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Up High, Hot and Dry: Individual Reproductive Output in Subalpine Bees Declines With Increasing Drought Severity

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ABSTRACT

Wild bees play indispensable ecological roles in many ecosystems, yet declines in many species have been documented in recent years. These declines have been linked to numerous anthropogenic pressures, including climate change, which can influence bee populations directly (i.e., via physiological mechanisms) and indirectly (e.g., through changes to floral resource quantity and quality). Widespread changes in the distributions and abundances of many bee species have been linked to climate change at large spatial scales; yet, the local-scale processes that generate these broad-scale patterns are little known. Specifically, it is unclear how climate change influences the fitness of individual bees, despite the fact that broad-scale patterns of decline must be driven by individual-level processes. Our study examines the individual fitness responses (i.e., reproductive output) of five solitary bee species in the genus *Osmia* to variations in local climate variables in subalpine habitats. Over nine years, we tracked brood cell production in over 700 individual female bees, conducted repeated surveys of floral abundance (while taking into account the specific floral host taxa used by each bee species), and recorded local precipitation and temperature at seven sites. Our data revealed both direct and indirect (floral resource-mediated) negative effects of drought: the total number of brood cells produced by nesting females decreased significantly in summers characterized by greater drought severity and high temperatures—a relationship driven partly by significant decreases in floral host-plant availability in hotter and drier years. Our study highlights how the negative consequences of climate change for bee populations can manifest at the level of individuals and the role of floral resources in mediating these relationships. Overall, our results suggest that the increasingly warm and dry conditions forecasted for our study area will have net negative effects on the demographic success of these solitary bees.

1 | Introduction

The consequences of climate change for biodiversity are becoming increasingly apparent (Pörtner et al. 2021; Scheffers et al. 2016). A growing number of studies have documented widespread population decline in many taxonomic groups in response to rising temperatures and increased frequency and intensity of climate extremes (e.g., Lister and Garcia 2018; Spooner

et al. 2018). Many of these studies have taken a broad-scale approach, documenting changes in the distributions, ranges, and extinction risks of many species in aggregate across large spatial scales. While their findings have helped to quantify the overall rate and magnitude of biodiversity decline due to climate change, the mechanisms driving the observed patterns remain difficult to decipher. Ultimately, broad-scale patterns of biodiversity loss due to climate change represent the cumulative response of

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individuals within populations to changes in their local climate conditions. Understanding the processes that drive the consequences of climate change for biodiversity requires empirical studies at local scales that document relationships between climate variables and individual fitness, all while considering the idiosyncrasies of species, populations, and their habitats.

Studies that quantify metrics of lifetime individual fitness in natural animal populations are relatively rare (Clutton-Brock and Sheldon 2010; Sheldon et al. 2022). Individuals within a population must be caught, identified, and continuously tracked throughout their lifetimes—requirements that may be impractical or even impossible for many animals, especially those that have long lifespans and for which access to sufficiently high densities of recognizable individuals is limited. Quantifying climate predictors such as temperature and moisture in ways that meaningfully capture the conditions directly experienced by individuals may pose an additional challenge, especially for animals that are migratory or for those that have unknown or large home ranges. Moreover, in addition to the direct (i.e., physiological) impacts of climate, individual fitness can be influenced by climate indirectly through its effects on extrinsic variables such as resource abundance, habitat suitability, and interspecific interactions. Capturing the net effects of climate change on individual fitness would therefore require that these indirect climate pathways be considered along with direct physiological effects. Nevertheless, challenges may arise in quantifying indirect pathways if we lack knowledge of the organism's natural history traits, e.g., their dietary preferences, life cycles, habitat requirements, and interactions with mutualists, competitors, predators, and pathogens. Overall, studies that consider both direct and indirect pathways between climate and individual fitness may be critical for understanding the processes underlying large-scale biodiversity decline, yet are rare due to the practical challenges associated with gathering individual-level data in natural populations and inadequate natural history knowledge for many species.

Solitary bees are ideal candidates for studying the effects of climate on individual fitness. Each female solitary bee constructs her own nests and performs tasks such as provisioning offspring and defending the nest from parasites and predators over a single breeding season that typically lasts only for a few weeks (Danforth et al. 2019). Most species are small-bodied, central-place foragers (females build nests in fixed locations) with flight ranges spanning no more than a few hundred meters (Greenleaf et al. 2007; Zurbuchen et al. 2010). Species-specific natural history traits such as dietary and nesting resource requirements are also relatively easy to observe for most species, facilitating the incorporation of these variables into study designs (Dorian et al. 2024). These traits alleviate some of the challenges frequently associated with quantifying individual fitness in natural populations. Over 75% of the 20,000 described bee species are solitary, and despite their important contributions as pollinators in both natural and agricultural systems, they receive little attention relative to social bees such as honey bees and bumble bees (Danforth et al. 2019).

Over recent years, climate change has been linked to broad-scale declines in both social and solitary bee species, although most studies have focused on the former (Jackson et al. 2022;

Kammerer et al. 2021; Kerr et al. 2015). Substantial variation in the direction and magnitude of the responses of bees to climate change has also been documented, with populations of some species remaining stable and others even showing positive trends (Kammerer et al. 2021; Kazenel et al. 2024; Powney et al. 2019). This variation may in part be attributable to the fact that bees inhabit highly diverse environments and exhibit widely divergent natural history traits (e.g., degrees of sociality, pollen specialization, nesting habits, life cycles, body sizes, etc.) (Michener 2007). Studies that aim to understand the processes driving relationships between bees and climate may therefore benefit from a focused approach with fewer species and a careful consideration of their natural history traits. For the most part, the processes that underpin the responses of bees to climate change remain unknown, despite the fact that this information may be necessary for predicting the responses of species to future environmental change (but see Kazenel et al. 2024).

We conducted a nine-year field study in which we documented the relationships between seasonal weather variables (drought severity, precipitation, and temperature) and individual reproductive output in natural populations of five species of wild solitary bees in the genus *Osmia*. We also considered the pollen requirements of each species by quantifying local floral resource abundance based on the floral host usage of each species and examined the potential indirect, resource-mediated relationships between climate and bee fitness. Our study took place in subalpine meadows in the Rocky Mountains of Colorado in an area that has experienced relatively little anthropogenic land-use change, allowing for the effects of changing climate conditions on bee populations to be investigated independently of other potential stressors (e.g., urbanization, pollution, and pesticides). The state of Colorado and much of southwestern North America is highly drought-prone and predicted to sustain increasingly severe climatic changes including reduced snowpack, earlier snow melt, heat waves, and reduced summer rainfall (Rhoades et al. 2018; Wahl et al. 2022). Many of these changes have already manifested. Montane species may be especially vulnerable to rising temperatures as rates of warming may be amplified at high elevations (Trew and Maclean 2021). At the same time, positive effects of drought for high-elevation species are also conceivable. For example, warmer temperatures and reduced rainfall events may benefit bees and other fair-weather foragers by increasing favorable foraging opportunities—which may be especially limited in our study area given the brevity of the season, the generally cool temperatures, and frequent summer storms. Overall, the demographic effects of drought on many organisms in the region remain unclear.

