bouts (Brosi, 2016), though such an assertion would require far more research to confirm. Such a broad-scale pattern of increased specialization within a particular thermal window would also provide support for the persistence of generalization among many plant and pollinator species, which should be at odds with the transfer of conspecific pollen between flowers that underlies the plant–pollinator mutualism (Arceo-Gómez et al., 2016; Morales & Traveset, 2008).

Increasing temperatures, among other consequences of climate change, are expected to threaten the persistence of many plant and pollinator species (Deutsch et al., 2008; Dormann et al., 2008). Conserving plants, pollinators and their interactions is thus an important global priority. Many modelling frameworks for predicting the effects of climate change assume that organisms will shift their geographic distributions to follow preferred climatic niches, usually defined by temperature and precipitation (e.g. Rafferty, 2017). However, our evidence that pollinators change their foraging preferences with temperature presents another important pathway through which pollinators may adapt to climate change—in addition to potentially shifting their ranges, they may also shift their interaction patterns. This could be a crucial, yet overlooked, component of the intersection between climate change and plant–pollinator community ecology. Effective conservation will need to account for both of these possible responses to global environmental change in order to effectively predict and manage changes to plant–pollinator communities, though the relative importance of each response will depend on the goals of specific conservation action. For instance, conservation of an imperilled insect pollinator might primarily involve planting floral resources that this pollinator is expected to visit under new, warmer temperatures. In contrast, conservation actions focused on protecting pollination function may prioritize regions of a pollinator's suitable habitat in which it is expected to successfully pollinate a particular plant of concern, and possibly even deprioritize areas of that plant's current habitat where it is likely to lose

access to pollination services. Across conservation goals, however, efforts to counter the impacts of climate change on ecological communities will benefit from a stronger understanding of the ways in which temperature might impact not only the presence of plants and pollinators in a particular location but also the patterns of interactions between these groups.

AUTHOR CONTRIBUTIONS

K. C. Arrowsmith and Berry J. Brosi conceived of the ideas and designed methodology. K. C. Arrowsmith, Madeleine D. Strait, Manogya Chandar and Annie Schiffer were involved in data collection and insect curation. K. C. Arrowsmith conducted data analysis and led the writing of the manuscript with support from Berry J. Brosi. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to the many people who contributed to the data collection for this project: C. Anderson, A. Baker, M. Cathcart, S. Dewey, D. Lahn, T. Lamperty and K. Woytek. The Rocky Mountain Biological Laboratory staff, especially J. Reithel and I. Breckheimer, provided critical support for this work. We had fruitful conversations about ectotherm energetics with L. Buckley and J. Litle and received valuable feedback on this manuscript from B. Abrahms, L. Buckley, E. Theobald, S. Jha, four anonymous reviewers and the editorial staff at the *Journal of Animal Ecology*. Funding for these activities was provided by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-2140004 and Postdoctoral Research Fellowship in Biology under Grant No. DBI-2305867. Additional support came from NSF grants DEB-2129759 and DEB-1834487. The research reported here was funded in part by DEVCOM ARL, ARO through a Multidisciplinary University Research Initiative Grant (#W911NF1910231). The research, interpretations and perspectives reported here are those of the authors and should not be attributed to the Army or the Department of Defence.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and a fully replicable Rmarkdown of the analysis are available on Zenodo at <https://doi.org/10.5281/zenodo.17049963>.

STATEMENT ON INCLUSION

Our study took place in the Rocky Mountains of Colorado, on land that is the ancestral home of the Ute people. All authors have spent multiple summers working and living in this area, but are not originally from this area and do not have ties to the indigenous and other local communities in the area. Our research team included researchers that spanned a diverse range of races, genders, sexual orientations, disabilities and national origins. Our team provided opportunities for multiple undergraduate researchers experiencing their first field ecology experience, including one of our authors (MC).

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SUPPORTING INFORMATION

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

Data S1. Study system and summary information.

Data S2. Results of statistical analyses.

How to cite this article: Arrowsmith, K. C., Strait, M. D., Chandar, M., Schiffer, A., & Brosi, B. J. (2025). Temperature influences pollinators' choice of floral partners independently of community composition. *Journal of Animal Ecology*, 94, 2390–2402. <https://doi.org/10.1111/1365-2656.70158>