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Warming-Mediated Decreases in Nectar Quality Translate Into Lower Energy Reserves of the Monarch Butterfly (*Danaus plexippus*)

Katherine Peel[1] | Greg W. Mitchell[2] | Christopher G. Guglielmo[3] | Heather M. Kharouba[1]

[1]Department of Biology, University of Ottawa, Ottawa, Ontario, Canada | [2]Wildlife Research Division, Environment and Climate Change Canada, National Wildlife Research Centre, Ottawa, Ontario, Canada | [3]Department of Biology, Western University, London, Ontario, Canada

Correspondence: Heather M. Kharouba (hkharoub@uottawa.ca)

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ABSTRACT

Warming can alter plant–pollinator interactions through indirect, plant-mediated pathways, yet the consequence for pollinators remains poorly quantified. We tested whether modest warming (0.57°C) negatively impacts nectar plants and whether these changes carry over to affect the body condition of migratory monarch butterflies (*Danaus plexippus*). We conducted a field warming experiment at the northern edge of the eastern monarch breeding range (Ottawa, Canada) using open-top chambers deployed on three frequently used late-season nectar species: *Monarda fistulosa*, *Solidago canadensis*, and *Symphyotrichum novae-angliae*. Our design allowed adults to feed on warmed plants while spending nonfeeding time outside chambers, isolating plant-mediated effects from direct warming effects. Across most species, warming reduced floral abundance (12.9% fewer open flowers per stem) and decreased nectar sucrose concentration by ~24%, while nectar volume in *M. fistulosa* did not differ between treatments. We then conducted 5-day feeding trials in which adult monarchs foraged on warmed versus control plants and quantified body composition (fat, lean, and water mass). Monarchs feeding on warmed plants had ~26% lower fat mass than controls. Our findings provide experimental evidence that even modest warming can depress nectar quality and floral display, with measurable carry-over effects on pollinator energy stores. Because fat reserves fuel migration and overwinter survival, warming-induced declines in nectar quality may impair monarch performance during the critical late-season fueling period. These results highlight the need to prioritize late-season floral resources that maintain nectar quality under warming and to integrate plant thermal responses into habitat restoration and climate-adaptation strategies for migratory pollinators.

1 | Introduction

Climate change is increasingly becoming a major factor in biodiversity loss. In the longer term (50–100 years), climate change is likely to rise to the forefront of threats to biodiversity (Arneth et al. 2020; McElwee 2021). In recent decades, it has caused a wide range of impacts on biodiversity, ecosystem functions, and human welfare (Habibullah et al. 2022; Shivanna 2022). Among the most affected groups of animals are insects (Harvey et al. 2023). Many, but not all, insect populations are declining across the biosphere due in part to climate change (Marshall et al. 2020; Harvey et al. 2023). However, it is difficult to anticipate the far-reaching community-level effects of these changes (e.g., declines in flowering plants; Scaven and Rafferty 2013) because we do not know yet why insect responses to climate change have been so variable (Harvey et al. 2023).

One reason for this knowledge gap may be that research has focused more on the direct (physiological) effects of warming on insects than on the indirect, plant-mediated pathways, which

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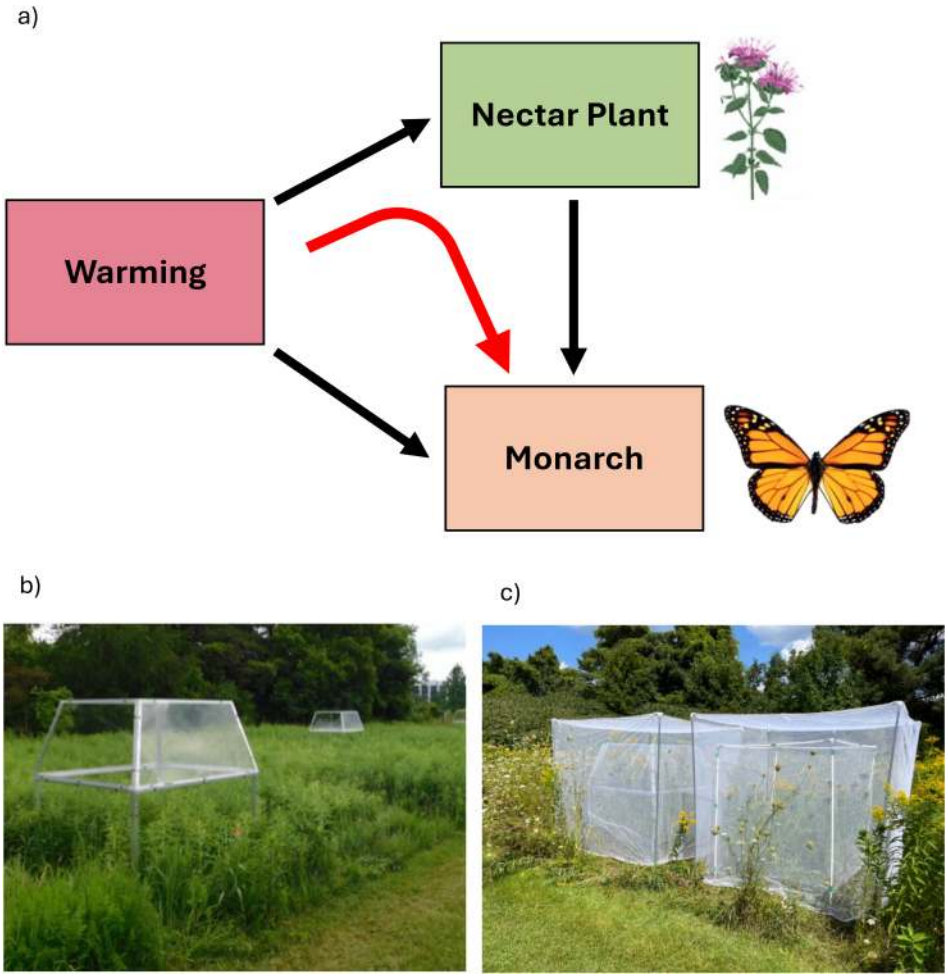


FIGURE 1 | Conceptual and experimental design. (a) Conceptual diagram illustrating the effects of warming on nectar plants and monarch butterflies. Warming may influence nectar plants and monarchs directly (black arrows), but can also influence monarchs indirectly, mediated by warming-induced changes in nectar plants (red arrow). Nectar plants may directly influence monarchs independent of warming (black arrow). Panels (b, c): Experimental design of temperature treatment and controls. (b) Open-top chambers on stems of *Solidago canadensis* in the Fletcher Wildlife Garden-Canadensis Botanical Garden complex on June 9, 2023. (c) An example of a pair of an open-top chamber (left) and control chamber (right) on stems of *S. canadensis* on August 20, 2023, in the FWG-CBG complex. The control chamber was made of PVC piping. Both chambers are wrapped in mesh tulle (hidden in picture). Large enclosures made of steel garden pegs with mosquito netting are built around the chambers with 30+ cm of clearance around all sides to allow space for the monarchs to move around in the enclosures. The open-top chambers and PVC control chambers are 1.5 m tall and 1.2 m wide at the base.

are often more complex (Jamieson et al. 2012; Kharouba and Yang 2021). A major indirect pathway involves warming-driven changes in the timing, availability, and quality of food resources (Figure 1; Saavedra et al. 2003; Descamps et al. 2021; de Manincor et al. 2023; Alquichire-Rojas et al. 2024). For example, climate change can disrupt the synchrony between flowering and insect activity, increasing the likelihood of phenological mismatches that reduce nectar availability (e.g., Kharouba et al. 2018; Crone et al. 2024). Other studies show that heat stress in plants can reduce the availability and quality of floral rewards, but this is not always consistent (Alquichire-Rojas et al. 2024). Few studies have considered how such changes then affect the fitness of insect pollinators (de Manincor et al. 2023; Alquichire-Rojas et al. 2024). For example, de Manincor et al. (2023) found that 4°C of experimental warming reduced floral area and increased nectar concentration in three annual plants, causing bees to become less selective of plant species in their foraging. However, without evaluating changes in both nectar quality and pollinator fitness, it remains difficult to determine whether warming will have detrimental effects on pollinators.

