

## ARTICLE

## Climate Ecology

# Warming temperatures affect meadow-wide nectar resources, with implications for plant–pollinator communities

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## Abstract

Nectar production may be a point of sensitivity that can help link primary and secondary trophic responses to climate shifts, and is therefore important to our understanding of ecosystem responses. We evaluated the nectar response of two widespread native forbs, *Balsamorhiza sagittata* and *Eriogonum umbellatum*, to experimental warming in a high-elevation sagebrush meadow in the Teton Range, WY, USA, over two years, 2015 and 2016. Warming treatments reduced the occurrence of nighttime freezing and nectar volume but increased sugar concentration in nectar in both species in both years. Warming effects were also evident in a consistent increase in the number of flowers produced by *B. sagittata*. Our research suggests that warming associated with climate change has the potential to induce shifts in the nectar-feeding community by changing nectar characteristics such as volume and sugar concentration to which nectar feeders are adapted.

## KEYWORDS

*Balsamorhiza sagittata*, climate change, *Eriogonum umbellatum*, flower production, montane meadow, nectar, pollinator resources

## INTRODUCTION

The worldwide number of animal species that visit flowers to consume nectar may total nearly 300,000 (Kearns et al., 1998; Willmer, 2011), and of the 352,000 species of angiosperms, around 88% depend on animal visitors for pollination (Ollerton et al., 2011). Flower visitors that consume nectar at least occasionally include taxa from five classes—Arachnida, Insecta, Reptilia,

Aves, and Mammalia—and 15 orders (Nicolson, 2007). The total nectar resources available to nectarivores in any particular habitat is a function of three factors: the total number of flowers in the habitat, the percentage of those flowers that produce nectar, and the specific characteristics of the nectar (e.g., nectar volume and sugar concentration). Research into the potential effects of climate change suggests that some or all of these factors could be altered by increasing temperatures (Anderson, 2016;

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Byers & Chang, 2017; Mu et al., 2015; Parmesan & Hanley, 2015; Sherwood et al., 2017; Takkis et al., 2015).

Altered nectar production and composition can have both immediate effects on flower visitor activity and energetics, and longer-term consequences for fitness (Parachnowitsch et al., 2018; Scaven & Rafferty, 2013). Variation in nectar quantity and quality can change the abundance, diversity, and activity of nectarivores with which the plants interact (Junker et al., 2013; Nicolson, 2007; Palmer et al., 2015; Parachnowitsch et al., 2018; Potts et al., 2006; Willmer, 2011). Changes in nectar resources therefore have the potential to propagate upward through trophic levels, potentially causing shifts in ecological communities.

Mouth and body morphology, and water and energy requirements at least partly determine a nectarivore's potential resources and food needs. In general, bee- and fly-pollinated flowers offer lower nectar volumes with higher sugar concentrations, while flowers pollinated by birds, bats, butterflies, and moths have higher volumes with more dilute sugar solutions (Baker & Baker, 1983). Temperature is the environmental variable that is most often related to the volume of nectar offered by a flower (Jakobsen & Kristjánsson, 1994; Mu et al., 2015; Nocentini et al., 2013; Pacini et al., 2003; Pacini & Nepi, 2007; Petanidou & Smets, 1996; Takkis et al., 2015). Additionally, water availability (O'Brien et al., 1996; Pacini & Nepi, 2007; Wyatt et al., 1992) and CO<sub>2</sub> levels (Lake & Hughes, 1999) can also affect nectar volume. Sugar concentration, on the contrary, is usually less dependent on abiotic factors and more consistent throughout the day and the flowering season (Mu et al., 2015; Nocentini et al., 2013; Takkis et al., 2015; Villarreal & Freeman, 1990). These differences have been interpreted as adaptive—nectar production in plants balances costs and benefits given pollinator requirements and abiotic conditions (Pacini & Nepi, 2007).

Studies into the effects of temperature on total flower production demonstrate a variety of responses to increased temperatures. Some species in some environments reduce flower production or increase aborted buds when exposed to higher temperatures (Mu et al., 2015; Saavedra et al., 2003; Wood, 1968), while others increase flower production or reduce aborted buds under warming treatments (Arft et al., 1999; Sherwood et al., 2017). Past research into the percentage of flowers that produce nectar has focused on evolution and fitness (Baker & Baker, 1983; Mu et al., 2015; Nicolson, 2007; Pacini et al., 2003; Pyke, 1991; Southwick, 1984); both theoretical (Bell, 1986) and empirical (Thakar et al., 2003) studies suggest that producing a mixture of nectarful and nectarless flowers confers an adaptive advantage to plants. To our knowledge, there have been no studies examining how abiotic ecological factors such as

temperature might influence the percentage of flowers that produce nectar.

