RESEARCH ARTICLE

Climate driven disruption of transitional alpine bumble bee communities

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Abstract
Pollinators at high elevations face multiple threats from climate change including heat stress, failure to phenological match advancing flower resources and competitive pressure from range-expanding species of lower elevations. We conducted long-term multi-site surveys of alpine bumble bees to determine how phenology of range-stable and range-expanding species is responding to climate change. We ask whether bumble bee responses generate mismatches with floral resources, and whether these mismatches in turn promote community disruption and potential species replacement. In alpine environments of the central Rocky Mountains, range-stable and range-expanding bumble bees exhibit phenological mismatches with flowering host plants due to earlier flowering of preferred resources under warmer spring temperatures. However, workers of range-stable species are more canalised in their foraging schedules, exploiting a relatively narrow portion of the flowering season. Specifically, range-stable species show less variance in phenology in response to temporally and spatially changing conditions than range-expanding ones. Because flowering duration drives the seasonal abundance of floral resources at the landscape scale, we hypothesize that canalisation of phenology in alpine bumble bees could reduce their access to earlier or later season flowers. Warmer conditions are decreasing abundances of range-stable alpine bumble bees above the timberline, increasing abundance of range-expanding species, and facilitating a novel and more species-diverse bumble bee community. However, this trend is not explained by greater phenological mismatch of range-stable bees. Results suggest that conversion of historic habitats for cold-adapted alpine bumble bee species into refugia for more heat-tolerant congeners is disrupting bumble bee communities at high elevations, though the precise mechanisms accounting for these changes are not yet known. If warming continues, we predict that the transient increase in diversity due to colonization by historically low-elevation species will likely give way to declines of alpine bumble bees in the central Rocky Mountains.

KEYWORDS
alpine, bumble bees, climate change, counter-gradient selection, phenological mismatch, range shift, transitional communities
**INTRODUCTION**

Mutualisms are fundamental to species persistence and distribution, yet generally involve partners with large differences in mobility, generating potential disruption under conditions promoting range shift. Pollination mutualisms involve associations between largely sedentary plants and more mobile animals. When environmental conditions undergo rapid degradation, such associations are vulnerable to disruption (Aslan et al., 2013; Keeler et al., 2021). Climate change is driving this process via multiple pathways, with unclear outcomes for biodiversity in novel and transitional communities (Gérard et al., 2020; Shah et al., 2020).

Climate impacts on plant-pollinator interactions potentially affect ≥70% of flowering plants and 200,000 species of insects (Ingram et al., 1996). Since pollination mutualisms confer essential ecosystem services, when habitats gain or lose pollinators, impacts cascade through ecosystems. As pollinators colonize landscapes occupied by ecologically similar taxa, diversity can increase if conditions favor coexistence. Availability of empty niches, superabundant floral resources, and/or new opportunities for resource partitioning could promote coexistence between novel and extant taxa. However, Schweiger et al. (2010) postulate that when colonists are more generalized in their food choices than resident species, displacement is likely to ensue. Understanding how global change affects the likelihood of displacement is critical for management of wild pollinators and the ecological networks in which they are embedded.

Recent warming has reconfigured ecological communities by causing range shifts, habitat loss and population declines. These disruptions impact biodiversity in cold regions through climate stressors acting in tandem with the influx of organisms from warmer regions. Extreme temperatures, early snow melt, and summer drought advance the seasonal activity of plants and pollinators by about 4 days per °C (Abrol, 2012) and impact phenological resource partitioning among consumer species (Duchenne et al., 2020). For plants, phenological advancement generates pollination deficits and shifts in pollinator composition (Gallagher & Campbell, 2021). Warming reduces abiotic barriers to colonization, functioning as an ecological ratchet for movement of warm-adapted pollinator taxa into historically colder environments (Biella et al., 2017; Marshall et al., 2020; Osland et al., 2021; Rafferty, 2017; Shah et al., 2020; Suzuki-Ohno et al., 2020). Pollinators have colonized new environments throughout their evolutionary history (Williams & Jackson, 2007), yet the process has accelerated with rapid latitudinal and elevational shifts in species’ thermal niche boundaries (Gérard et al., 2020; Herrera et al., 2018; Kerr et al., 2015; Ploquin et al., 2013; Rafferty, 2017).