Climate change appears to be the primary driver of the current declines in the eastern migratory population of the monarch butterfly (*Danaus plexippus*), an endangered species in Canada and the United States (Zylstra et al. (2021); Shirey and Ries 2023). Zylstra et al. (2021) found that weather conditions during the breeding season were the most important factors in explaining monarch summer population size, which in turn was directly correlated with the size of the overwintering population. A recent study also suggested that the majority of forest degradation on the overwintering grounds in Mexico since 2007 is due to climate change (Zylstra et al. 2020). However, it remains unclear how nectar plants that adult monarchs depend on respond to warming temperatures (Takkis et al. 2015; Descamps et al. 2021) and how these changes impact monarchs. Adult monarchs use sugar from nectar as a primary

energy source (Alonso-Mejía et al. 1997; Brower et al. 2006; Sinclair and Marshall 2018), and rely on high-quality nectar to fuel their fall migration to Mexico and sustain them through the winter in Mexico (Brower et al. 2006). Therefore, monarchs could face even greater population declines if high-quality nectar sources are negatively impacted by climate change.

Here, we conducted a field warming experiment in Ottawa, Canada, at the northern edge of the eastern population of monarchs' breeding range to test how warming affects monarchs indirectly through changes in nectar resources of three frequently used late-season nectar plants (*Symphyotrichum novae-angliae*, *Solidago canadensis*, *Monarda fistulosa*). Our experimental design allows adult monarchs to feed on warmed nectar plants while spending nonfeeding times outside of the warming treatment, thereby isolating plant-mediated effects from the direct warming effects (Figure 1). We hope that a better understanding of these impacts could improve the selection and introduction of floral resources in habitat restoration projects, a critical strategy for monarch conservation.

We first tested how warming influences nectar-producing plants relative to their thermal optima (H1; Figure 1; Jakobsen and Kritjánsson 1994). Moderate warming can sometimes enhance nectar production (Nicolson et al. 2007; Nocentini et al. 2013) but not always (Alquichire-Rojas et al. 2024). Warming beyond the thermal optima can cause stress and may reduce nectar volume and sugar content (Petanidou and Smets 1996; Pacini et al. 2003; Takkis et al. 2015). Because the three plant species share similar life history strategies and co-occur in the same community, we predicted similar responses across species to warming (H2). We tested these hypotheses via changes in vegetative and floral development and nectar production to warming.

We then evaluated the indirect effects of warming on adult monarch body composition (fat, lean, and water mass) using feeding trials with live warmed and control plants (Figure 1). These body composition metrics are important for successful migration and reproductive success in monarchs (Sinclair and Marshall 2018; Enriquez and Visser 2023). Since sucrose is predominantly converted to fat in monarchs to use as a primary energy source (Alonso-Mejía et al. 1997; Brower et al. 2006; Sinclair and Marshall 2018), we predicted that warming-driven changes in nectar quality (H1) would lower fat reserves (H3). We further predicted that water content would reflect warming-driven changes in nectar quality given that monarchs rely on nectar for hydration (Contreras et al. 2022) but no change in lean mass, as nectar is not an important source of protein for adult monarchs (H4; Campbell and Carr 1987).

2 | Methods

2.1 | Study System

2.1.1 | Monarch Butterfly

The eastern population of the monarch butterfly undergoes an annual long-distance migration from their breeding grounds in southeastern Canada and the eastern United States to their overwintering grounds in oyamel fir forests in Mexico (Brower 1996). Population sizes of the monarch have fluctuated greatly over the last 30 years, but the general pattern is a consistent, dramatic decline (Mitchell et al. 2025). As a result, it is currently listed as "Endangered" under Canada's Species at Risk Act (Environment and Climate Change Canada 2023) and is being considered for an "Endangered" listing in the United States of America (U.S. Fish and Wildlife Service 2024).

Monarchs are multivoltine with two to three distinct breeding generations, followed by a third or fourth migratory generation that does not breed until the following spring (Brower et al. 2006). While adults of breeding generations have a life span of 2–5 weeks, the migratory generation of monarchs can live up to 9 months (Brower et al. 2006). Males and females of this late-season, migratory generation are in reproductive diapause, a state that conserves energy by suppressing non-essential physiological functions (Koštál 2006). Monarchs in this study were reared during the late season to align with the migratory generation in reproductive diapause.

2.1.2 | Plant Species

We used three late-season nectar sources that are frequently used by monarch butterflies in the Ottawa region (Pekos et al. 2025). They are also on native plant seed lists used in Ottawa for habitat restoration projects, e.g., by the Canadian Wildlife Federation (https://cwf-fcf.org/en/resources/downloads/booklets-handouts/Seed-Calculator-Companion-Jan-23-CWF.pdf). Each species reproduces sexually via seeds and vegetatively via short rhizomes.

Symphyotrichum novae-angliae (New England Aster) is a forb in the family *Asteraceae* that flowers from August to late October. It is native to central and eastern North America and grows in typically moist habitats, including meadows, prairies, marshes, fens, forest edges, and disturbed anthropogenic sites (National Plant Data Team 2024).

Solidago canadensis (Canada Goldenrod) is a tall forb also in the family *Asteraceae* that flowers from July through October. It is native to northeastern and north-central North America and can grow under many conditions. It is often one of the first plants to colonize an area after a disturbance (National Plant Data Team 2024).

Monarda fistulosa (Wild Bergamot) is a forb in the family *Lamiaceae* that flowers from July to September. It is native to much of North America, typically growing in dry fields, thickets, and clearings (National Plant Data Team 2024).

2.2 | Warming Experiment

2.2.1 | Location

We conducted the field warming experiment from June 8 to September 25, 2023, at the Fletcher Wildlife Garden (FWG)-Canadensis Botanical Garden (CBG) complex, located in the urban core of Ottawa, Ontario, Canada (Figure S1a). FWG is

a roughly 6 ha wildlife refuge, comprised of forests, wetlands, meadows, and old fields managed as agricultural land by Agriculture and Agri-Food Canada until 1990. CBG is 13.8 ha of semi-managed meadow. The experiment took place in four open areas at the site (Figure S1b).

2.2.2 | Experimental Design: Warming Treatment and Controls

We used open-top chambers (OTC) as a passive warming treatment. OTCs have been shown to significantly alter temperature and minimize unwanted effects such as modified precipitation and humidity (Marion et al. 1997; De Frenne et al. 2010; Welshofer et al. 2018). While OTCs have been frequently used in plant ecological studies (Marion et al. 1997; Kudernatsch et al. 2008; De Frenne et al. 2010; Welshofer et al. 2018), they have not been widely used in insect studies (but see Dollery et al. 2006; Grainger and Gilbert 2017). It is even more rare to study flying insects because of the difficulty in keeping flying insects enclosed within OTCs while excluding the direct impacts of warming on insects (e.g., Kharouba and Yang 2021; Yang et al. 2021).