2 | Methods

2.1 | Study Sites

Data were collected every year from 2013 to 2022 (except 2020 due to COVID-19 travel restrictions) in seven subalpine sites around the Rocky Mountain Biological Laboratory (RMBL), Colorado, USA (38.9592° N 106.9897° W; 2900 m) (Figure 1a). Sites span an elevational gradient of approximately 700 m, from 2729 to 3440 m. Not all sites were monitored in every year of the study (Table S1). In each year, data were collected starting in

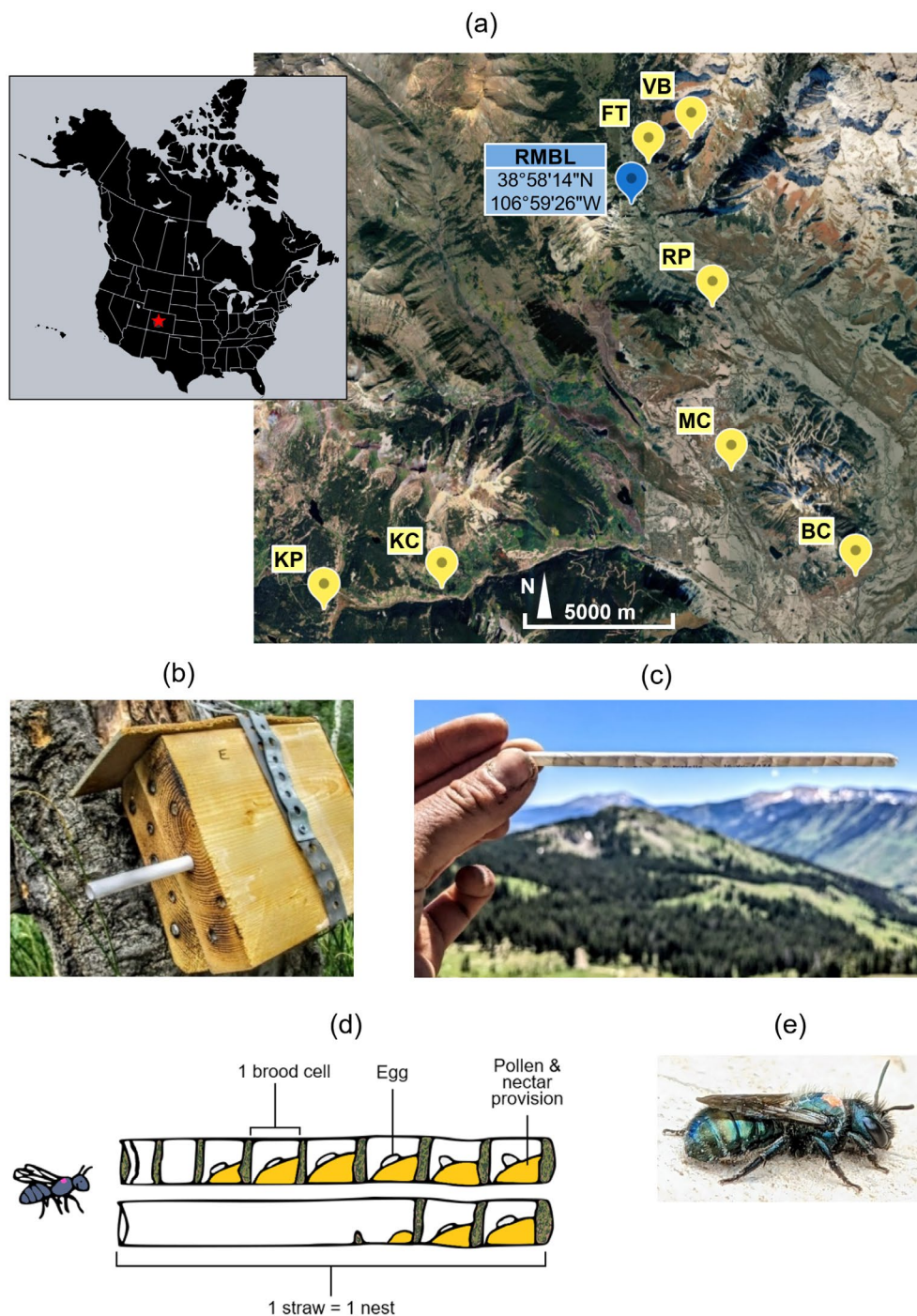


FIGURE 1 | (a) Location of the seven study sites (yellow markers) where bee brood cell production and flower data were collected between 2013 and 2022 and the RMBL (long-term study site; blue marker) where flower data were collected from 1976 to 2022. See Table S1 for site details and abbreviations. (b) Wooden trap nest attached to a tree with one paper nesting straw partially extracted. Cavities are of three diameters: 4.5 mm, 6.1 mm, and 8.2 mm. (c) Paper straw containing an *O. tristella* nest. Brood cells are visible and can be counted when the straw is held up against the light. This nest contains approximately 20 brood cells. (d) Diagram of nest interiors with an individual bee (marked with pink paint) who has two nests, i.e., she has so far used two paper straws throughout her nesting period. Nests consist of a linear series of brood cells each of which contains an egg and pollen-and-nectar provision. We counted the number of eggs produced by each individual across all their nests to determine the total individual lifetime reproductive output. In this illustration, the upper nest is complete (it has an outer seal in addition to the outermost brood cell wall), while the lower nest is still in progress. In the field, this individual's reproductive output would have been scored as a decimal value (e.g., ~8.3–8.4 brood cells) given the partially complete brood cell in her second nest and lack of egg. If no additional progress were to be made in this nest by the end of the season, this individual's reproductive output would have been rounded down to 8 in statistical models. (e) *Osmia tristella* female marked with a dot of orange paint on mesosoma. Photo & illustration credit: L.H.W.

late May or early June until mid- to late-August. Sites contained 12–24 wooden trap nests attached to the trunks of dead or dying trees located at a meadow edge. Trap nests consisted of wooden blocks containing ten 14-cm deep holes of three diameters (4.5, 6.1, and 8.2 mm) that attracted cavity-nesting Hymenoptera (bees and wasps). Holes were lined with semitransparent paper straws, allowing for nests to be temporarily removed and for the number of brood cells contained in them to be counted without disturbing actively nesting females (Figure 1b,c).

2.2 | Study Organisms

Numerous cavity-nesting bee species have been recorded nesting in the trap nests at our sites (Forrest and Thomson 2011); however, the total brood cell production of individual females was only consistently recorded for a subset of species—primarily those that were relatively common at the sites and for which brood cells were not concealed in nesting material. We selected the five most well-represented species across sites and years: *Osmia coloradensis* Cresson, *O. iridis* Cockerell and Titus, *O. montana* Cresson, *O. subaustralis* Cockerell, and *O. tristella* Cockerell. All are solitary bee species that occur throughout western North America and nest in pre-existing cavities in wood (Michener 2007; Wilson et al. 2010). In our study area, adult bees typically emerge between late May and mid-June, the specific timing varying by species and site (Wong and Forrest 2021). Individuals mate, and females locate nesting cavities and construct nests. Nests consist of a linear series of brood cells, with each cell containing a mass of pollen and nectar along with a single egg (Figure 1d). A female bee may construct multiple nests, almost always sequentially, over her lifetime. Upon hatching, larvae progress through several instars over the course of the summer before entering diapause for the winter. All five species are typically semivoltine in our study area, emerging as adults two years later, although one-year lifecycles are observed occasionally (Forrest et al. 2019).

2.3 | Bee Reproductive Output

Most sites were visited every 3–5 days (Table S1). During each site visit, we checked trap nests for nesting activity by temporarily extracting the paper straws and inspecting their contents. Upon identifying a new active nest at a site, we watched the nest entrance until the nest owner (nesting female) appeared. Females were then caught and marked with unique color combinations of non-toxic paint (Testors Hobbyist's paint: Vernon Hills, Illinois, USA; Figure 1e). The paint marks allowed us to track individual bees as they constructed successive nests because approximately a third of all individuals built more than one, i.e., used multiple paper straws (Figure 1d). Females were released after being marked and continued nesting. Once nests were completed and sealed, we quantified each female's reproductive output by summing the total number of brood cells they had produced across all their nests. Although this study design does not account for brood cells constructed outside of the trap nests in naturally occurring cavities at our sites (if any), females who built multiple nests typically began nesting in a new hole within the same trap nest immediately after completing the first. Species identifications of nesting individuals were ascertained

using a combination of species-identifying morphological features visible in the field, as well as nest pollen contents (see “Floral resources”). Further details on trap nest monitoring protocols are in Wong and Forrest (2021).