While climate change clearly reshuffles local pollinator communities through loss of extant biodiversity coupled with gain of migrants from warmer regions (Williams & Jackson, 2007), what is less understood is how the two processes interact to shape species composition (Gibson-Reinemer et al., 2015; Shah et al., 2020). We address this gap for bumble bee communities in rapidly warming alpine regions.

**1.1 Bumble bees: A model system for investigating climate change impacts**

Climate change acts through multiple pathways to affect growth and reproduction in bumble bees (Aldridge et al., 2011; CaraDonna et al., 2014; Gezon et al., 2016; Høye et al., 2013; Pyke et al., 2016; Stemkovski et al., 2020). Summer heat increases demands for cooling (fanning) by workers in the nest, reducing the forager pool (O’Donnell & Foster, 2001) and causing physiological stress in species adapted to cooler conditions (Martinet et al., 2015; Oyen et al., 2016). Additionally, warming impacts bumble bees indirectly by creating gaps in resource availability (Ogilvie et al., 2017) and degrading resource quality (Descamps et al., 2021; Russell & McFrederick, 2021). Phenological synchrony with floral resources is reduced when partners differ in responses to climate cues (match-mismatch theory; Kerby et al., 2013; Ploquin et al., 2013). Conversely, convergence in cue use between partners could maintain phenological matching despite climate variance (Hegland et al., 2009; Inouye, 2020; Roslin et al., 2021). While conceptually straightforward, documenting such convergence is prone to spurious conclusions if forager and flower abundances are monitored together (Forrest & Thomson, 2011).

Linkages between sequential life history stages also may drive temporal mismatches between bumble bees and flowers. Bumble bee queens overwinter, emerging and establishing nests the following spring, with workers maturing several weeks later. For organisms with such complex life histories, climate events at one life cycle stage may affect the timing of critical functions at later stages. For example, in migratory birds, climate cues in the winter habitat influence phenological synchrony with prey in the breeding range (Dunn & Winkler, 2010). Emerging bumble bee queens avoid starvation during prolonged nest searching by resorbing their ovaries (Sarro et al., 2022), potentially delaying worker production and reducing worker synchrony with floral resources.

As alpine environments warm, range-expanding bumble bees from hotter regions may better track advancing flowering schedules than resident species (Soroye et al., 2020; Wadgymar et al., 2015). Research on developmental timing in amphibians shows that warmer and longer growing seasons at low elevations select for developmental plasticity, while cold-delayed seasons at higher sites favor rapid, early maturation and more canalised developmental schedules (counter-gradient selection, Berven et al., 1979). If bumble bee development has been shaped similarly by past climate regimes, range-expanding and range-stable species may diverge in synchrony with floral resources and experience different levels of resource stress.

We consider two pathways for reconfiguration of bumble bee communities under a warming alpine climate coupled with colonization by range-expanding species. First, we test the hypothesis that discrepancy in responses to changing climate cues between bumble bees and flower resources contributes to partners’ phenological mismatch; that the magnitude of mismatch in turn reduces bumble bee abundance; and that such losses are amplified by the lack of phenological flexibility in range-stable alpine taxa. Alternatively, we postulate that regardless of phenological...
mismatch, range-expanding bumble bees from lower elevations are better suited to a warmer alpine environment than cold-adapted, range-stable congeners. Both scenarios predict that colonizing bumble bees will replace alpine residents, but by different pathways. To address these hypotheses, we evaluated (1) climate cues affecting flowering time in the host plant-community, (2) cues driving foraging phenology of colonizing versus resident bumble bee species, (3) impacts of climate cues on synchrony of colonizers and residents with floral resources, and (4) relationship of phenological mismatch to abundances of resident and colonizing species.