The OTCs used in this study had an aluminum frame and polycarbonate sides, measuring 1.2 m^2 at the bottom, tapering to a 0.9 m^2 opening at the top (1.5 m tall; Figure 1b). Photosynthetically active radiation (350–750 nm) spans the visible light portion (380–700 nm) of the electromagnetic spectrum (McCree 1971). The polycarbonate sides are estimated to allow 86% visible and ultraviolet light transmission (De Frenne et al. 2010).

Our control chambers had the same dimensions as the OTCs and were constructed using PVC piping. There was nothing covering the outsides of the control chambers from June to August. Just before the adult feeding trials began (August 19, 2023), we wrapped a fine white mesh tulle around the PVC frame of the control chambers (Figure 1c) so that monarchs would encounter the same physical barrier to get to the nectar in the flowers (i.e., monarchs would have to fly up over chamber sides to get into the chamber) as they would with the OTCs. To ensure visual similarity between treatments, OTCs were also wrapped in the same fine white mesh tulle.

From August 15–30, 2023, we constructed 2 m^3 insect enclosures over the OTC and control chambers (Figure 1c). The polycarbonate sides remained on the OTCs even after the monarchs were introduced into the enclosures. The enclosures were built using steel garden poles, bamboo poles, and the same fine white mesh described above. They were designed with enough space to allow the monarchs to spend their non-feeding time outside of the chambers (Figure 1c). Any flowers in the space between the chamber and the mesh enclosure (~30 cm) were removed so that nectar was only available inside the chamber. Together, this design allowed us to separate the direct (i.e., warmed monarchs) and indirect effects of warming on monarchs (i.e., warmed nectar; Figure 1a) and minimize the direct warming effect of the OTC on the butterflies. While the polycarbonate sides remained on the OTCs after the monarchs were removed.

2.2.3 | Experimental Design: Location of Chambers

On June 8, 2023, we placed 15 OTCs and 15 control chambers on existing stems of *S. novae-angliae*, *S. canadensis*, and *M. fistulosa* (single species per chamber, five chambers per species per treatment) at the FWG-CBG site (Figure S1). Each OTC was paired with a nearby control chamber (< 2 m) of the same plant species (known together as a "pair") to ensure similar environmental conditions. Distance between pairs was at least 6 m to minimize the risk of genetic similarity between replicates due to vegetative reproduction. We selected the location of the pairs based on: (i) the availability of each nectar plant species at the site; (ii) a relatively equal cover of each plant species between the pairs; and (iii) the avoidance of daytime shading on the OTCs from trees (Figure S1).

2.2.4 | Monarch Rearing

From July 18 to August 2, 2023, we caught five female and five male adult monarchs from the FWG-CBG site. We mated and reared them in controlled conditions at the University of Ottawa (refer to Appendix S1 for details). Once the monarchs' wings were fully expanded after eclosion (~5–12 h), we added them to the experimental enclosures. The first set of adults was introduced into the experiment on August 19, 2023. Until August 28, only female monarchs were used in the experiment to avoid sex effects. However, due to seasonal time constraints and rearing more males than females, males were also included in the experiment from August 28 to September 14. Adults were allowed to feed ad libitum on the nectar in the chambers for 5 days.

2.3 | Measurements

2.3.1 | Temperature and Soil Moisture

Hourly temperature measurements were taken using 12 HOBO temperature data loggers (Onset HOBO Pendant Temperature/Light 64K Data Logger, ±0.53°C, HOBO Data Loggers, Bourne, MA, USA) in six treatment pairs across the 30 experimental units from July 18th to the end of the experiment. Loggers were hung from 15 cm tall garden posts to minimize ground temperature effects.

To compare soil moisture between temperature treatments, we measured soil moisture in all chambers using a bi-metal probe (RapiTest Moisture Meter) that measures conductivity and indicates moisture content on a scale from 1 to 10. We placed the probe into the soil and allowed the meter to calibrate (~5 s) before recording the reading. We measured soil moisture in each corner and the center of each chamber 1–2 times per week based on logistics during the experiment. We then took the daily average per sampling day.

2.3.2 | Plants

In early June 2023, we flagged and labelled 10 random stems from each chamber using a 1 m^2 quadrat. We chose the stems

closest to the string intersections (every 10 cm). All plant measurements were taken on labelled stems. Stem height was measured from the root crown to the apical leaf of the main stem 1–3 times per week throughout the season.

Floral measurements were recorded from July 5 to October 11, 2023 (Figure S2). We recorded the phenophase of all flowers 1–3 times per week using the flower phenophase classification protocol from the USA-National Phenology Network (Denny et al. 2014). We considered "flowering onset," or the date of the first open flower, as the phenophase. The flowering period for *S. canadensis* and *S. novae-angliae* ended after the experiment (Figure S2) so we did not consider the length of the flowering period in the analysis. To estimate nectar availability, we counted the number of open flowers or floral units (Tew et al. 2021; see Appendix S1 for details) of *S. novae-angliae* and *M. fistulosa*. A flower was considered open when the petals revealed the reproductive structures. We excluded *S. canadensis* from this analysis due to the difficulty in counting the small, dense, and copious number of flowering heads.

To estimate nectar quality, we measured nectar sucrose concentration on 12 days from July 26 to September 25, 2023, which encompassed the main flowering windows and peak nectar production of the species (Figure S2). We sampled on all days that met our sampling criteria to maintain consistent environmental conditions. Sampling frequency varied through the period from every 1–2 days in July to every 5 days on average in September. Measurements for *M. fistulosa* took place prior to the introduction of monarchs into the enclosures but not for *S. canadensis* and *S. novae-angliae* given the timeline of the experiment (Figure S2). Most plant food sources for Lepidoptera are sucrose-dominant, with more than 60% of sugar coming from sucrose (Wolff 2006). We wanted to capture nectar production rate, so we placed 15 cm × 20 cm mesh fruit protection Organza bags over open flowers 24 h before nectar extraction to exclude monarchs or other insects from visiting flowers before nectar measurement and allow the flowers to replenish their nectar. We avoided measuring nectar if it had rained within 24 h, and all measurements were taken between 08:00 and 11:00 to minimize time of day effects.

To measure nectar sucrose concentration, we first extracted nectar from flowers using microcapillary tubes (1–8 μL) with extracted volumes ranging from 1 to 8 μL depending on the size of the flower (Drummond Microcaps, Drummond Scientific Company, Broomall, PA, USA). We displaced nectar from the microcapillary tubes onto a handheld low-volume refractometer (Eclipse 0-50°BRIX Handheld Refractometer). Sucrose concentration was measured in degrees BRIX, a measure of dissolved solids in a liquid (i.e., 1° of BRIX = 1 g of sucrose in 100 g of solution). Sucrose concentrations of the three species used here (range: 0-50°BRIX, mean: 29.9°BRIX; Figure 2d) were similar to those reported for butterfly-pollinated flowers, which generally have concentrations between 20 and 25°BRIX (Nicolson and Thornburg 2007; Willmer 2011). Despite using the smallest microcapillary tubes available (see below for details), the small size of the *S. canadensis* flowers made nectar collection difficult, resulting in a small sample size of sucrose concentration measurements ($n = 15$, compared to *M. fistulosa* $n = 155$, *S. novae-angliae* $n = 97$).