In this study, we investigate how higher temperatures (especially nighttime temperatures), such as those expected under climate change, interact with three important variables to determine total floral resources in a meadow—specific nectar characteristics (volume and sugar concentration), the presence or absence of nectar in a flower, and the total number of flowers produced by a plant. We established control and passive warming plots in a high-elevation montane meadow in Grand Teton National Park, WY, USA, and compared the nectar offered by two important nectar producers that occur across a wide range of upland plant community types in western North America—*Balsamorhiza sagittata* and *Eriogonum umbellatum*.

The study site is located in a cold-desert montane community, where vigorous plant growth occurs when water is abundant in spring (May–June), but slows due to water limitations in the mid-to-late season (July–August). Because *B. sagittata* emerges early in the growing season, we expected increased flower production in *B. sagittata* in the warmed plots compared with the control plots due to an increase in frost-free nights. We expected plants in the warmed plots to produce lower nectar volumes but similar sugar concentrations as control plots, consistent with previous findings in the literature (Mu et al., 2015; Takkis et al., 2015), and we expected this effect to be stronger in *E. umbellatum* than in *B. sagittata* because *E. umbellatum* blooms later in the growing season, and plants may reduce nectar production due to water limitations in the late season. A mixed strategy of producing nectarful and nectarless flowers has been shown to be evolutionarily stable, and the ideal ratio is mainly decided by characteristics of the pollinators rather than the environment (Bell, 1986; Thakar et al., 2003). We therefore expected the proportion of flowers offering nectar to remain approximately the same between control and warmed plots.

## METHODS

### Site location and experimental design

The study was conducted during 2015 and 2016 in a flat montane meadow in Grand Teton National Park, WY, USA, at an elevation of 2100 m. The meadow is composed of a relatively homogeneous plant community that includes sagebrush (*Artemisia arbuscula* ssp. *thermopola* in plots, mixed with *Artemisia tridentata* ssp. *vaseyana* in the surrounding area), flowering forbs and grasses, and a high percentage (~50%) of bare ground (Sherwood

et al., 2017). The typical growing season for forbs and grasses lasts from mid- to late May until late August to early September, with maximum greenness occurring approximately mid-June (Debinski et al., 2000).

We established 12 2.4-m<sup>2</sup> plots approximately 5 m apart and regularly assigned alternating plots as control or warmed treatment ( $n = 6$  for each). Sites were marked for the duration of the experiment using 12-cm-wide plastic landscape edging around the perimeter of each plot. The edging did not affect the movement of invertebrates, small vertebrates, or rain. The warming treatment involved passive warming of plots by an open-sided chamber (Germino & Smith, 1999) with a roof of clear plastic (see below), which increases daily minimum temperatures of plant and soil surfaces by passively increasing the downwelling infrared (longwave or thermal) radiation to plant and soil surfaces (see Germino & Smith, 1999, for validation of radiation effects). Each chamber consisted of a 2.4 × 2.4 m wood frame open to the environment on all sides, with tops designed to trap ground-emitted longwave radiation ( $\sim 50 \text{ W m}^{-2}$ ).

In 2015, chamber tops were louvers of 4-cm-wide clear acrylic panels (>95% transmittance of sunlight) placed at 50° angles every 10 cm. This design effectively trapped longwave radiation and heated soil and plant leaf temperatures  $\sim 1\text{--}3^\circ\text{C}$ , mostly at night (Germino & Smith, 1999), while allowing precipitation to pass through to plots with minimal impedance (Germino & Demshar, 2008). In 2016, the acrylic louvers were replaced with greenhouse film (Sun Selector Clear IR AD Greenhouse Film, 88% light transmission, 25% light diffusion) stretched across the tops of the frames and perforated to allow rain to pass through. The tops of the chambers were approximately 30 cm from the ground so as not to interfere with the growth of the vegetation. The chambers were placed on the site annually from late April to early May and remained until the end of the growing season (late September to mid-October).