2 | METHODS

2.1 | Study system

Subalpine bumble bees have moved upward since the mid-1900s and currently nest above treeline (~3500 m) in the Colorado Rocky Mountains (Miller-Struttmann et al., 2015). In our alpine (above treeline) study sites (Colorado, USA), we classified bumble bees as resident or range-stable if pre-1980 records showed them completing their entire life cycle above treeline (B. kirbiellus and B. lapponicus sylvicola, formerly B. baltatus and B. sylvicola, respectively; Byron, 1980). Observations of B. lapponicus likely included the recently discovered cryptic taxon “incognitus” as it overlapped in distribution and is morphologically indistinguishable (Christmas et al., 2021). Species were deemed colonizing or range-expanding if populations before 1980 were commonly found in lower subalpine and montane habitats and nesting was not observed above treeline (B. bifarius, B. flavifrons, B. frigidus, B. melanopogus, B. mixtus, and B. nevadensis; Byron, 1980; Macior, 1974). Flowering phenology and floral density were monitored for nine plant species that together accounted for 90% of floral resources used historically by alpine bumble bees: Trifolium dasyphyllum, T. parryi, and T. nanum, Penstemon whippleanus, Pedicularis groenlandica, Castilleja occidentalis, Mertensia lanceolata, Polemonium viscousum, and Rhodiola rhodantha (Byron, 1980; Macior, 1974; Miller-Struttmann et al., 2015). Table 1 delineates the design of our study, showing how sampling effort was distributed among sites, years, elevational zones, and focal species.

Floral resources were surveyed as part of a long-term phenological study (13 year between 1977 and 2019; Table 1) on Pennsylvania Mountain, Colorado (39°15.803’N, 106°8.564’W; 3600–3970 m). Timing and abundances of bumble bee foragers were monitored from 2012 to 2014 in elevationally stratified zones of two Front Range sites (Niwot Ridge [low alpine: 40.0567°N, 105.5916°W, 3564 m and mid-alpine: 40.0585°N, 105.6119°W, 3700] and Mount Evans [low alpine: 39.6454°N, 105.5925°W, 3550 m; mid alpine: 39.6334°N, 105.6046°W, 3700 m; and high alpine: 39.5964°N, 105.6275°W, 3850 m]) where L. W. Macior (1974) documented the historic ranges (1966–1969) and flowering hosts of species sampled in this study. Host plants and bumble bees were sampled weekly throughout the flowering season (June–August) in alpine habitats including krummholz vegetation, rocky fellfields, exposed ridges, mesic tundra meadows, and swale or marsh vegetation.

Recent warming has occurred at all our study sites, as evidenced by increasing spring and summer temperatures (Miller-Struttmann et al., 2015) and decreasing episodes of extreme cold spring conditions when temperatures averaged below 0°C in May (15% of 20th century records vs. 6% of the 21st; Table S1 and Figure S1; PRISM, Daly et al., 2008; Strachan & Daly, 2017; see below for details). Current temperature regimes in our alpine field sites are converging on historical norms in the surrounding subalpine regions, consistent with more rapid warming at high elevations (Shah et al., 2020; Figure S1).

2.2 | Spatial and temporal characterization of climate

Climate records were obtained from PRISM point interpolation data. For Pennsylvania Mountain where flower survey plots were distributed along a continuous elevational gradient, PRISM climate data were taken from one point at median elevation (3750 m) to represent the entire transect. At Mount Evans and Niwot Ridge, where bee and flower surveys were clustered in discrete elevational zones, climate data were obtained from mid-points in each zone. In mountain habitats, PRISM point interpolation data most accurately predict climate conditions at the spatial scale of bumble bee foraging (~1 km; Geib et al., 2015; Strachan & Daly, 2017). Spatial variation in climate with elevation and latitude generates a range of short-term conditions representative of longer-term climate variance (Figure S2). Accordingly, 3 years of bumble bee monitoring (2012–2014) over the elevational and geographic gradients characterizing Niwot Ridge and Mount Evans captured long-term interannual climate variation in these alpine habitats (range in mean May temperature: −0.6 to 4.5°C; summer maximum temperature, 13.5–19.0°C; winter precipitation, 22.07–77.02 cm; and summer precipitation, 14.91–38.50 cm). Collinearity among climate variables was weak (Table S2), with the variation explained (R²) ranging from 0.0016% to 30% (maximum variance inflation factor of 1.4).