To measure the nectar volume of *M. fistulosa*, we measured the length of the nectar column in the microcapillary tube before displacement onto the refractometer. We calculated the volume of the nectar from the known length and volume of the microcapillary tube and the length of the nectar column ($V_{nectar} = V_{tube} \times L_{nectar}/L_{tube}$). Note that nectar was extracted from each flower until no more nectar could be collected. Flowers of *S. canadensis* and *S. novae-angliae* were too small to extract nectar using the microcapillary tubes described above. Instead, we used a small torch to melt the tubes and slowly pulled the glass using forceps to make the tube narrower in the middle before breaking it apart and using the narrow ends to extract nectar (Corbet 2003). Because tubes were no longer standardized, we could not calculate nectar volume for *S. canadensis* or *S. novae-angliae*.

2.3.3 | Monarchs

We conducted 5-day feeding trials and weighed adult mass on days 0, 1, 3, and 5 of the trial. Five days match typical monarch stopovers and refueling bouts, during which energetic stores and metabolic performance shifts (Walton and Brower 1996; Hobson et al. 2023; Shephard et al. 2023). As well, diet driven adult plasticity within days can influence longevity and performance (Hobson et al. 2023; Shephard et al. 2023). To weigh them, we gently removed the butterflies from the enclosures and placed them in a small container on a scale with an accuracy of four decimal places (Research R300S Analytical Balance Digital Laboratory Scale, Satorius, Göttingen, Germany) located on site. The scale was tared with the measurement container before weighing. In total, there were 59 five-day feeding trials from August 20 to September 21, 2023.

At the end of the feeding trial, the adults were humanely euthanized by freezing and sent to Western University for measurement of body composition. Monarch samples were analyzed for wet, fat, dry lean (hereafter, lean), and water mass (Table S1; Marden 1989). To measure wet mass, samples were placed in individual envelopes and weighed, with the envelope weight subtracted to obtain the total mass of the butterfly (i.e., the body mass of the adults before processing). Given a strong correlation between the weight of live adults on day 5 of the feeding trial and the weight of preserved samples ($n = 59$; $R^2 = 0.90$), as well as the increased reliability of measuring the mass of sedentary samples, we used wet mass as an estimate of total mass instead of the weight measurements taken in the field.

After wet mass was measured, samples were transferred to a drying oven at 70°C for 3 days. Mass was checked periodically, and all samples had reached a constant mass at the time of the final measurement of dry mass. The difference between wet and dry mass is water mass, which was used here as an indicator for the degree of hydration. Monarchs rely on nectar as a major source of moisture and to avoid dehydration (Contreras et al. 2022), and given their large surface area to volume ratio, they face a high potential for desiccation, leading to mortality if water intake is too low (O'Donnell 2022). Monarchs also need water to successfully migrate and survive the winter because they feed and drink less through these periods than during breeding (Brower et al. 2006; Sánchez-Tlacuahuac et al. 2023).

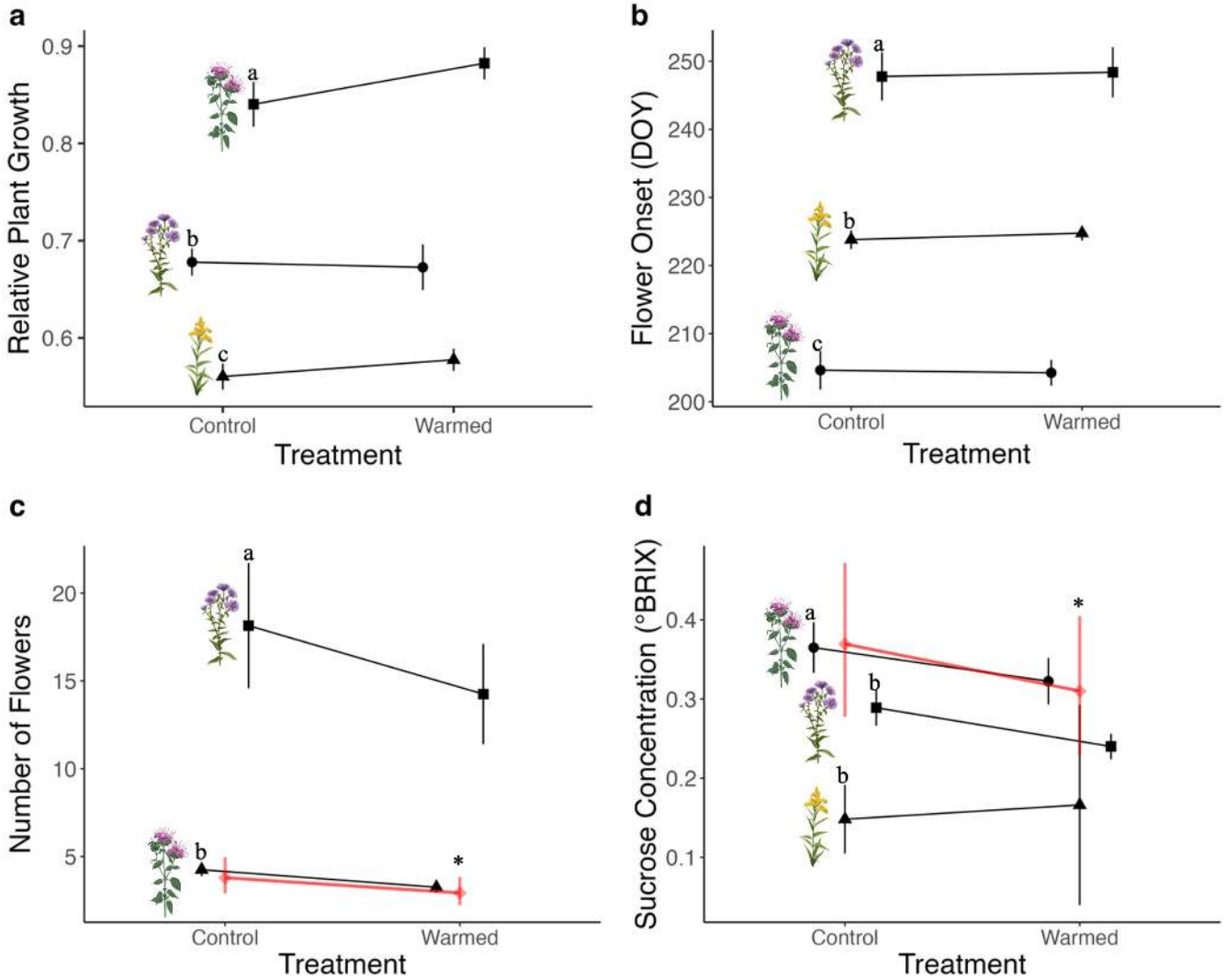


FIGURE 2 | Plant responses to temperature treatment (control and warmed). Shown is: (a) relative stem growth, (b) day of flower onset (DOY), (c) number of flowers, and (d) nectar sucrose concentration (°BRIX). The black symbols indicate the mean estimate based on the raw data with 95% confidence intervals for each species: *Monarda fistulosa* (circles), *Solidago canadensis* (triangles), and *Symphyotrichum novae-angliae* (squares). The red line represents the overall difference (when present) between temperature treatments (Table 2). Means with 95% confidence intervals are shown. "*" denotes a statistically significant effect based on model output ($p < 0.05$). Letters represent statistically significant pairwise comparisons ($p < 0.05$).

To measure fat mass, the samples then underwent petroleum ether extraction in a Soxhlet extractor. This process removes all lipids except for membrane phospholipids. Monarchs were re-dried for another 8 h and re-weighed, with the difference in dry weight before and after extraction representing the butterfly's total lipid mass (or fat mass). Fat mass is one of the most important measurements of body composition for monarchs migrating south (Dockx 2012) because fat fuels their flight and monarchs rarely feed over the winter (Gibo and McCurdy 1993; Sinclair and Marshall 2018). Fat content has also been frequently related to overall condition in insects, with higher fat mass generally resulting in better condition (Zwaan et al. 1991).