2.4 | Floral Resources

We quantified floral resources following the protocol of Forrest and Chisholm (2017). These data were used to characterize the relationship between climate variables and the floral resources available to nesting bees, as well as the relationship between floral resources and bee reproductive output. Floral surveys were conducted during every site visit in the first seven years of the study (every 3–5 days; 2013–2019) and weekly in 2021 and 2022. The first flowering of some taxa was missed at some sites in 2013 as floral surveys were initiated only when bees started nesting that year. During surveys, we counted open flowers only of plant taxa identified as potential pollen sources for our focal bee species (floral hosts) since four of the five species were pollen specialists: *Osmia coloradensis*, *O. montana* and *O. subaustralis* are specialists on plants in the Asteraceae family (Rust 1974); *O. iridis* are specialists on plants from the tribe Fabeae or possibly the broader “IRLC” clade of papilionoid legumes (Fabaceae; at our sites, these were primarily *Lathyrus lanszwertii* Kellogg and *Vicia americana* Muhl. Ex Willd.) (The Legume Phylogeny Working Group 2013). *Osmia tristella* are pollen generalists (Rivet et al. 2024). Floral hosts were confirmed by examination of pollen samples from bee nests at our study sites (for details, see Forrest 2024; Spear et al. 2016; Wong and Forrest 2021). All plant taxa (typically species or genera, sometimes groups of related genera with indistinguishable pollen) found in pollen samples and present at our sites were included in surveys. Taxa that were identified as floral hosts partway through the study and missed in earlier years were included in all subsequent surveys; we ascertained that their contribution to our metrics of floral resources did not qualitatively influence our results. See Forrest (2024) for details on plant taxa. Hereafter, “floral group” refers to all floral hosts used by each bee species; these include Asteraceae (*O. coloradensis*, *O. montana*, *O. subaustralis*), tribe Fabeae (*O. iridis*), and generalist hosts (*O. tristella*) (Table S2).

In addition to conducting floral surveys at our study sites, we accessed two multidecadal datasets from the RMBL to further examine the relationship between climate variables and floral resource abundance. The RMBL is located within 15 km of all our study sites (Table S1); climate conditions, floral species composition, and phenology are therefore similar. The first dataset contained floral abundance and phenology records of 45 of the 49 plant species we surveyed (missing taxa represented 10% of the floral hosts of the generalist bee species in our study, *O. tristella*). Counts of these species from this dataset were combined according to the three floral groups. Briefly, each year from 1976 to 2022 (except 1978 and 1990), all open flowers in twenty-one 2 × 2 m plots were counted every 2–3 days throughout the growing season (generally May to September; methodological details and metadata in Inouye (2008) and Inouye et al. (2022)). The second dataset contained long-term weather data amalgamated from several local sources with the same temporal coverage as the long-term floral abundance dataset (Prather et al. 2023). Although

TABLE 1 | Final versions of models tested. Models are written in the form: Response ~ predictor. Model types include linear mixed-effects models (LMMs), linear models (LMs), and negative binomial generalized linear mixed-effects models (NB-GLMMs). Variable transformations and temporal coverage of precipitation, temperature, and drought severity are described in the main text. A priori versions of models contained interactive effects between climate variables and floral group or bee species for models (1–2) and (3–4) respectively. These interactions were removed as they were found to be non-significant; the statistical results reported in the text reflect these reduced models.

Model type	Response	Model predictors	#
LMM	Maximum floral density (2013–2022)	~ Drought severity + Floral group + (1 Site) + (1 Year)	1a
		~ Precipitation * Temperature + Floral group + (1 Site) + (1 Year)	2a
LM	Total floral density (1976–2022)	~ Drought severity + Floral group	1b
		~ Precipitation * Temperature + Floral group	2b
NB-GLMM	Bee reproductive output (2013–2022)	~ Drought severity + Nesting date + Max. floral density + (1 Site) + (1 Year) + (1 Bee species)	3
		~ Precipitation * Temperature + Nesting date + Max. floral density + (1 Bee species)	4

these data do not perfectly represent the flower and climate conditions experienced by the bees at our sites, we incorporated them in our study as they allow for the floral resource–climate relationship to be examined over a timeframe that captures greater climate variation than our nine-year dataset.

2.5 | Climate Variables

At each of the seven sites, an unshielded HOBO temperature logger (Onset Computer Corp., Bourne, Massachusetts, USA; accurate to $\pm 0.5^\circ\text{C}$) was attached beneath one centrally located trap nest and provided hourly readings throughout the entire duration of the study (additional details in the [Supporting Information](#)). Because we did not have in situ measures of precipitation at the seven sites, we acquired daily precipitation for each site and year using the parameter-elevation regressions on the independent slopes model (PRISM Group, Oregon State University, accessed October 18, 2023). These data were used to generate metrics of precipitation and temperature, and to calculate a drought index that combines precipitation and temperature, which were our predictor variables (models described below).

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to quantify drought severity as it includes both precipitation and temperature and can be quantified at varying temporal grains and windows, i.e., indices can be calculated over durations of time relevant to a particular organism and with respect to varying calendar dates (Vicente-Serrano et al. 2010). For example, a 3-month SPEI ending in October characterizes conditions averaged over the months of August through October. SPEI is a normalized index; values of zero indicate no change relative to historical values. We used negative SPEI values ($-1 * \text{SPEI}$) in our models and figures to make results more intuitive to interpret and visualize; large positive values indicate severe drought, and large negative values indicate cool and wet conditions. The Hargreaves method was used to calculate monthly potential evapotranspiration (Beguería et al. 2014). All SPEI values were calculated using the R package “SPEI” (Beguería et al. 2023). Hereafter, we refer to (negative) SPEI as “drought severity.”

2.6 | Data Analysis

2.6.1 | General Approach

We used linear models to examine relationships between climate variables and two response variables: (1) floral density and (2) total brood cell production (individual lifetime reproductive output). For each response variable, we ran two models—one with drought severity as the sole climate predictor (hereafter “drought severity model”) and a second with temperature, precipitation, and their interaction as predictors (hereafter “component variable model”). The goal of the drought severity models was to test the consequences of the specific combination of climate variables associated with drought (i.e., high temperatures, low precipitation), while the component variable model aimed to delineate potentially more nuanced relationships between our response variables and temperature and precipitation. The temporal coverage of drought severity, temperature, and precipitation varied depending on the response variable in the model. Models are described in detail below and a list of all final models is in Table 1.

All analyses were conducted in R (version 4.4.1) (R Core Team 2024). For all models, we examined pairwise correlations between continuous predictor variables and calculated Variance Inflation Factors (VIFs) using the “check_collinearity” function in the package “performance” (Lüdtke et al. 2021), and the “vif” function in base R. VIFs and correlations between predictor variables were generally low (Figures S8 & S9; maximum VIF = 2.23). Models where predictors were strongly correlated, and where we suspected multicollinearity may have influenced our findings, are noted in the results. Homoscedasticity was assessed by visually inspecting residual plots; data were transformed in cases where plots indicated model heteroscedasticity (transformations specified below).

2.6.2 | Floral Density Models

For both datasets, we only included floral counts between June 7 and August 16 because these dates correspond to the

latest survey start date and earliest survey end date over the duration of trap nest monitoring at our seven study sites. Drought severity was calculated over a 12-month 'water-year' from September 1 of the previous year to August 31 of the current year. This time window incorporates winter snow accumulation and summer rainfall, both of which are known to influence flower phenology and abundance in our study area (Inouye 2008). Total precipitation was also summed over this time window. Mean temperature was averaged over a four-month period from May to August (hereafter "summer"), reflecting the period during which most species flower. Hereafter, we refer to these climate metrics as "water-year drought-severity," "water-year precipitation," and "summer temperature." Precipitation and temperature were scaled and centered to mean = 0 and standard deviation = 1.