Climate predictors were chosen to reflect critical conditions for different bumble bee life cycle stages and host-plant reproduction. Mean daily May temperature was selected along with winter precipitation (sum of precipitation or snowfall from January through May), because together these have pronounced impacts on snowmelt timing and the accumulation of growing degree days for plants and insects in alpine regions. Specifically, spring warming coincides with emergence from torpor and colony initiation for bumble bee queens (Szabo & Pengelly, 1973) and onset of new growth in their host plants (Gezon et al., 2016). Summer maximum temperatures and summer precipitation (respectively, mean of monthly diurnal high temperatures and sum of June, July, and August precipitation) were used as they influence accumulation of energy resources in the nest via production and activity of foraging workers (Maebe et al., 2021) and duration of flowering in host plants via soil and plant water
TABLE 1  Sampling design for data addressing the specific aims of this study. Observations of bumble bees (queens [Q], workers [W]) and their host plants were made at several geographically isolated sites and altitudinal zones, over varying time scales to probe effects of climate change on community dynamics. Because not all species were found in all zones, total replication was reduced in some cases.

| Objective(s) | Response variables | Units of measurement | Years sampled per location | Number of species by range type | Number of sampling zones | Unit of replication | Total replication |
|--------------|--------------------|----------------------|----------------------------|------------------------|-------------------------|--------------------|------------------|
| 1-4          | Climate (from PRISM) | May mean (°C) Summer (June–August) maximum (°C) Winter (January–May) precipitation (cm) Summer (June–August) precipitation (cm) | PM: 1977–1981 and 2012–2019 NR & ME: 2012–2014 | — — | PM: 1 NR: 2 ME: 3 | Zone×Year | PM: 13 NR: 6 ME: 9 |
| 1. Drivers of flowering phenology | Day of first flower | Day of peak flower density | Day of year Flower density: N flowers per species, m², and day | PM: 1977–1981 and 2012–2019 | — 9 | PM: 23 Species×Zone×Year | 2691 |
| 2. Drivers of bee foraging phenology | Day of queen emergence | Day of worker emergence | Day of peak worker density Bee density: N bees per species, caste, week, and person hour | NR & ME: 2012–2014 | Q: 3 W: 6 Q: 2 W: 2 NR: 2 ME: 3 | Species×Zone×Year | Q: 48 W: 80 |
| 3. Causes of phenological mismatch | Day of queen emergence—day of first flower Day of peak worker density—day of peak flower density | Number of days Flower density: N flowers per m² per day Bee density: N bees per species, caste, day, and person hour | NR & ME: 2012–2014 | Q: 3 W: 6 Q: 2 W: 2 NR: 2 ME: 3 | Species×Zone×Year | Q: 48 W: 80 |
| 4. Pathways of climate impact on bee abundances | Cumulative bee abundance | | | NR and ME: 2012–2014 | W: 6 W: 2 NR: 2 ME: 3 | Species×Zone×Year | W: 80 |

Abbreviations: ME: Mount Evans; NR: Niwot Ridge; PM: Pensylvania Mountain.
baskets (Galen, 2000; Gallagher & Campbell, 2021; Olliff-Yang & Mesler, 2018).

2.2.1 Climate cues affecting flowering time in the host plant-community

Twenty-three 2 × 10 m plots were established on Pennsylvania Mountain by P. G. Kevan and surveyed weekly from the onset to the end of the flowering season in 1977–1981. Plots were located non-randomly to sample prevalent alpine habitat types (Byron, 1980). Using aerial photographs and maps in 2012, we found at least one edge of each original plot and established a larger survey area that included the original plot in its entirety (Miller-Struttmann et al., 2015). To account for larger sampling scale from 2012 to 2019, flower density was based on the average flower density in all possible independent 2 × 10 m subplots within the larger plots. Open flowers or inflorescences were counted weekly to provide comparable data to surveys from 1977 to 1981. Inflorescence counts at randomly chosen points were used to estimate the average number of open flowers per m². From flower counts we extracted day of first flowering, day of peak flowering, and cumulative flower density (total flowers produced per m² over the entire season) for each of the nine host-plant species (Table 1).

All statistical analyses were conducted in R version 4.0.2 (R Development Core Team, 2020), and all datasets and R scripts are openly available in Dryad (Miller-Struttmann et al., 2022). To test for climate drivers of day of first flowering, we compared three linear mixed-effects models constructed via lmer in the lme4 package version 1.1-23 (Bates et al., 2015) that tested for the effects of May mean temperature, summer maximum temperature, and winter and summer precipitation (Table S3). For day of peak flowering, we included as predictors the same climate variables as well as day of first flowering to account for potential developmental (carryover) effects. Because our focus was on community-scale resources, here and elsewhere plot and plant species were treated as random effects (Table S3). Models were compared via ΔAICc calculated by aictab in the AlCmodavg package version 2.3–1 (Marc & Mazerolle, 2020). Models with a ΔAICc less than 2 from the best model were considered equivocal. However, for all analyses in this manuscript, model averaging was not required because one model always outperformed the competing models by ΔAICc greater than 2. For the top performing model, we calculated test statistics using type III sums of squares via the Anova function in the car package version 3.10-0 (Fox & Weisberg, 2019), and the partial R² for each explanatory variable was extracted via r2beta in the r2glmm package version 0.1.2 (Jaeger, 2017). Here and elsewhere, we tested whether our data met the assumptions of parametric statistics, and if they did not, we used transformations as explained, when necessary.