Last, lean mass was measured as the remaining weight of the butterfly after water and lipid extraction. It is used as a proxy for total amount of chitin (exoskeleton) and protein in butterflies (muscle tissue, nonlipid organ tissue; O'Regan et al. 2012; Giulivi and Ramsey 2015).

2.4 | Statistical Analysis

2.4.1 | Overview

All statistical analyses were performed using R 4.1.2 (R Core Team 2021). Analyses were split into three sections: (i) "environmental models" to investigate potential differences in environmental conditions between the OTCs and control chambers; (ii) "plant models" to investigate effects of warming on plant growth and development; and (iii) "monarch models" to examine effects of warming on monarch body composition.

Model fitting followed the same framework in all three sections. When random effects were required and assumptions were met, we used linear mixed-effects models (LME; lme4 package; Bates et al. 2015, 2022). When data violated Gaussian assumptions in the presence of random effects, generalized linear mixed-effects models (GLMM) were fitted using glmmTMB (Brooks et al. 2017, 2023). When random effects could not be estimated

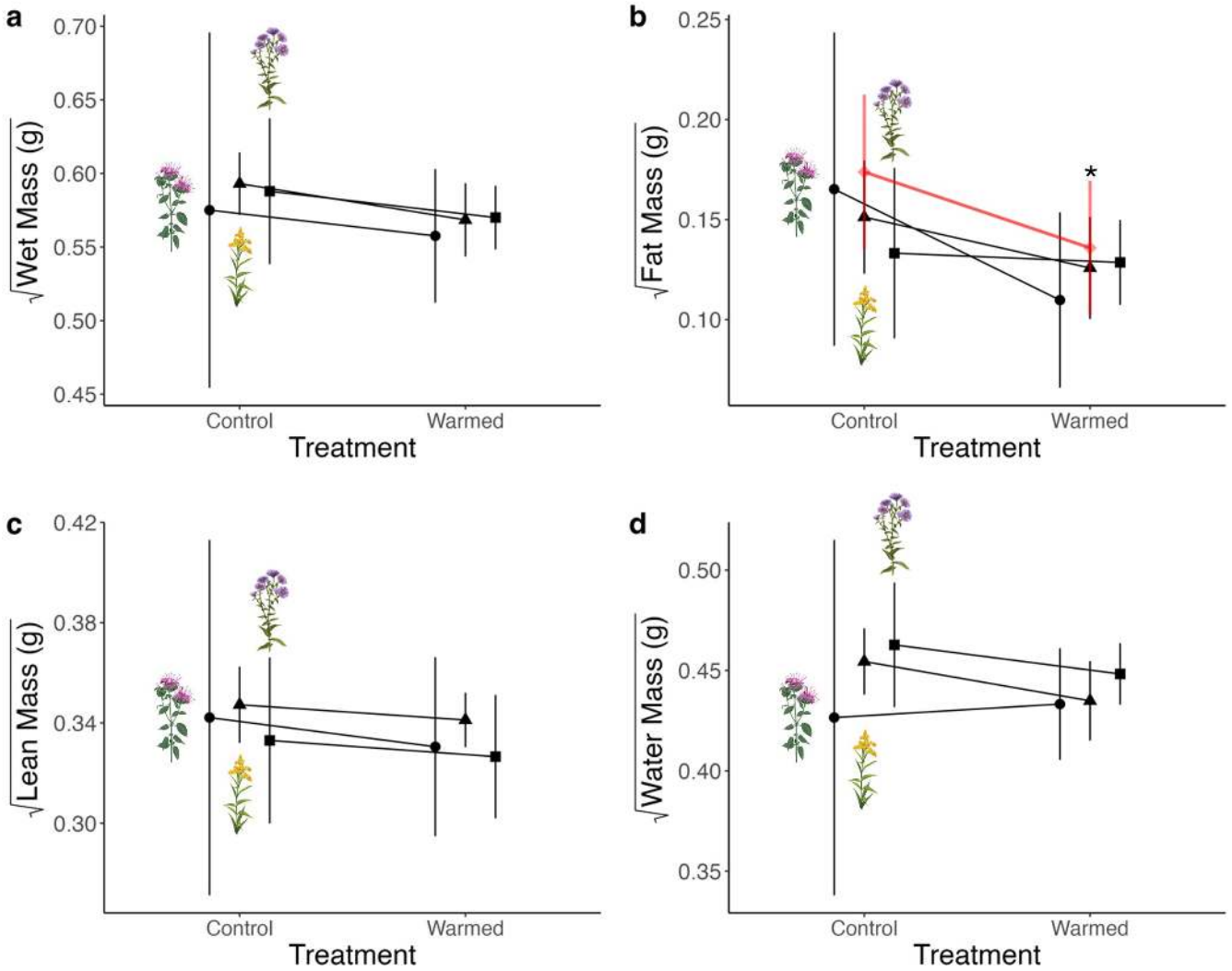


FIGURE 3 | Monarch body condition and composition responses to temperature treatment (control and warmed). Shown is: (a) monarch wet mass (g), (b) monarch fat mass (g), (c) monarch lean mass (g), and (d) monarch water mass (g). All variables have been square-root transformed. The black symbols indicate the mean estimate based on raw data with 95% confidence intervals for each species: *Monarda fistulosa* (circles), *Solidago canadensis* (triangles), and *Symphyotrichum novae-angliae* (squares) under each treatment. The red line represents the overall difference (when present) between temperature treatments (Table 3). "*" denotes a statistically significant effect based on model output ($p < 0.05$).

and data met assumptions, we used linear models (LM). When data violated assumptions of normality, response variables were transformed as necessary.

When possible, "pair" ($n = 15$; an OTC and adjacent (< 2 m) control) was included as an intercept-only random effect to control for repeated measures. "Day of year" (DOY) was included in all models either as a fixed effect to account for seasonal trends or as a random effect to account for temporal autocorrelation. Despite the same experimental structure, sample size varied across the experiment for reasons beyond our control (Table S2).

We assessed model diagnostics using the DHARMa package (Hartig 2022) to evaluate residual normality and homoscedasticity for LM and LME models, and to test for under- and over-dispersion in GLMMs. When model convergence failures occurred due to singular fits, random effects were systematically tested. When nonconvergence was associated with unstable DOY estimates, DOY was first mean-centered; if convergence was still not achieved, DOY was removed from the model.

We evaluated goodness of fit of models using conditional and marginal *R*-squared values for LME models and conditional and marginal pseudo-*R*-squared values for GLMMs using the performance package (Ludecke et al. 2021). All two-way interaction terms were initially included but were only retained in final models when statistically supported; otherwise, they were removed to enable interpretation of main effects (Table S3). To compare differences between levels of all combinations of categorical variables, we used a TukeyHSD pairwise comparison test.

The summary of all models can be found in Table S4. Figures 2 and 3 were created using ggplot2.

2.4.2 | Environmental Models

To determine temperature differences between the OTC and control chambers over the season, we calculated three metrics of temperature: (i) mean daily temperature (°C) between

TABLE 1 | Comparison of mean daytime temperature (°C), nighttime temperature (°C), and temperature fluctuation (°C) between the OTCs and control chambers ($n = 560$ measurements).