For the flower data collected at the seven study sites, we used the maximum floral density observed for each floral group in each site and year as our response variable (i.e., for each sampling occasion, we summed the densities of all taxa in a given floral group and extracted the maximum value observed for each year and site). We used maximum density instead of total or average density because the first and last flowering of early and late-blooming taxa, respectively, were missed in some years at some sites. In these models, each replicate represented a yearly metric of floral density for a given floral group in a given site and year. Maximum floral density was naturally log-transformed to improve the homoscedasticity of residuals. For the RMBL (long-term) data, we combined floral counts across all 21 plots, treating all plots as a single site since they were all located within 1 km of one another. For each floral group, we generated annual metrics of total floral density by summing floral counts across all plant taxa in the group, and across all plots and census days for each year. We then divided total floral counts by the total area surveyed in that year (the number of plots surveyed multiplied by 4 m²) to account for differences among years in the number of census days. Total floral density was fourth-root transformed to improve homoscedasticity of residuals.

We ran linear models to test relationships between floral density and water-year drought (drought severity model), as well as water-year precipitation, summer temperature, and their interactive effects (component variable model). For the floral data from the seven sites, we used linear mixed-effects models (LMMs) with site and year (seven and nine levels, respectively) included as random-intercept effects. Slope estimates were obtained using the "lmer" function in the "lme4" package (Bates et al. 2015), and the significance of fixed factors was evaluated with Satterthwaite-approximated degrees of freedom using the "lmerTest" package (Kuznetsova et al. 2017). We used simple linear models for the RMBL data as each replicate represented floral density for one floral group in a given year. For both datasets, we considered potential variation in responses to climate across the three floral groups by including the floral group as an interactive effect with all climate variables (i.e., drought severity * floral group and temperature * precipitation * floral group for the drought severity and component variable models, respectively).

2.6.3 | Bee Reproductive Output Models

To test the relationships between bee reproductive output, drought severity, precipitation, temperature, and floral abundance, we ran negative binomial generalized linear mixed-effects models (NB-GLMMs) using the "glmer.nb" function in the "lme4" package (Bates et al. 2015). Drought severity, precipitation, and temperature were calculated over a four-month period from May 1 to August 31 ("summer drought severity," "summer precipitation," and "summer temperature"), reflecting the months during which female bees were provisioning nests. As with the floral density models, we accounted for potential interspecific variation in responses to climate by including bee species as an interactive effect with all climate variables. In these models, each replicate represents an individual female of a given species and the total number of brood cells she produced in a given year and site (i.e., lifetime reproductive output). Total brood cell production was recorded as a non-integer variable in the field as we included partially complete brood cells (Figure 1d); however, values were rounded to the nearest integer for statistical analysis. Maximum floral density was log_e-transformed to reduce the influence of extreme values. The day of the year on which individual bees were first observed to be nesting (nesting date) was included as a covariate because nesting timing is a known predictor of reproductive success in our study system (Wong and Forrest 2021). Nesting date, precipitation, and temperature were each scaled and centered to mean = 0 and standard deviation = 1. We used the "dispersion_glmer" in the package "blmeo" to verify that models were not over-dispersed (Korner-Nievergelt et al. 2015).

2.6.4 | Structural Equation Models

We also examined the relationships among climate variables, floral resources, and bee reproductive output at our sites using structural equation models (SEMs), as they facilitate the detection of direct and indirect relationships and allow for causal inferences to be made from observational data (Shipley 2016). SEMs were constructed and evaluated using the "piecewiseSEM" package in R (Lefcheck 2016).

We constructed two a priori causal networks: the first used drought severity as the predictor for floral density and bee reproductive output; the second used component variables as predictors (Figure 4). A priori component models were modified versions of Models 1a and 3 (drought severity) and Models 2a and 4 (component variable) in Table 1. In a priori models, we only included interactions that were found to be significant in the linear models described above. The floral group (3 levels) was included as a random effect in component models predicting floral density because including it as a fixed effect (as in the LMMs) complicated results interpretation (standardized estimates cannot be generated for some pathways when models contain categorical fixed effects). The calculation of standardized coefficients has not yet been implemented for NB-GLMMs through the piecewiseSEM package, so we calculated coefficients for all pathways leading to brood cell production using the observation-empirical approach (Grace et al. 2018). We included

all pair-wise combinations of correlations between climate variables to account for any covariance between precipitation and temperature, or between climate variables covering different time windows (e.g., summer and water-year drought severity). Response variables and predictors were transformed as in linear models, and continuous variables were automatically scaled by piecewiseSEM. Table S9 contains a summary of all component models.

We evaluated model goodness-of-fit using Fisher's C ($p > 0.05$ indicating adequate fit) and Shipley's tests of directed separation (d-sep) to identify missing pathways among variables (significant independence claims) (Shipley 2016). When d-sep tests indicated that a priori networks were missing biologically plausible significant relationships, we revised component models and reran SEMs (Arif and MacNeil 2023).

3 | Results

3.1 | Climate

From 2013 to 2022, our study region sustained two periods characterized by extremely hot and dry conditions: in 2018 and between 2020 and 2021, drought indices neared or surpassed 1.5 for more than half the year, suggesting that conditions were outside the range of normal climatic variation (review in Slette et al. 2019) (Figures S1 and S2a). Since the start of the long-term flower monitoring in 1976, there have only been three other similarly extreme droughts in terms of magnitude and duration (Figure S1a) (1977, 1981, and 2012; Prather et al. 2023). Relative to the baseline period of 1976–2012, total annual precipitation fell below the 15th percentile in 2013, 2018, and 2021 (Figure S1b), and mean annual temperatures at the RMBL surpassed the 90th percentile in 2015, 2017, and 2018 (Figure S1c).

3.2 | Floral Density

The effects of drought severity, temperature, and precipitation did not vary significantly by the floral group; interactions between climate variables and the floral group were therefore removed, and we present the reduced models here (final forms of models in Table 1). Floral density decreased with increasing drought severity in both datasets, although this relationship was only marginally significant at the seven sites (RMBL: Figure 2a; $\beta = -0.06$, $SE = 0.01$, $t = -4.22$, $p < 0.01$; seven sites: Figure S3a; $\beta = -0.18$, $SE = 0.08$, $t = -2.24$, $p = 0.06$). At the RMBL, this decrease represented a halving of the number of flowers per m^2 (per floral group) between the least and most severe drought years. The interactive effect of water-year precipitation and summer temperature was a significant positive predictor of floral density at the RMBL and at our seven study sites (RMBL: $\beta = 0.05$, $SE = 0.01$, $t = 3.52$, $p < 0.01$; 7 sites: $\beta = 0.16$, $SE = 0.07$, $t = 2.46$, $p = 0.02$). Visual inspection of interaction plots for both datasets suggested that hot summers had stronger negative effects on floral density when they were also dry (RMBL: Figure 2b–d; seven sites: Figure S4). We note that water-year precipitation and mean summer temperature at the seven sites were highly correlated, so the slopes characterizing the effects of these variables should

be interpreted with caution ($r = -0.75$; Figures S8a and S9e). See Table S4 for detailed model results.

3.3 | Bee Reproductive Output

Over nine years, across all sites, we observed the nesting activity of 723 female bees (362 *O. iridis*, 86 *O. coloradensis*, 115 *O. montana*, 115 *O. subaustralis*, 45 *O. tristella*), of which 694 (96%) were successfully paint-marked. Nests constructed by unknown individuals were excluded from analysis; however, we included 29 unmarked individuals in our analyses because we had ascertained that they were the only unmarked individuals of their species at the given site in that year. On average, females constructed between 6 and 8 brood cells in total (Table S3). Collectively, all individuals in the study produced 5111 brood cells.