To ask whether variation in flowering phenology influences the seasonal accumulation of floral resources, we ran a single mixed-effects multiple regression with species and plot as random effects using the lme in the nlme package version 3.1-149 (Pinheiro et al., 2020). We included day of first flowering and day of peak flowering, as independent fixed effects in the model. Cumulative flower density was the dependent variable and was log transformed to meet the assumption of normality. Test statistics were estimated via the anova.lme function in the nlme package version 3.1-149 (Pinheiro et al., 2020), and the partial R² for each explanatory variable was extracted via r2beta in the r2glmm package version 0.1.2 (Jaeger, 2017).

2.2.2 Cues driving foraging phenology of colonizing versus resident bumble bee species

In the Front Range (Niwot Ridge and Mount Evans), we collected and identified to species and caste all bumble bees observed foraging on flowers without regard to plant taxon, during weekly, 1-h walking surveys in each elevational zone (median area of 4.22 ha, and range of 2.13–6.57 ha; Miller-Struttmann et al., 2015). Individuals were anesthetized, photographed, marked with nontoxic paint, and released. In the rare event that a marked bee was recaptured, it was released without additional data collection and was not included in the analyses presented here. A small subset of individuals was lethally collected for archival purposes and deposited in the Enns Entomology Museum at the University of Missouri.

Samples were pooled elevationally to characterize bumble bee communities within the average flight distance of alpine bumble bees (<1 km: Geib et al., 2015) for a total of five elevational zones in the Front Range (Niwot Ridge and Mount Evans). Species abundances were weighted by collection effort in person hours for each elevational zone (median = 663; range: 198–840 person hours). For queen and worker bumble bees of each species encountered, we estimated the timing of emergence and peak foraging activity. Respectively, emergence was operationally recognized as the day of year (DOY) of the first observation of that species/caste, and peak activity as the DOY when the maximum number of foraging individuals were observed in a given elevational zone. We use sightings rather than estimating phenological events via modeling, because model estimates of first occurrence do not provide biologically realistic results for this system. Weibull estimates (Belitz et al., 2020) were, on average, 12.02 days earlier than first sightings (range: 1.06–60.17 days), predicting emergence when mean daily temperatures were well below that required for flight (Heinrich, 1975; Lundberg, 1980). Day of queen emergence was natural log transformed to meet the assumption of normality.

To test for effects of climate and range status on the timing of key phenological events for each caste, we compared mixed-effects analysis of covariance (ANCOVA) models that included the effects of range status (expanding or stable), climate conditions during or prior to the event of interest, and interactions of climate factors with range status (Table S4). Specifically, for day of queen emergence, fixed effects included range status, May
mean temperature, winter precipitation and their interactions, with species treated as a random effect. Queens of three colonizing species (B. flavifrons, B. melanopygus, and B. mixtus) were infrequently collected (fewer than five populations sampled over 3 years) and therefore excluded from these analyses. As above, competing models were constructed via lme in the nlme package version 3.1-149 (Pinheiro et al., 2020) and compared via ΔAICc calculated by aictab in the AiCcmoadaug package version 2.3-1 (Marc & Mazerolle, 2020). Model averaging was not required, because one model always outperformed the competing models by ΔAICc greater than 2. For the top performing model, we calculated test statistics using type III sums of squares via the anova.lme function in the nlme package version 3.1-149 (Pinheiro et al., 2020), and the partial R² for each explanatory variable was extracted via r2beta in the r2glmm package version 0.1.2 (Jaeger, 2017). We similarly compared competing models for timing of worker emergence and peak activity (Table S4). Day of queen emergence did not predict worker emergence timing (F1,39 = 0.080, p = .78) and was removed from the competing models. Mixed effect ANCOVAs tested for fixed effects of range status, summer maximum temperature, and summer precipitation on timing of worker emergence and peak activity, with species as a random effect. For peak worker activity day, we also included as a fixed effect worker emergence day, to test for a carryover effect. When there was an interaction between range status and a climate variable, we ran separate mixed-effect regressions for each range type (i.e., expanding or stable).