Response	Fixed effect	Effect size	SE	DF	F	R^2	p
Mean daytime temperature (°C)	**Treatment**	**0.57** (°C)	**0.28**	**1, 552**	**4.18**	**0.22**	**0.046**
	DOY	**−0.090**	**0.0081**	**1, 537**	**122.36**		**< 0.001**
Mean temperature fluctuation (°C)	Treatment	0.59 (°C)	0.044	1, 553	1.76	0.01	0.19
Mean nighttime temperature (°C)	Treatment	0.45 (°C)	0.24	1, 481	3.40	0.02	0.066

Note: Shown is the effect size (mean difference or β), standard error (SE), degrees of freedom (DF), F-values (F), conditional R^2 values, and p-values (p) for the fixed effects (temperature treatment, day of year [DOY]), with pair as a random effect. Models are fit with linear mixed effects models. Bold font indicates statistical significance ($p < 0.05$).

TABLE 2 | The response of vegetative and floral development, and nectar production of three plant species to the warming treatment.

Response	Fixed effect	Effect size	SE	DF	F/z	p	R^2 (conditional, marginal)
Relative stem growth (%)	Treatment	1.8	3.1	1, 270	0.5	0.48	0.18, 0.17
	Species	**NA**	**NA**	**2, 270**	**29.38**	**< 0.001**	
Flower onset (DOY)	Treatment	0.0021	0.0030	1, 177	0.7	0.48	0.96, 0.86
	Species	**NA**	**NA**	**2, 177**	**NA**	**< 0.001**	
# of flowers	**Treatment**	**−0.25**	**0.055**	**1, 531**	**−4.62**	**< 0.001**	**0.54, 0.31**
	Species	**NA**	**NA**	**2, 531**	**3.76**	**< 0.001**	
Nectar concentration (°BRIX)	**Treatment**	**−0.27**	**0.066**	**1, 229**	**−4.03**	**< 0.001**	**0.78, 0.26**
	Species	**NA**	**NA**	**2, 229**	**NA**	**< 0.001**	
Nectar volume (mL)	Treatment	−0.072	0.057	1, 143	1.61	0.21	0.35, 0.01

Note: Responses are relative stem growth (%; $n = 301$), day of year of flower onset (DOY; $n = 183$), number of flowers ($n = 147$), nectar sucrose concentration (°BRIX; $n = 250$), and nectar volume (mL; $n = 155$). Relative stem growth is fit with a linear model, and nectar volume with an LME model. Flower onset, number of flowers, and nectar concentration are fit with GLMMs. Shown is the effect size (mean difference), standard error (SE), degrees of freedom (DF), F-values (F) for LME models, z-values for GLMMs, and p-values (p). Conditional R^2 (first) and marginal R^2 (second) are reported for each model. Fixed effects are temperature treatment, species, and statistically significant two-way interactions. For nectar volume, only temperature treatment was included as a fixed effect. Pair is a random effect for all models except for relative stem growth. Day of year (DOY) is included as a random effect in the number of flowers, nectar concentration, and nectar volume models. Bold font indicates statistical significance ($p < 0.05$).

8:00 and 20:00; (ii) nighttime temperatures (i.e., 20:00–8:00); and (iii) daily temperature fluctuation between temperature treatments (maximum daily temperature-minimum daily temperature). LME models were used. Treatment and DOY were included as fixed effects in the mean daily temperature model. DOY was not included in the models for temperature fluctuation or nighttime temperature given lack of model convergence.

To evaluate soil moisture differences between the OTC and control chambers, we used average soil moisture per chamber per day. To accommodate the bounded response variable, we used a GLMM with a beta distribution. The model included warming treatment and DOY as fixed effects.

2.4.3 | Plant Models

To estimate relative stem growth, we focused on the period of most rapid growth that occurred before flowering began. We measured the relative change in stem height from day 1 until the date of flower onset of each plant stem and calculated relative growth as (final height-initial height)/initial height. Relative stem growth was measured on DOY 193 for *M. fistulosa*, 221 for *S. canadensis*, and 243 for *S. novae-angliae* (Figure S2). To determine if the warming treatment influenced relative stem growth, we modelled it as a function of the warming treatment and species. Given difficulties with model convergence (i.e., singular fit), we used an LM for plant relative growth.

To determine if the warming treatment influenced the timing of flowering onset, we used a GLMM with a gamma distribution because of overdispersion (mean: variance = 221.9:412.5) and because residuals were not normally distributed. We used DOY of flower onset for each of the 10 flagged stems per chamber and modelled it as a function of temperature treatment and species.

To determine if the warming treatment influenced number of flowers, we modelled number of open flowers per stem on each of the 10 flagged stems per chamber as a function of temperature treatment and species, with pair and DOY as crossed random effects to account for repeated sampling on different days throughout the season. We used a GLMM with negative binomial distribution and logarithmic link because

TABLE 3 | The response of four monarch body condition metrics to the indirect effects of warming from the temperature treatment.

Response	Fixed effect	Effect size	SE	DF	F	p	R^2
Wet mass (g)	Treatment	−0.028	0.018	1, 51	1.18	0.18	0.17
	Sex	0.012	0.026	1, 51	2.57	0.12	
	Species	NA	NA	2, 51	0.59	0.56	
	DOY	0.0030	0.0027	1, 51	0.19	0.89	
	Body length	0.015	0.0065	1, 51	3.64	0.063	
Fat mass (g)	**Treatment**	**−0.038**	**0.016**	1, 51	**3.17**	**0.020**	0.15
	Sex	−0.021	0.023	1, 51	0.027	0.87	
	Species	NA	NA	2, 51	0.22	0.80	
	DOY	**0.0052**	**0.0024**	1, 51	**4.68**	**0.035**	
	Body length	0.0037	0.0057	1, 51	0.30	0.59	
Lean mass (g)	Treatment	−0.015	0.011	1, 51	0.41	0.41	0.24
	Sex	−0.0010	0.016	1, 51	0.63	0.56	
	Species	NA	NA	2, 51	0.92	0.53	
	DOY	0.0016	0.0016	1, 51	0.99	0.37	
	Body length	**0.013**	**0.0039**	1, 51	**11.74**	**0.0012**	
Water mass (g)	Treatment	−0.0046	0.013	1, 51	1.56	0.22	0.23
	Sex	**0.037**	**0.020**	**1, 51**	**6.37**	**0.015**	
	Species	NA	NA	2, 51	0.35	0.84	
	DOY	0.0012	0.0020	1, 51	0.20	0.62	
	Body length	**0.010**	**0.0047**	**1, 51**	**3.23**	**0.042**	

Note: All responses are square root transformed and include wet mass (g) ($n = 59$), fat mass (g) ($n = 59$), lean mass (g) ($n = 59$), and water mass (g) ($n = 59$). All models are fit with linear models. Shown is the effect size (mean difference or β), standard error (SE), degrees of freedom (DF), F-values (F), p-values (p), and model-associated marginal R^2 values. Fixed effects are temperature treatment, sex, species, day of year (DOY), body length. Bold font indicates statistical significance ($p < 0.05$).

number of open flowers is an integer and is overdispersed (mean: variance = 5.2:30.8).

To determine if the warming treatment influenced nectar sucrose concentration, we modelled it as a function of warming treatment and species, with pair and DOY as crossed random effects to account for repeated sampling on different days throughout the season. We used a GLMM with beta distribution given the response was a percentage.

To determine if the warming treatment influenced nectar volume in *M. fistulosa*, we included warming treatment as a fixed effect, with pair and DOY as crossed random effects to account for repeated sampling on different days throughout the season.