Interactions between bee species and climate variables were non-significant in both the drought severity and the component variable models. Models were therefore rerun with bee species (five levels) as a random-intercept effect. Brood cell production decreased with increasing summer drought severity (Figures 3a and S6a; $\beta = -0.12$, $SE = 0.06$, $Z = -2.25$, $p = 0.03$), falling from an average of 7.4 to 4.6 cells per female in sites and years characterized by the lowest and highest drought severity, respectively. Summer precipitation was not a significant predictor of brood cell production (Figures 3b and S6b; $\beta = -0.003$, $SE = 0.06$, $Z = -0.057$, $p = 0.95$); however, hotter summers were associated with significantly lower reproductive output (Figures 3c and S6c; $\beta = -0.17$, $SE = 0.08$, $Z = -2.10$, $p = 0.04$). Total brood cell production fell from an average of 10.2 to 4.3 cells per female between the coolest and hottest sites and years. Maximum floral density was a significant positive predictor of total brood cell production in both the drought severity and component climate models (Figures 3d and S6d; drought severity model: $\beta = 0.12$, $SE = 0.03$, $Z = 3.67$, $p < 0.01$, component variable model: $\beta = 0.12$, $SE = 0.03$, $Z = 3.90$, $p < 0.01$). In all models, nesting date was a significant negative predictor of total brood cell production; bees who nested earlier in the season produced more offspring (Figure S7; drought severity model: $\beta = -0.38$, $SE = 0.04$, $Z = -10.56$, $p < 0.01$; component variable: $\beta = -0.38$, $SE = 0.03$, $Z = -10.57$, $p < 0.01$). See Table S5 for detailed model results.

3.4 | Structural Equation Models

The a priori model fit for the drought SEM was inadequate (Fisher's $C = 14.20$, $df = 6$, $p = 0.03$). The path between summer drought severity and maximum floral density was identified as a significant missing pathway (Fisher's $C = -2.15$, $df = 22.31$, $p = 0.04$; a priori, summer drought severity was only a predictor for bee reproductive output). Model fit was adequate after the addition of this path (Fisher's $C = 7.37$, $df = 4$, $p = 0.12$). No additional missing paths were suggested in the revised model, which suggested both direct and indirect negative effects of drought on bee brood cell production (Figure 4a). Increased summer drought severity directly lowered bee brood cell production ($p = 0.03$) but also had a direct negative effect on maximum floral density ($p = 0.04$) which in turn positively affected brood cell production ($p < 0.01$).

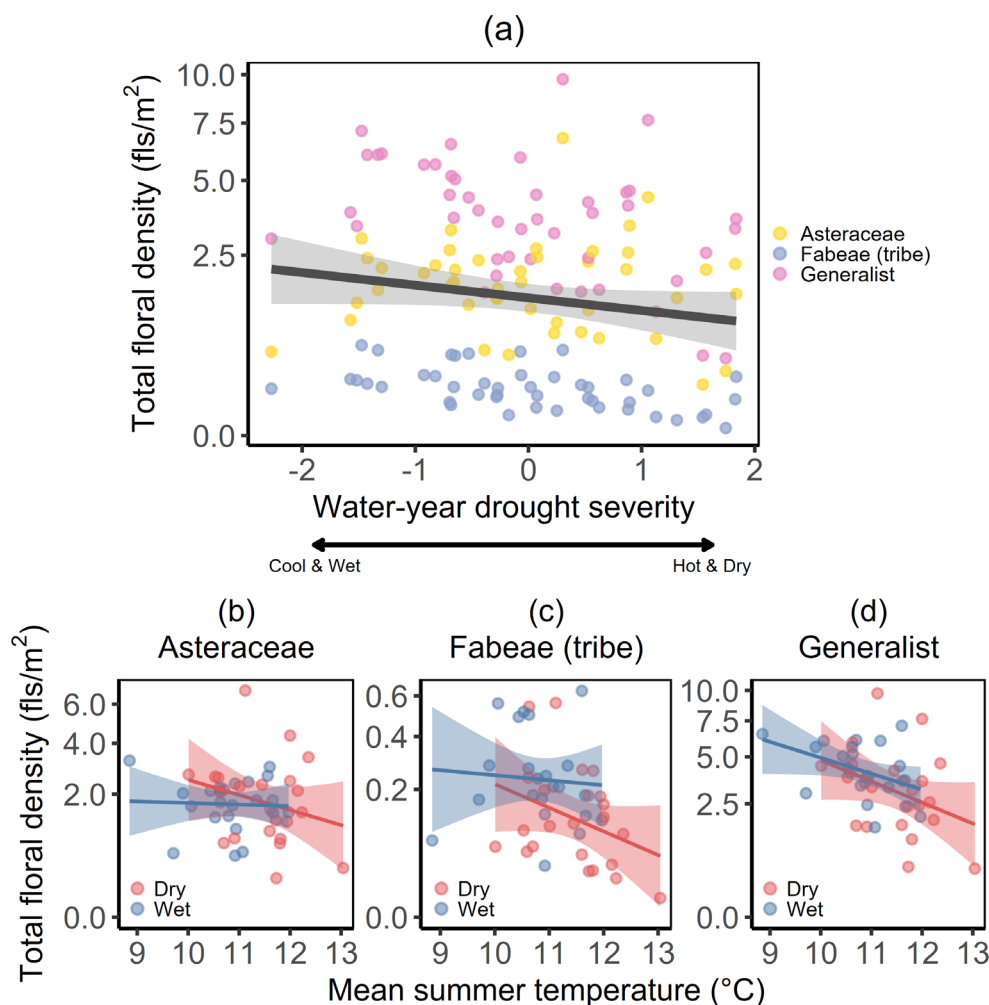


FIGURE 2 | (a) Total floral density at the RMBL (1976–2022) as a function of water-year drought severity (-1×12 -month Standardized Precipitation-Evapotranspiration Index) for all three floral groups. A water-year covers the period between September 1 of the previous year to August 31 of the current year. (b–d) Total floral density at the RMBL as a function of mean summer temperature for each floral group separately. Data are divided into two equal precipitation categories based on total water-year precipitation to visualize the interactive effects of temperature and precipitation. “Dry” and “Wet” correspond to water-year precipitation totals less than and greater than the median water-year precipitation (806 mm), respectively. Red lines have more negative slopes than the blue lines. Each datapoint represents total floral density observed for a given year; $N=45$ years for each floral group. Bands indicate 95% confidence intervals for the slope of simple univariate linear models. Marginal R^2 values are in Table S6. The y-axis was square-root scaled in all panels to better visualize all datapoints.

Model fit of the a priori component variable SEM was adequate (Fisher's $C=5.515$, $df=6$, $p=0.48$) and revealed significant direct and indirect negative effects of warmer and drier conditions on brood cell production (Figure 4b). Increased mean summer temperature was directly associated with lower bee brood cell production ($p=0.04$). The interactive effects of water-year precipitation and summer temperature were directly associated with maximum floral density ($p<0.01$), which in turn directly increased bee brood cell production ($p<0.01$).

4 | Discussion

Our observations of over 700 female bees, repeated surveys of floral abundance, and records of precipitation and temperature over nine years suggest that bee reproductive success in our study system declines with warmer and drier climate conditions

and increasing drought severity. We discuss the putative direct and indirect mechanisms that may be at play herein, as well as the potential consequences for populations of bees and other flower-visiting insects in our study area if droughts become increasingly frequent and severe.