Soil surface temperatures were measured hourly using HOBO Pendant temperature data loggers (Onset Computer, Bourne, MA, USA) placed in the center of each plot. The average difference between median 5:00 AM soil temperatures in the warmed plots versus the control plots was 1.75°C (SD = 1.35°C) in 2015, and 1.43°C (SD = 0.94°C) in 2016 (data not shown), consistent with findings from Sherwood et al. (2017) and Germino and Smith (1999). The Intergovernmental Panel on Climate Change projects mean annual temperatures in western North America to increase by 1.1–4.3°C by the year 2100 (IPCC, 2013), primarily at night and in cool-season months. The warming treatment therefore increased temperatures, on average, on the low end of

the range predicted by regional climate models, but in the same season and at the same time of day.

## Nectar measurements and plant flower production

We collected nectar and conducted vegetation surveys for two dominant perennial plant species: arrowleaf balsamroot (*B. sagittata*) and sulfur-flower buckwheat (*E. umbellatum*). *Balsamorhiza sagittata* is an early-emerging deciduous perennial forb with large showy composite inflorescences on relatively long, individual stalks. The flowers and leaves senesce during the summer months, typically around late June/early July. *Eriogonum umbellatum* is a woody perennial that forms broad mats with many small evergreen leaves that green up in the spring. Each plant produces multiple flower stalks with a single umbel containing clusters of small florets. In mid- to late June, *E. umbellatum* begins to flower as *B. sagittata* begins to senesce, and flowers of *E. umbellatum* are typically available to flower visitors through late July (Sherwood et al., 2017).

We collected nectar samples between 7:00 and 9:00 AM every day during the flowering season when no water droplets (dew or rain) were visible on plants. For *B. sagittata*, we sampled eight flowers per plot, or as many flowers as were in the plot if there were fewer than eight. For each plant with at least one flower fully flowering (i.e., not in bud, senescing, or senesced) with at least five open disk florets, we chose the flower that was most likely to have nectar (i.e., disk floret yellow instead of orange and dried up, stigmas emerged and not curled up). We sampled from the flower most likely to have nectar on the first plant, then moved to the next plant with at least one flower and sampled from the flower most likely to have nectar on that plant. We continued until the flower most likely to have nectar on all plants with flowers had been sampled. If there were more flowers and we had not yet taken eight samples from the plot, we returned to the first plant and sampled from the next flower most likely to have nectar, etc.

For *E. umbellatum*, our methods were similar to *B. sagittata*, except that (1) sampling was by plot quadrant because *E. umbellatum* forms mats with multiple stems individually rooted per genet and (2) we sampled three florets with one microcapillary pipette because of the low volume of nectar produced by each floret (Lanza et al., 1995). Each individual data point for *E. umbellatum* is therefore an aggregate of nectar samples from three florets in the same umbel. In 2015, nectar sampling of *B. sagittata* began on 2 June and ended on 13 June ( $n = 156$ ), while in 2016, we sampled from 5 June through 16 June ( $n = 264$ ). For *E. umbellatum*, sampling

began in 2015 on 18 June and ended on 30 June ( $n = 471$ ), while in 2016, we sampled from 23 June through 30 June ( $n = 534$ ).

The nectary in both species is at the bottom of the flower above the sepal. To collect a nectar sample, we gently inserted a microcapillary pipette into the flower, and capillary action pulled the nectar into the glass tube. For each sample, we recorded the length (in millimeters) of nectar within the tube, and the concentration of nectar on the BRIX scale (percentage sucrose equivalent: grams sucrose per 100 g solution; Corbet, 2003). BRIX was measured in the field with Bellingham and Stanley Eclipse sugar refractometers modified for nectar. For each sample, we calculated total volume (in microliters) of nectar by comparing the length of the column of nectar with the total length and volume of the microcapillary tube. We also recorded the number of sampled flowers in each plot that produced nectar.

To determine the total number of flowers produced by each *B. sagittata* plant, we counted the number of buds, aborted buds, fully flowering, senescing, and senesced flowers, and the number of stalks (due to herbivory) apparent on each plant, 3–4 days/week over the growing season (24 May 2015 through 26 June 2015 and 28 May 2016 through 25 June 2016). We sampled 59 plants on 16 days in 2015 (plants with flowers = 43,  $n = 944$ ) and 9 days in 2016 (plants with flowers = 55,  $n = 531$ ). In most cases (83% of plants), determining the total number of flowers was straightforward. However, for 18 plants (17%), the recorded number of flowers fluctuated inconsistently across several survey dates, most likely as a result of observer variation. In those cases, we looked at the recorded number of senesced flowers and the recorded total number of flowers at the end of the season to determine the total number of flowers produced by the plant.