2.4.4 | Monarch Models

To determine if the warming treatment indirectly influenced monarch body composition, we modelled wet mass, fat mass, lean mass, and water mass as a function of the warming treatment, plant species, sex (to account for physiological variation between sexes; 2-level factor), DOY of eclosion (to account for seasonal trends), and body length (to account for the monarch's inherent size upon eclosion). Given difficulties with model convergence (i.e., singular fit), we used LMs for all monarch body composition models. All body composition metrics were square root transformed to meet normality assumptions of residuals. We checked for collinearity between fixed effects using Generalized Variance Inflation Factor (GVIF) and none of the variables were correlated (GVIF < 3).

3 | Results

3.1 | Environmental Effects of OTCs

Mean daytime temperatures of OTCs were 2.02% (0.57°C [0.028 SE]) warmer than control chambers ($F = 4.18_{1,522}$, $p = 0.046$, Table 1, Figure S3a). Average daily range of temperatures for the OTCs was 17.6°C–32.8°C (range: 15.2°C), and average daily range of temperatures for the control chambers was 17.6°C–32.3°C (range: 14.7°C). The highest recorded temperature in OTCs was 45.7°C, while the highest in control chambers was 43.5°C.

For both OTCs and control chambers, daytime temperatures decreased over the season (−0.090°C/day [0.0081 SE], $F = 122.36_{1,537}$, $p < 0.001$; Table 1, Figure S3a). There was no

difference in nighttime temperatures, daily temperature fluctuation between OTCs and control chambers (Table 1).

There was no difference in soil moisture between OTCs and control chambers (−0.11 conductivity units [0.078 SE], $z = -1.35_{1,186}$, $p = 0.18$). Soil moisture increased over the season for both OTCs and control chambers (0.024 conductivity units/day [0.00197 SE], $z = 12.29_{1,186}$, $p < 0.001$; Figure S4).

3.2 | Plant Responses

We made 6466 stem height observations from June 9 to October 11, 2023. Overall, the warming treatment did not affect relative stem growth of any plant species (Table 2, Figure 2a). There was no interaction between warming treatment and species on relative stem growth (Table S3). Relative stem growth differed among species ($F = 29.38_{2,270}$, $p < 0.001$; Table 2, Figure 2a; Table S5) with *S. novae-angliae* growing the most (Figure 2a).

The warming treatment did not change timing of flowering onset (Table 2, Figure 2b). Timing of flowering onset differed among species ($z = 8.0_{2,177}$, $p < 0.001$; Table 2, Figure 2b) with *M. fistulosa* flowering first (Figure 2b, Table S5, Figure S2). We found no evidence for an interaction between the warming treatment and species on timing of flowering onset (Table S3).

There were 12.9% fewer flowers per stem in the warming treatment than in the controls (−0.25 flowers [0.055 SE], $z = -4.62_{1,531}$, $p < 0.001$; Table 2, Figure 2c). *Symphyotrichum novae-angliae* had more flowers than *M. fistulosa* (1.35 flowers [0.30 SE] $z = 3.76_{1,531}$, $p < 0.001$; Table 2, Figure 2c; Table S5). We found no evidence for an interaction between the warming treatment and species on number of flowers (Table S3).

Nectar sucrose concentration was 23.6% lower in the warming treatment than the control (−0.27°BRIX [0.066 SE], $z = -4.03_{1,229}$, $p < 0.001$; Table 2, Figure 2d). Species differed in nectar sucrose concentration ($z = -3.0_{2,229}$, $p < 0.001$; Table 2; Figure 2d, Table S5) with *M. fistulosa* having the highest sucrose concentration (Figure 2d). We found no evidence for an interaction between the warming treatment and species on nectar sucrose concentration (Table S3).

The nectar volume of *M. fistulosa* was the same between warming and control treatments (Table 2).

3.3 | Monarch Responses

The response of monarchs differed across body composition metrics. There was no difference in wet mass between the warming and control treatment (Table 3; Figure 3a). Wet mass did not differ across plant species (Figure 3a), sexes, or vary with DOY or body length (Table 3). We found no evidence for an interaction between the warming treatment and any predictors on wet mass (Table S3).

Fat mass was 25.9% lower in the warming treatment than control (−0.038 g [0.016 SE], $F = 3.17_{1,51}$, $p = 0.020$; Table 3, Figure 3b). Monarchs which eclosed later in the season had greater fat mass (0.0052 g [0.0024 SE], $F = 4.68_{1,51}$, $p = 0.035$; Table 3). Adult fat mass did not differ across plant species (Figure 3b), sexes, or vary with body length (Table 3). We found no evidence for an interaction between the warming treatment and any predictors on fat mass (Table S3).

There was no difference in lean mass between warming and control treatments (Table 3, Figure 3c). Monarchs with longer bodies had greater lean mass (0.013 g [0.0039 SE], $F = 11.74_{1,51}$, $p = 0.0012$; Table 3). Adult lean mass did not differ across plant species (Figure 3c), sexes, or vary with DOY (Table 3). We found no evidence for an interaction between the warming treatment and any predictors on lean mass (Table S3).

There was no difference in water mass between warming and control treatments (Table 3, Figure 3d). There was evidence for longer monarchs having greater water mass (0.010 g [0.0047 SE] $F = 3.23_{1,51}$, $p = 0.042$; Table 3). Water mass did not differ across plant species (Table 3; Figure 3d) or vary with DOY (Table 3). We also found no evidence for an interaction between the warming treatment and any other of the predictors on water mass (Table S3).

4 | Discussion

Our experiment revealed consistent indirect effects of warming on monarch fat mass and flower production across three plant species. First, we found monarchs feeding on experimentally warmed flowers had ~26% less fat mass than monarchs feeding on control flowers. Notably, the magnitude of this decrease in fat content could be biologically significant. The predicted average fat content of monarchs that fed on control nectar in this experiment was 0.032 g, which falls in the range of previously studied nonreproductive monarchs (0.019–0.037 g; James 1984). Conversely, monarchs that fed on warmed nectar had an average fat content of 0.0196 g, which falls at the lowest end of that range (James 1984). Given that stored lipids are used as fuel for migration and overwinter survival (Alonso-Mejía et al. 1997; Brower et al. 2006; Sinclair and Marshall 2018; Enriquez and Visser 2023), our study indicates that climate warming has the potential to reduce monarch migration success and overwinter survival. Future work is needed to determine the cumulative effects on monarch physiology and longer-term adaptive responses to these changes in nectar.

The decrease in fat content of monarchs who fed on warmed nectar was most likely driven by the lower nectar sucrose concentration we measured in warmed plants relative to control plants. This finding is consistent with our hypothesis, and with other studies that have found elevated temperatures decrease sucrose concentrations in nectar (Scaven and Rafferty 2013; Takkis et al. 2015; although refer to de Manincor et al. 2023). Warmer temperatures could have led to lower nectar sucrose concentration by increasing enzyme activity leading to an acceleration of the hydrolysis of sucrose into glucose and fructose (Borghi et al. 2019) or by increasing microbial activity which affects nectar sugar composition (Russell and McFrederick 2022). Given that relatively few studies have investigated the effects of climate warming on sucrose concentration, identifying how

warming led to lower nectar sucrose concentration is an important avenue of future research.

It is unlikely that the brief periods of warming monarchs experienced while feeding caused the observed declines in fat mass given the small proportion of time butterflies spend feeding relative to other activities (25–30%; Bąkowski et al. 2010; Popović et al. 2022; Evans et al. 2020). Anecdotally, we observed them to spend most of their time at the top of the enclosures resting. Nevertheless, future studies should investigate whether warming influences feeding behaviour in monarchs.