4.1 | Direct Effects of Climate Variables on Bee Reproduction

4.1.1 | Temperature

For many ectotherms, numerous physiological processes including those involved in egg maturation and oviposition are highly temperature-sensitive (Berger et al. 2008; Howe 1956; Kingsolver and Huey 2008; Zhang et al. 2015). In our data, bee brood cell production declined with increasing drought severity

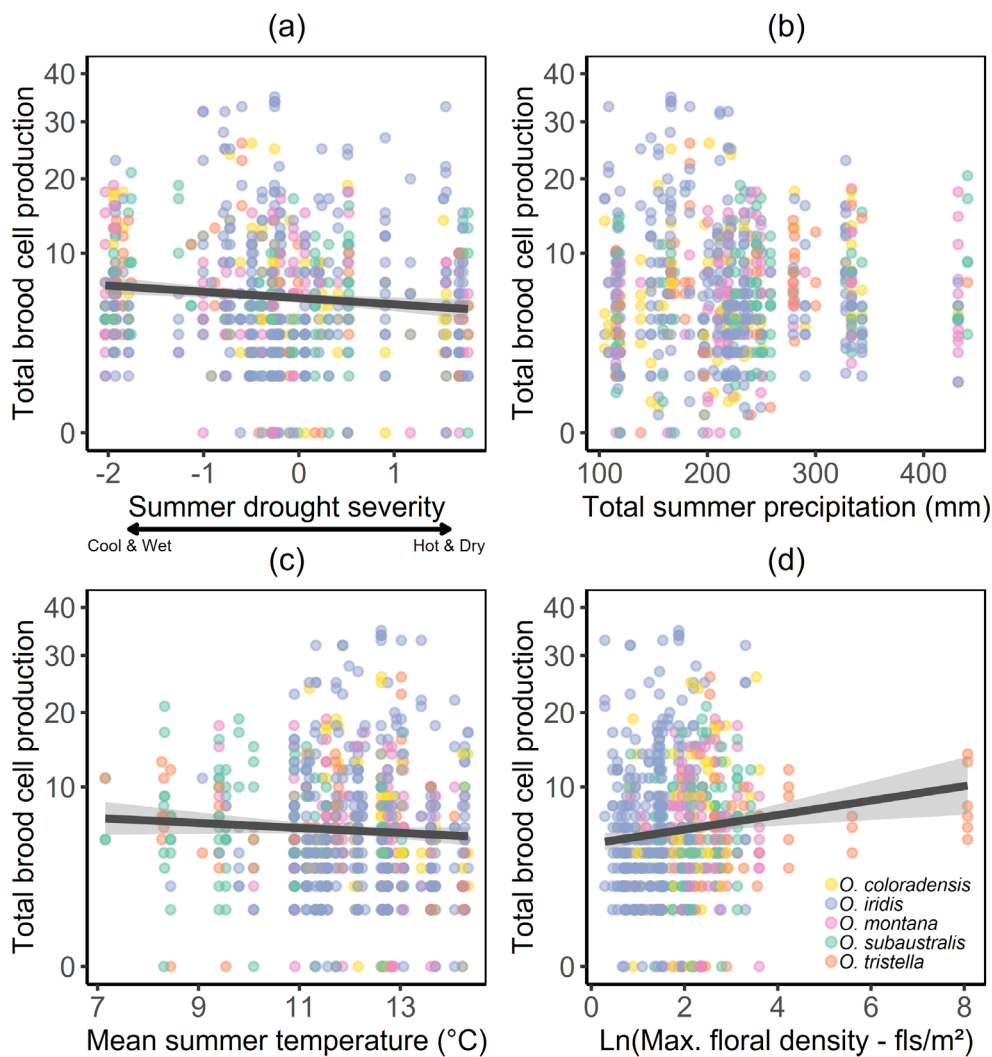


FIGURE 3 | Total brood cell production as a function of (a) summer drought severity ($-1 \times$ Standardized Precipitation-Evapotranspiration Index), (b) total summer precipitation, (c) mean summer temperature, and (d) maximum floral density (natural log transformed). Summer = May–August. Each datapoint represents the lifetime reproductive output of one female bee. An extreme outlier was omitted here for visualization but was retained in all analyses (figures including this bee in Figure S5). Solid lines indicate significant ($p < 0.05$) relationships in the multivariate models described in the text. Species-specific trendlines were not included as we did not detect significant interactions between predictors and bee species, but figures for each species separately are in Figure S6. The y-axis was square-root scaled in all panels to better visualize all datapoints on the same graph. Marginal R^2 values for each predictor are in Table S6.

and warmer mean summer temperatures, independently of floral density. This pattern could reflect physiological relationships between temperature and reproduction; many insects oviposit only within specific temperature ranges, and egg maturation may be disrupted if temperatures exceed certain thresholds (Engelmann 1970). In laboratory studies with *Osmia* species, higher temperatures have been shown to accelerate oocyte degeneration and arrest oocyte development (Maeta and Kurihara 1971).

The negative relationship we observed between drought conditions and brood cell production could also be driven by the effects of temperature on other aspects of physiology not directly related to egg production. High temperatures can increase oxidative damage and mutation rates in many animals, leading to decreased survival and longevity (Burraco et al. 2020; Pearl 1928; Ritchie and Friesen 2022) and ultimately shortening

the time available for reproduction. Indeed, negative effects of high temperatures on longevity, and the resulting loss of time to reproduce, have been previously suggested in our study system (Wong and Forrest 2021) and in another *Osmia* species (Müller et al. 2025). In both studies, the number of days over which females actively nested declined with warmer temperatures, and shorter nesting duration was associated with lower total brood cell production.

Many physiological traits in ectotherms initially respond positively to warmer temperatures but decline rapidly once a species-specific threshold is surpassed (Huey and Stevenson 1979). Although the thermal thresholds of our focal species have not been quantified, laboratory studies with other *Osmia* species have suggested that temperatures exceeding optimal ranges by 3°C – 4°C can generate significant negative physiological responses, including decreased body size, longevity, and survival

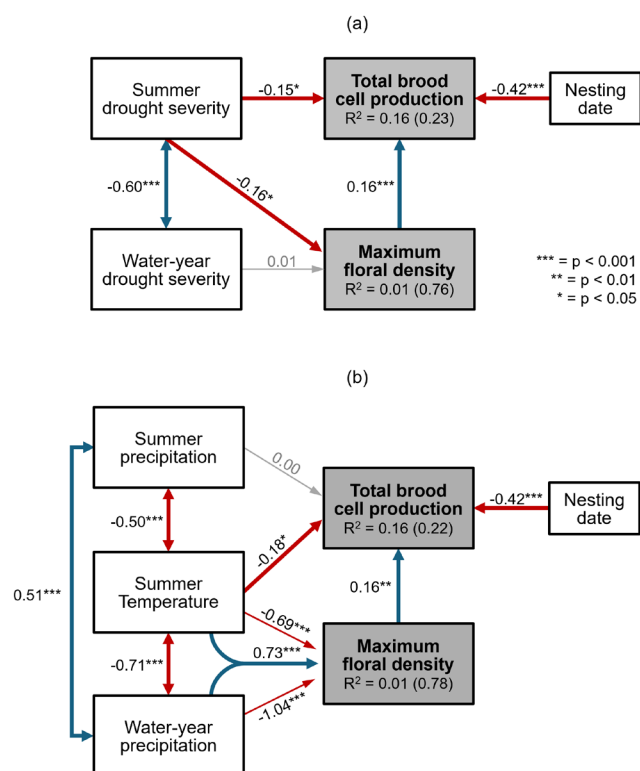


FIGURE 4 | Structural equation model relating (a) drought severity and (b) climate variables to maximum floral density and total brood cell production of female bees (5 bee species, 7 sites, 9 years; $N=723$ female bees; sample size by species in Figure 3). Single-headed arrows represent unidirectional relationships (“direct effects”). Double-headed arrows represent correlations. Blue and red lines denote significant positive and negative pathways respectively. Grey lines indicate non-significant paths specified in the a priori model. The merged arrow in (b) represents an interaction. Standardized regression coefficients are in standard deviation units. Marginal and conditional R^2 values (in parentheses) are reported for each response variable (grey boxes). Component models for both SEMs are listed in Table S9.