## Statistical methods

Datasets were cleaned, and all analyses were performed in R version 4.0.2 (R Core Team, 2021). To examine possible differences in nectar volume and concentration (BRIX), we ran linear mixed-effects models using the “lmer” function in the lme4 package (Bates et al., 2015). Nectar volume was log-transformed to improve the homogeneity of variance. Predictor variables included year, species, treatment, and all two- and three-way interactions, as well as a random intercept for a plot. We used the emmeans package in R (Lenth, 2021) to perform a type III ANOVA to identify significant predictors in the model, and computed least-squares mean contrasts to

obtain estimates (on the log scale where appropriate) and  $p$  values. We considered  $p \leq 0.05$  to be significant with a type I error rate of  $\alpha = 0.05$ .

To analyze possible differences between treatments relating to the presence or absence of nectar in flowers, we ran a binomial generalized linear mixed-effects model using the function “glmer” in lme4 with a logit link function, a random intercept for a plot, and the same predictor variables listed above (Bates et al., 2015). To examine the number of flowers produced per plant for *B. sagittata* plants that produced flowers, we ran a Poisson generalized linear mixed model with a log link function, a random intercept for a plot, and year, treatment, and their two-way interaction as predictor variables. Estimates, contrasts, and  $p$  values were obtained from the emmeans package in R (Lenth, 2021).

## RESULTS

### Nectar volume and concentration

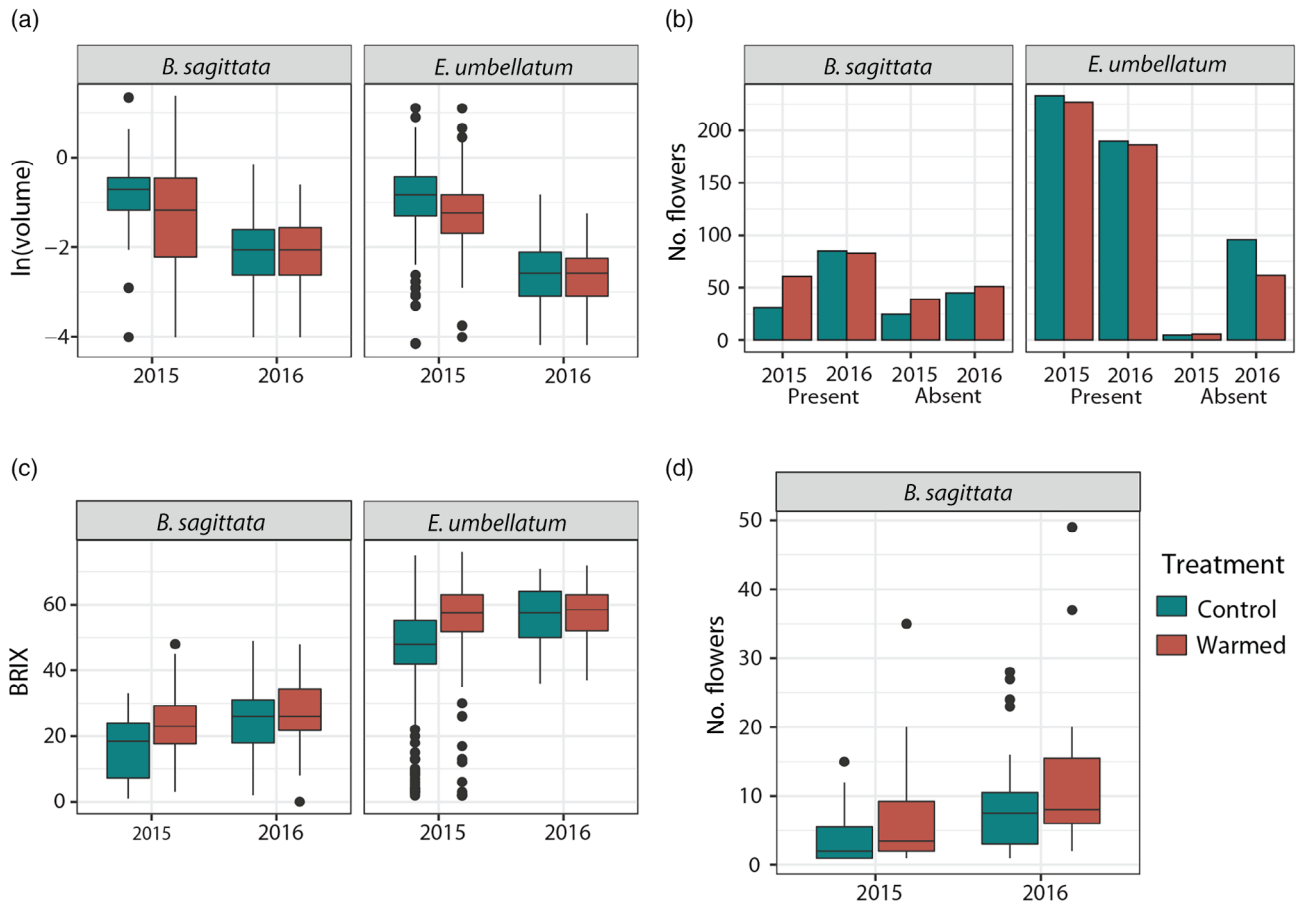
ANOVA results indicated that year, species, treatment, the year  $\times$  treatment, and the year  $\times$  species interaction all produced a significant effect on nectar volume (Appendix S1: Table S1). Significant predictors for sugar concentration were year, species, treatment, and year  $\times$  treatment interaction (Appendix S1: Table S2). The effect of warming on both nectar volume and sugar concentration was consistent across both species in both years, with lower nectar volumes and higher concentrations compared with the control plots (Figure 1a,c).