Second, consistent with previous warming experiments (Liu et al. 2012; Moss and Evans 2022; de Manincor et al. 2023), we found fewer flowers per stem under elevated temperature, likely reflecting thermal inhibition of floral meristem development (Saavedra et al. 2003; Zinn et al. 2010). As flower number influences the plant fecundity and pollinator resources (Sun et al. 2018), these reductions could cascade through pollination networks. However, while warming reduced flowers per stem, overall nectar availability was probably unaffected because stem density remained high in all chambers, as observed in similar experiments (Moss and Evans 2022). However, even if climate warming increases stem densities, reduced floral availability could still limit nectar resources for the broader pollinator community where stem density is low and interspecific competition is high. Future studies should examine the relationship between flower and stem density to disentangle the relative effects of reduced sucrose quality and floral availability on fat gain in pollinators.

4.1 | Similarities and Differences Across Plant Species

Our analysis suggests that the warming treatment had similar effects on the majority of the plant species we considered. This is consistent with our prediction that these species would have similar responses to warming because of their shared history and similar life history strategies (e.g., seasonality, reproductive strategy). However, given the low replication (nectar sucrose concentration) and/or inability to measure all traits (i.e., number of flowers, nectar volume) for *S. canadensis*, it is unclear whether this species had a similar response to the warming treatment as the other two species (Figure 2d). In particular, plots of the raw data suggest some evidence for a lack of effect of the warming treatment on nectar sucrose concentration for *S. canadensis*, thus increasing the risk of a Type II error. A study that was able to extract nectar from *S. canadensis* found much higher levels of nectar sucrose concentration than we found (Jachuła et al. 2020). Future studies should consider species with more divergent life history strategies and physiological tolerances to heat stress to better understand which traits have the potential to contribute to the resilience of ecosystems to climatic changes.

Independently of warming, plant species varied in nectar sucrose concentration and flower number, but these differences did not affect monarch fat mass. In natural settings, this could arise because monarchs are considered nectar-foraging generalists (i.e., they can forage on a wide variety of flower species; Dumroese et al. 2016), fulfilling their nutritional requirements from different species. Experimentally, we expected differences in monarch body composition across species given previous findings from our research groups (Veselovsky et al. In prep). We suggest that the lack of difference we found across plant species here could be explained by compensatory feeding. Here, monarchs may have compensated for the lower quality nectar in *S. canadensis* and *S. novae-angliae* relative to *M. fistulosa* by consuming larger amounts of nectar or feeding more often (Simpson et al. 1989; Slanksy and Wheeler 1991), eliminating species-level differences in quality and quantity. Importantly, even if compensatory feeding can occur when sucrose concentrations are lower, the reduced fat mass of monarchs we found feeding on warmed flowers relative to control flowers suggests that this strategy was not enough for monarchs to overcome the warming-induced declines in nectar quality.

4.2 | Lack of Warming Effects

We found no effect of warming-induced changes in nectar quality on lean mass or water mass of monarchs. This was expected for lean mass, as nectar provides little protein and most adult protein reserves are accumulated during the larval stage (Campbell and Carr 1987). However, the results may have been different for another butterfly species; though not a high protein source, nectar does contain 16 of the 20 essential amino acids, and other butterfly species do use amino acids from nectar to build protein (Nepi et al. 2012; Borghi et al. 2019). There is also evidence that monarchs may use protein derived from amino acids in nectar as additional energy reserves for migration or to build and recover muscle tissue (Giulivi and Ramsey 2015). Regardless, the unchanged lean mass suggests that climatic warming is unlikely to impact the availability of key amino acids in nectar for monarchs.

In contrast, the lack of effect on water mass was more surprising because monarchs rely on nectar for hydration (Contreras et al. 2022) and warming typically increases nectar evaporation (Nicolson 2022). However, high ambient humidity in our study region during the summer (~80% relative humidity; weather-atlas.com) likely minimized evaporative losses, consistent with the tendency for nectar water content to equilibrate with ambient humidity (Nicolson 2022). Any small reductions in nectar volume may also have been offset by compensatory feeding, though the lack of difference we found in nectar volume of *M. fistulosa* across treatment suggests this might not be the case. Together, these results suggest that moderate warming may not substantially increase dehydration risk for monarch populations preparing for migration at the northern limit of their breeding range.

The warming treatment did not change relative stem growth or date of flower onset and the lack of response for both variables was unexpected. Warmer temperatures generally accelerate plant development by increasing metabolic rates (Kudernatsch et al. 2008; Jamieson et al. 2012; Tait and Schiel 2013). Temperature is a primary driver in regulating plant phenology (Parmesan and Yohe 2003; Jamieson et al. 2012; Thackeray et al. 2016). There is also considerable evidence for the advancement in timing of flowering with climate or experimental warming (e.g., Hollister and Webber 2000; McEwan et al. 2011; Rafferty et al. 2020), although substantial interspecific variation in degree and direction of change in timing has also been observed (Stuble et al. 2021). It

could be that the magnitude of the warming effect from the OTCs was not large enough and/or straddled the optimum of the thermal performance curve where the curve is the shallowest (Kharouba and Yang 2021). Alternatively for timing of flower onset, cues for the timing of flowering often occur earlier in the season and/or the previous year (Evers et al. 2021), so our warming treatment may not have begun early enough to influence flower phenology (Ettinger et al. 2018). We note this is challenging to do in a natural field setting where the exact locations of plants are not known year-to-year and thus, the experiment can only begin once plants are identifiable in late spring. Finally, it could also be that the species we used are considered late-season species (i.e., those that flower after the peak of summer heat) which have been shown to be less sensitive to climatic warming than early-season species (e.g., before the peak of summer heat) (Sherry et al. 2007; Chmura et al. 2019). Future field warming experiments that have more extreme warming changes will be necessary to better understand the effects of warming on plant-insect interactions.

4.3 | Effectiveness of the Experimental Treatments

As in most field-warming experiments, our experimental treatment likely influenced multiple environmental factors beyond temperature (e.g., CO_2 concentrations, UV-B radiation; Wolkovich et al. 2012). Our OTCs may have reduced soil moisture to some extent, as our measure of soil moisture was coarse. However, since we found no change in the nectar volume in *M. fistulosa*, and anecdotally found no indications of drought stress in the plants in the warming treatment (e.g., no scorching, yellowing, wilting, premature senescence; Seleiman et al. 2021), it is likely that there were minimal soil moisture-related effects of the warming treatment.

The mean daytime increase of 0.57°C was smaller than regional long-term projections for our study region (average temperature increase: 3°C–8°C by 2100; Gough et al. 2016) but consistent with microclimatic warming expected over coming decades (De Frenne et al. 2019; Lembrechts et al. 2022). Field-based manipulations rarely reproduce the full magnitude of macroclimatic projections due to soil thermal inertia, vegetation structure, and fluctuating weather conditions (Hollister et al. 2022). Even modest experimental warming (< °C) has been shown to produce biologically meaningful effects in phenology, species interactions, and soil biogeochemistry (Wolkovich et al. 2012; Hu et al. 2021; Roth et al. 2023). Thus, our design provides a conservative yet ecologically realistic simulation of near-term climate change.

Our study provides the first experimental evidence that warming-mediated declines in nectar quality can reduce monarch body fat reserves, a critical resource for migration and overwinter survival. These findings highlight the urgent need to identify flower species and restoration strategies resilient to rising temperatures.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Open Science Framework at https://osf.io/g2smx/?view_only=19641ad81ec14a60a8f0cc82dedb7c36.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** gcb470001-sup-0001-Supinfo.docx.