(e.g., Kemp and Bosch 2005; Ostap-Chec et al. 2021; Sgolastra et al. 2012). Given that summer temperatures in our study covered a 7°C range across sites and years, it is plausible that the negative association between drought and brood cell production (independent of floral resources) reflects some direct physiological effects of temperature on nesting females, though we cannot identify the specific mechanisms implicated.

4.1.2 | Precipitation

We detected no direct effects of precipitation on bee brood cell production. In general, adult bees are thought to be less sensitive to desiccation than most terrestrial insects, given their nectar diet and ability to generate metabolic water during flight (Nicolson 2009). However, other studies have suggested that bees are prone to desiccation should humidity levels fall below their taxon-specific thresholds, and that desiccation tolerances of bees can predict their abundances (Burdine and McCluney 2019; Kazenel et al. 2024). Separating the effects of precipitation from temperature in observational studies can be challenging, as periods of high temperatures typically co-occur

with decreased precipitation. This was the case in our study system, but the correlation between temperature and precipitation was sufficiently modest that we were able to statistically disentangle the effects of both variables (Pearson's r for summer precipitation and temperature = -0.5 ; Figures S8d and S9a). Our results suggest that the direct harmful effects of high temperatures exceeded those of low precipitation.

4.2 | Indirect Effects of Climate Variables on Bee Reproduction

4.2.1 | Floral Density

Floral abundance declined in years characterized by greater drought severity (albeit non-significantly at the seven study sites). This result was unsurprising given that water and heat stress can decrease rates of photosynthesis (Pandey et al. 2015), leaving plants with fewer resources to invest in flower production and/or floral rewards, among various other physiological responses (e.g., reduced vegetative growth, shifts in tissue composition, increased investment in chemical defenses; Descamps et al. 2018; Morrison and Stewart 2002; Waser and Price 2016). Notably, many plant taxa in our study area are considered relatively drought-tolerant as long-lived perennials with deep tap-roots; however, the degree to which floral density decreased with increasing drought suggests that drought conditions in our study region reached severity levels beyond the tolerance of even these taxa. We note that there may have been site-specific responses with regard to the effects of hot and dry conditions on floral density. Specifically, floral density at our highest elevation site actually increased with increasing summer drought severity (data not shown), suggesting that the negative effects of relatively hot and dry conditions may be less severe at sites that were historically cooler and wetter.

The impacts of drought sustained by plants can have cascading effects on the demographic success of organisms at higher trophic levels—a relationship that has been shown in a range of taxa, e.g., herbivorous insects, frugivorous birds, grazing mammals, seed predators (Fuaborg 1982; Kansman et al. 2021; McCluney et al. 2012). The magnitude of plant-mediated indirect effects may depend in part on the strength of the relationship between plants and their consumers. Females of most bee species are dependent on floral resources to provision offspring and to sustain their own energy demands (review in Roulston and Goodell 2011)—a relationship apparent in our data, which suggested positive relationships between brood cell production and the abundance of the specific floral hosts used by each bee species. While numerous studies have documented positive relationships between floral resource availability and bee abundance and diversity (e.g., Carvell et al. 2004; Hines and Hendrix 2005; Williams et al. 2015), few have directly linked brood cell production in individual bees to local floral resource availability (but see Minckley et al. 1994; Wong and Forrest 2021). Our data build on the general correlations between bee abundance and floral resources shown in other studies by providing demographic evidence that local floral abundance can increase reproduction, and that brood cell production can be limited by floral resources rather than by physiological limitations on egg production (cf. Minckley et al. 1994). Indeed, we even observed

female bees constructing nests consisting only of mud wall partitions, but devoid of pollen provisions and eggs, during periods of low flower abundance, often coincident with a lack of rainfall (personal observations). Overall, the positive relationship we observed between brood cell production and floral resources, coupled with our finding that floral resources declined in hot and dry years, suggests that drought had an indirect negative effect on bee fitness via changes in resource availability.

4.2.2 | Other Indirect Pathways

While we explicitly quantified floral density as a mediator of the effects of drought, we acknowledge that other extrinsic variables may have also mediated indirect relationships between drought and bee reproduction. Indeed, any unmeasured variable that covaried with drought and bee reproductive output but not with floral density could have contributed to the ‘direct’ effects of drought severity and temperature in addition to the possible physiological mechanisms described above.

For example, bee nests can be attacked by a variety of predators, pathogens, parasitoids, and parasites, including brood parasites (Roulston and Goodell 2011)—the prevalence and activity levels of which can be influenced by temperature (Meeus et al. 2018; Palmer-Young et al. 2019). In our study system, one of the most abundant brood parasites is a sapygid wasp (*Sapyga* sp.). Female sapygids opportunistically enter bee nests while they are in progress and oviposit through the cell partition nearest the nest entrance. Sapygid larvae consume host eggs along with the pollen provision supplied by the nesting female bee. Female bees in our study system have been observed prematurely sealing nests that have been parasitized (i.e., sealing cavities even if they only contain one or two brood cells instead of fully exploiting the length of the cavity; personal observations). Increased parasite activity with warmer temperatures, a pattern previously documented at our sites by Forrest and Chisholm (2017), may have resulted in female bees allocating more time and energy toward nest-sealing and locating new cavities instead of provisioning more brood cells. It is also possible that upon perceiving more parasite activity in their nesting environment, female bees spent less time away from their nests foraging to remain on guard for parasites, although Forrest and Chisholm (2017) suggest that this was not the case, at least for *O. iridis*. Notably, sapygids, which attack only two of our five focal species—*O. iridis* and *O. tristella*—are not the only natural enemies attacking *Osmia* spp. in our study area: attacks by the kleptoparasitic bee *Stelis montana* (Megachilidae), chalcidoid wasps, and the predatory beetle *Trichodes ornatus* (Cleridae) have also been observed. Characterizing the role of natural enemies such as brood parasites in driving indirect relationships between climate and bees ultimately requires knowledge of host ranges and the responses of both hosts and parasites to rising temperatures.

The negative relationship we observed between drought and bee reproductive output could also be mediated by pollen and nectar quantity and/or quality (e.g., pollen macronutrients, nectar volume, and concentration). Our floral surveys captured changes in floral quantity; however, drought can decrease the quality and quantity of nectar and pollen available to foraging bees (Descamps et al. 2021), an effect that has been linked to

negative reproductive outcomes for bees, including *Osmia* (Walters et al. 2024). Warmer temperatures can also increase the activity of other flower-visiting insects, potentially causing further reductions in pollen and nectar availability for our focal species. This explanation is plausible given that floral visitors such as bumble bees and flies at our sites were typically far more abundant than our focal taxa (personal observations), and the foraging activity of these taxonomic groups often responds positively to temperature (Corbet et al. 1993; Goodwin et al. 2021; Totland 1994).