#### For *B. sagittata*

In flowers containing nectar, nectar volume decreased in warmed plots (W) versus control plots (C) over both years, and in 2015, the decrease was statistically significant (Table 1; Appendix S1: Table S5). Sugar concentration increased in warmed plots in both years, and the difference was significant in 2015 (Table 1; Appendix S1: Table S6).

#### For *E. umbellatum*

Nectar volumes in *E. umbellatum* were lower in the warmed plots than in the control plots in both years, and the difference was statistically significant in 2015 (Table 1; Appendix S1: Table S5). Sugar concentration increased in warmed plots in both years, and the increase was statistically significant in 2015 (Table 1; Appendix S1: Table S6).



**FIGURE 1** Observed values for *Balsamorhiza sagittata* and *Eriogonum umbellatum* in control plots and warmed plots, 2015 and 2016: (a) nectar volume in flowers containing nectar (natural log-transformed), (b) number of flowers in which nectar was present or absent, (c) sugar concentration (in degrees BRIX), and (d) number of flowers produced per plant for flowering *B. sagittata*.

## Presence of nectar and floral abundance

The warming treatment did not have a significant effect on the probability of nectar presence in a flower; however, year, species, and the year  $\times$  species two-way interaction all had significant effects (Appendix S1: Table S3). The warming treatment did have a significant effect on the number of flowers produced in *B. sagittata* plants that produced flowers, as did year, and the year  $\times$  treatment interaction (Appendix S1: Table S4). The effects of warming on the probability of a flower containing nectar were inconsistent across both species and years, but the warmed plots showed a consistent increase in the number of flowers produced by *B. sagittata* plants (Figure 1b,d).

In 2015, *B. sagittata* plants produced a higher proportion of flowers containing nectar in the warmed plots than in the control plots, while in 2016, the proportion in the warmed plots was lower, and neither difference was significant (Table 1; Appendix S1: Table S7). Warming had the opposite effect on nectar presence in *E. umbellatum*: In 2015, plants produced a lower proportion of flowers containing nectar in the warmed plots than in the control

plots, while in 2016, the proportion of flowers with nectar present was higher in the warmed plots, and again, neither difference was significant (Table 1; Appendix S1: Table S7).

The difference between the number of flowers produced per *B. sagittata* plant was significant in 2015 and marginally significant in 2016, and the rate of flower production was higher in the warmed plots in both years (Table 1; Appendix S1: Table S8).