4.3 | Relative Importance of ‘Direct’ and Indirect Effects of Climate

Ultimately, relationships between climate variables and the reproductive output of organisms reflect combinations of—and interactions between—numerous factors that can be intrinsic or extrinsic to the organisms themselves. In observational studies, the relative contributions of these factors can be difficult to determine, even when they are explicitly quantified. Structural equation modeling allows the relative strength of direct and indirect pathways between variables in observational studies to be evaluated by comparing the magnitude of standardized coefficients. The overall magnitude of indirect effects can be determined by multiplying the standardized coefficients of the component pathways (Figure 4). Our SEMs suggested that the negative effects of drought on bee reproductive output were only partially driven by its effects on floral abundance. The role of other mechanisms that were not quantified in this study—be they physiological (i.e., “direct” *sensu stricto*) or unquantified indirect effects extrinsic to the bees—had a greater influence in driving the observed negative relationship between drought conditions and bee reproductive output. This result contrasts with the findings of similar work in our study area which found that the negative effects of drought conditions on bumble bee abundance were driven mostly by indirect effects mediated by floral resources (Ogilvie et al. 2017). We note, however, that in addition to differences in how floral abundance and bee responses were quantified between the two studies, our focal species exhibit substantially different natural history traits from the bumble bee species studied by Ogilvie et al. (2017), which were larger-bodied, social pollen generalists, with better abilities to regulate their body temperature and that of developing brood (Heinrich and Esch 1994). Understanding the processes underlying climate-fitness relationships ultimately necessitates detailed knowledge of a given study system’s natural history such that important drivers of reproductive success—which may be taxon- or habitat-specific—can be identified and accounted for.

4.4 | Interspecific Variation in Responses to Climate

We did not detect taxonomic variation in climate responses; that is, interactions between climate variables and floral group or bee species were not significant. However, we may have lacked sufficient power to detect such interactions. Indeed, the marginally significant interaction between drought severity and floral group in the RMBL data ($p = 0.07$; Table S7) suggested that Fabeae (tribe) and generalist host floral density responded more

negatively to increasing drought compared to Asteraceae floral density. The Asteraceae species in our study area are generally more drought tolerant than non-aster taxa given their deep tap-roots (personal observations), possibly reducing the indirect negative effects of drought on brood cell production for bee species that forage from asters (all species except *O. iridis*). Variation in the responses of the five bee species to the effects of drought is also possible given that they exhibit differences in traits apart from pollen specialization. For example, the five species vary in body size, with average intertegular distance ranging from 1.75 mm for *O. tristella* to 2.70 mm in *O. montana* (appendix in McAulay et al. 2021). Body size is an important determinant of thermoregulatory ability in many ectotherms, given the general biophysical relationships between an organism's surface-area: volume ratio and excess heat dissipation (Porter and Gates 1969). Notably, whether small vs. large body size is favored in high-temperature conditions is highly variable across the studies that have examined this relationship in bees. Improved tolerance to high temperatures among larger species has been suggested by some studies, while others have suggested the opposite pattern or no relationship at all (Gonzalez et al. 2022, 2024; Pardee et al. 2022). The lack of a general relationship between body size and temperature tolerance may be due to the fact that body size is also linked to numerous ecological traits unrelated to thermoregulation, all of which may be implicated in the responses of bees to drought, e.g., nutritional requirements, competitive ability, and foraging distance (Gonzalez et al. 2022, 2024; Pardee et al. 2022). For example, indirect effects of drought mediated by floral resources may have stronger negative impacts on smaller bees as they may be unable to forage greater distances in search of sparsely distributed resources. Whether or not there are relationships between body size and drought response is unclear in our study as *O. coloradensis*, with intermediate body size relative to the other four species, seemed to be the most negatively influenced by drought (Table S8). Incidentally, individuals of this species were also most commonly observed at our lowest elevation (warmer) sites (personal observations; also, compare x-axes of Figure S6c across species). Future studies that aim to understand the processes underlying interspecific variation in the responses of bees to drought would require more information on species-specific physiological tolerances paired with direct observations of their behavior in the field. Despite differences in pollen specialization and body size, the five focal species in this study are similar in that they are congeneric and share traits such as a solitary lifestyle, cavity nesting, and semivoltinism. More conspicuous variation in climate responses may be expected among bees representing other genera, nesting habits, and degrees of sociality.

4.5 | Future Directions

Despite the negative implications of these findings for subalpine bee populations, we note that our predictors—climate, floral resources, and nesting date—explained a modest proportion of the variation in bee reproductive output ($R^2_m = 0.16$ in SEMs for brood cell production). The substantial unexplained variation suggests that brood cell production is affected by numerous other variables not quantified here. These variables may be extrinsic or intrinsic to the bees and may or may not be linked to climate. Intrinsic variation in individual reproductive success

likely encompasses heritable trait variation, which may influence the capacity of populations to respond adaptively to the increasingly severe droughts predicted for this region. Further work is needed to identify the genetic basis for traits that may confer increased tolerance to drought conditions. Non-genetic adaptive responses to climate change may also be possible; for example, range shifts toward higher elevations and latitudes have already been observed in many taxa, including bumble bees in our study area (Marshall et al. 2020; Pyke et al. 2016). The capacity for adaptive response to climate change in non-*Bombus* species remains little known but is likely to differ, since the life-history traits and habitat requirements of most bee species are unlike those of bumble bees—which represent less than 2% of all bees. We also note that our study focused on the reproduction component of bee life cycles, but that drought can influence bee fitness at any point in their lifecycle. How bees at juvenile stages will respond to changes in climate has been little explored in natural populations. Accurate predictions of the consequences of climate change on the persistence of local populations will require an understanding of their responses to climatic variation at all life stages.

5 | Conclusion

Despite the preponderance of studies that link changes in climate to widespread global biodiversity loss, the processes underlying many of these large-scale patterns remain unclear. Quantifying the in situ responses of individuals within a population to climate variation is one of the most direct ways to investigate the processes that underlie patterns at large spatial scales. We examined the responses of individually marked female bees of five focal species to variation in climate and found that warmer and drier years were associated with decreased individual lifetime reproductive output—a relationship partially mediated by declines in floral abundance, but also by additional negative effects of drought. The increasing frequency and severity of droughts predicted for this region (Chen et al. 2025; Garfin et al. 2022) may therefore have important negative consequences for the persistence of these populations if they are not capable of responding adaptively. Long-term individual-level data are critical for delineating the processes that underlie large-scale ecological patterns and for generating predictions about population persistence, yet they are difficult to obtain due to the practical challenges of following individuals over their lifetimes. Such datasets are consequently rare, and among those that exist, invertebrates such as insects are poorly represented, despite the ecological significance of these animals. Our study demonstrates the feasibility of individual-level studies on insects, and our findings highlight the importance of considering how individuals in naturally occurring populations are responding to environmental change.

Author Contributions

Lydia H. Wong: conceptualization, data curation, formal analysis, investigation, writing – original draft, writing – review and editing. **Brian D. Inouye:** data curation, funding acquisition, investigation, methodology, project administration, supervision, writing – review and editing. **Jessica R. K. Forrest:** conceptualization, data curation, funding

acquisition, investigation, methodology, project administration, supervision, writing – review and editing.

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The sites in this study are situated on the traditional lands of the Tabeguache Ute band (Núu-agma-tuvu-pu). Over the course of the nineteenth century, Ute territories were invaded by white settlers and mining prospectors backed by the U.S. government. Treaty agreements were violated, and the Utes were murdered or forcibly removed from their territories. The Rocky Mountain Biological Laboratory (Gothic, Colorado) was a mining town until the late 1800s. Much of the mining town infrastructure was retained and converted into research station infrastructure (housing for researchers, laboratory, and administration spaces). We are therefore the direct beneficiaries of colonialism (both historical and ongoing). We also acknowledge that the scientific approaches and methods of data interpretation used in this study reflect a knowledge system founded on the worldviews of those who colonized these lands. We are reflecting on our roles in perpetuating colonialism in ecological research and hope that other researchers will feel moved to do likewise.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.0rxwdbscj>. Data for the bee and flower data were obtained from the Environmental Data Initiative portal at <https://portal.edirepository.org/nis/mapbrowse?packageid=edi.890.4>. Data for the long-term flower data were obtained from the Open Science Framework portal at <https://doi.org/10.17605/OSF.IO/JT4N5>. Data for the long-term climate data are available in the Open Science Framework portal <https://doi.org/10.17605/OSF.IO/8EZKA>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.