## DISCUSSION

### Nectar characteristics and availability

Warming treatments reduced the occurrence of nighttime freezing and nectar volume but increased sugar concentration in nectar in both species in both years. The average difference between median 5:00 AM soil temperature in the warmed plots versus the control plots was greater in 2015 than in 2016 ( $\Delta = 1.75$  and  $1.43^\circ\text{C}$ , respectively), which may partly explain why the effect of warming was

**TABLE 1** Treatment comparisons: model contrasts for nectar volume (in microliters), nectar concentration (in degrees BRIX), nectar presence/absence, and total number of flowers.

| Contrast | Species              | Year | Estimate | 95% CI        | p       | Response      |
|----------|----------------------|------|----------|---------------|---------|---------------|
| W/C      | <i>B. sagittata</i>  | 2015 | 0.650    | 0.448, 0.944  | 0.024   | Volume        |
| W/C      | <i>E. umbellatum</i> | 2015 | 0.728    | 0.596, 0.8889 | 0.003   | Volume        |
| W/C      | <i>B. sagittata</i>  | 2016 | 0.869    | 0.680, 1.180  | 0.429   | Volume        |
| W/C      | <i>E. umbellatum</i> | 2016 | 0.950    | 0.769, 1.173  | 0.622   | Volume        |
| W – C    | <i>B. sagittata</i>  | 2015 | 7.713    | 1.487, 13.938 | 0.016   | BRIX          |
| W – C    | <i>E. umbellatum</i> | 2015 | 9.588    | 5.040, 14.135 | <0.0001 | BRIX          |
| W – C    | <i>B. sagittata</i>  | 2016 | 1.781    | –3.452, 7.014 | 0.492   | BRIX          |
| W – C    | <i>E. umbellatum</i> | 2016 | 2.136    | –2.584, 6.856 | 0.353   | BRIX          |
| W/C      | <i>B. sagittata</i>  | 2015 | 1.383    | 0.574, 3.329  | 0.470   | Presence      |
| W/C      | <i>E. umbellatum</i> | 2015 | 0.776    | 0.208, 2.892  | 0.705   | Presence      |
| W/C      | <i>B. sagittata</i>  | 2016 | 0.802    | 0.381, 1.690  | 0.563   | Presence      |
| W/C      | <i>E. umbellatum</i> | 2016 | 1.488    | 0.771, 2.873  | 0.236   | Presence      |
| W/C      | <i>B. sagittata</i>  | 2015 | 2.023    | 1.312, 2.120  | 0.001   | Total flowers |
| W/C      | <i>B. sagittata</i>  | 2016 | 1.383    | 0.941, 2.032  | 0.099   | Total flowers |

Abbreviations: C, control plots; W, warmed plots.

Note: “W – C” refers to an additive difference. Null hypothesis: W – C = 0. “W/C” refers to a multiplicative difference (odds ratio for presence/absence). Null hypothesis: W/C = 1.

stronger in 2015. While the direction of the warming effect was consistent across species and years, the size of the effect was only statistically significant (at  $\alpha = 0.05$ ) in 2015 for nectar volume and sugar concentration. Warming effects were also evident in a consistent increase in the number of flowers produced by *B. sagittata*; the size of the effect was statistically significant in 2015 (at  $\alpha = 0.05$ ) and marginally significant in 2016 (at  $\alpha = 0.1$ ). The increase in the number of flowers is consistent with and extends a previous study at this site, which found that warming treatments significantly reduce the number of frost-killed buds in *B. sagittata* plants (Sherwood et al., 2017). The effect of warming on the proportion of flowers containing nectar was inconsistent across both species and years, and in no case was the effect statistically significant. These results lend support to previous studies, finding a mixed strategy of producing nectarful and nectarless flowers is evolutionarily stable, and therefore, the proportion of flowers containing nectar may be robust to changes in environmental conditions (Bell, 1986; Thakar et al., 2003).

Studies conducted in growth chambers indicate that the volume of nectar per flower responds unimodally to temperature increases: Nectar volume increases with temperature up to a maximum, then decreases as the temperature is increased further (Jakobsen & Kristjánsson, 1994; Takkis et al., 2015). Field studies of natural populations find mixed results: On the Tibetan

plateau, 6 years of passive warming similar to the treatment used in this study also resulted in reduced nectar volume per floret (Mu et al., 2015), while studies of two Mediterranean species found that nectar volume depended more on changes in solar irradiance than on temperature (Petanidou & Smets, 1996; see also Nocentini et al., 2013). In the latter study, two species are found in different microhabitats (full sun vs. shade), and the authors attribute their findings to differential natural adaptation of the plants. Our results suggest that *B. sagittata* and *E. umbellatum* may be similarly adapted to their current environmental conditions and warming associated with climate change may reduce the volume of nectar found in florets, possibly affecting energy budgets associated with foraging in the nectarivores who visit these plants.

Most studies examining the effect of temperature on sugar concentration find no significant relationship between the two, either in field studies (Mu et al., 2015; Petanidou & Smets, 1996) or in growth chambers (Takkis et al., 2015; Villarreal & Freeman, 1990). One field study conducted in Texas found a significant negative relationship between temperature and sugar concentration (Freeman & Head, 1990), contrary to the findings reported here. It is possible that our results are anomalous since differences were only statistically significant in 1 year, but the direction of the effect was consistent in both years for both species, suggesting a possible trend. Further investigation over a longer period would help

resolve the question of whether these two populations in fact diverge from results found in previous studies, and if so, what mechanisms might be driving the differences.

Plant nectar production, and the a/biotic mechanisms that regulate the amount of sugar offered in nectar are connected with plant-wide control of all nonstructural carbohydrates (Adams et al., 2013; Bansal & Germino, 2008; Mooney, 1972), and may be influenced by the source of the sugar (phloem vs. nectary; Heil, 2011; Lüttge, 2013), the total amount of daily photosynthate (Pate et al., 1985; Southwick, 1984), and trade-offs between carbon allocated to nectar versus flowers and seeds (Kudo & Ida, 2010; Pyke, 1991; Zimmerman & Pyke, 1988). Furthermore, Takkis et al. (2015) note that plants have species-specific optimum ranges of temperatures for nectar production. The optimum temperature range for these two species is currently unknown, and the plant responses we observed could be driven by the local thermal regimes of the study site, the temperature tolerance of the plant and where in that tolerance range its environmental conditions fall, and/or the role of temperature cues in regulating flowering (Scaven & Rafferty, 2013). The results of our study suggest that, with respect to flower production, increasing temperatures by  $\sim 1.5^{\circ}\text{C}$  will most likely increase the number of flowers produced by *B. sagittata* in this and similar meadows in the region.

## Community effects

Significant changes in the total nectar resources available to nectarivores have the potential to alter the assembly, structure, and persistence of plant–visitor communities, changing characteristics such as community diversity, species range limits, community stability, and competition interactions in nectarivore species (Anderson, 2016; Byers & Chang, 2017; Palmer et al., 2015). A recent review of the literature on pollinator feeding preferences (Parachnowitsch et al., 2018) found that few studies have attempted to link nectar characteristics to community structure, as most studies focus on how nectar traits relate to floral signals. However, studies have demonstrated that variation in nectar traits leads to variation in the identity of visitors (Galen & Plowright, 1985; Hodges, 1995; Thomson, 1988; Thomson & Plowright, 1980) and that pollinator shifts within plant genera are associated with changes in nectar volume and sugar concentration (Nicolson, 2007).

Nectar is the base of the food chain for many animal communities. Changes in nectar resources therefore have the potential to propagate upward through trophic levels, possibly causing large-scale shifts in ecological communities. The need to improve our understanding of the

connection between nectar resources and the structure of plant–visitor communities is greater under the specter of climate change. Important questions include the following: (1) What are the tolerance limits of specific taxa to changes in nectar characteristics and abundance? (2) How might changes in nectar characteristics and the availability of nectar interact to affect a nectarivore's ability to satisfy its energy and water needs? (3) How might changes in nectar resources propagate up through trophic levels into animal communities? (4) What feedback effects might occur among different taxa that compete for nectar resources, and between plant species and their pollinators, if the community of nectarivores changes as a result of changes in nectar resources? These and other questions about if and how nectar might function as a mechanism for structuring communities point to an area of research long overdue for development.

## CONCLUSIONS

Warming temperatures associated with climate change have the potential to change the amount and characteristics of nectar available to nectarivores in montane meadows. This study found consistent effects and some significant differences between warmed plots and control plots for nectar characteristics (a decrease in nectar volume and an increase in sugar concentration in warmed plots) and the total number of flowers per plant (higher in warmed plots), but not for the proportion of flowers offering nectar. Mechanisms driving nonstructural carbon allocation—the amount of sugar offered in nectar—are not well understood, and the literature suggests that responses to increased temperatures are highly dependent on specific species and environmental characteristics. Different nectarivore taxa have different foraging needs depending on mouth and body morphology, and energy and water requirements. Changes in nectar traits, along with changes in the total nectar offered in a meadow, have the potential to cause structural shifts in communities of nectarivores. Because many nectarivores are also important pollinators, changes in nectar offerings also have the potential to cause feedback loops in plant–pollinator systems.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (McCombs, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6496287>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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