To address whether seasonal patterns of forager activity are more canalised for resident than colonizing bumble bees, we compared curves for temporal variation in forager activity over the season. The number of workers of each species on each date was calculated at the regional level by pooling samples from all locations and elevational zones. The activity curves for each species were tested for kurtosis using the PerformanceAnalytics package version 2.0.4 (Peterson et al., 2020), which quantifies the degree to which the peak of a curve is narrower or broader than expected for a normal distribution. Because our sample size was small (n = 2) for resident species, we tested for greater canalisation (more positive kurtotic scores) in resident than colonizing species using a nonparametric one-tailed Mann–Whitney test (wilcox.Test function in the base R package version 4.0.2; R Development Core Team, 2020). We then explored the degree to which local adaptation to alpine environments has favored canalisation in phenology, by testing for a relationship between the kurtosis of current (2012–2014) worker activity curves and the mean elevation at which a species was collected historically (1966–1969; Macior, 1974). We calculated the mean elevation at which bumble bees of each species were collected along the 2700 m elevational gradient (mean number of individuals per species = 1603). We predicted that if canalisation was favored in high-elevation habitats, species that occurred at higher elevations in the past should have lower variation in foraging phenology, and thus more positive kurtotic scores. We tested this hypothesis using the anova and lm functions in the base package version 4.0.2 (R Development Core Team, 2020).

### 2.2.3 Impacts of climate cues on synchrony of colonizers and residents with floral resources

We surveyed flowering weekly in the nine host-plant species using 12–15, 1 × 2 m plots placed within each elevational zone on Niwot Ridge and Mount Evans (Table 1). In 2012, we established an initial set of 10 1 × 2 m plots before the onset of flowering in each elevational zone. As the flowering season progressed, an additional 2–5 plots were established to survey areas of later-blooming. Open flowers or inflorescences for each of the nine host plants were counted weekly from onset to end of the flowering season and converted to number of flowers using the mean flowers per inflorescence for a sub-sample (3–30) of inflorescences per plot. For two species (T. dasyphyllum and T. parryi), we used published flower counts per inflorescence from Pennsylvania Mountain (Geib, 2010) and for one (C. occidentalis) flower counts from individuals outside of plots on Niwot Ridge and Mount Evans (2012–2013). Days of first and peak flowering and cumulative flower density were calculated for each elevational zone (Table 1).

For workers of each bumble bee species, we estimated the yearly phenological mismatch between foraging activity and flowering of the host-plant community in each elevational zone. To test for mismatch between worker foraging activity and flowering, we calculated the difference between day of peak worker foraging and day of peak flowering. Negative numbers indicate that worker activity peaked before flowering. We tested whether range status and/or climate predicted the phenological mismatch between peak worker activity and peak flowering by comparing competing models constructed via lme in the nlme package version 3.1-149 (Pinheiro et al., 2020). Predictor variables included range status, summer maximum temperature, summer precipitation, and their interactions, with species as a random effect (Table S5). Competing models were compared as above. For the top performing model, we calculated test statistics using type III sums of squares via the anova.lme function in the nlme package version 3.1-149 (Pinheiro et al., 2020), and the partial R² for each explanatory variable was extracted via r2beta in the r2glmm package version 0.1.2 (Jaeger, 2017).

### 2.2.4 Relationship of phenological mismatch to abundances of resident and colonizing species

Changing climate factors could influence abundances of range-stable versus range-expanding bumble bees by generating mismatches between seasonal foraging schedules and flowering times. Cumulative abundance of each bumble bee species was estimated as the sum of the weekly counts of all workers of that species weighted by collection effort over the season within an elevational zone. Relative abundance was calculated as the proportional contribution of a species to the bumble bee forager community. We tested whether cumulative and relative abundances of workers were predicted by alternative combinations of range status, mismatch with peak floral resources, summer maximum temperature, summer precipitation,
and their interactions (Table S6) using model comparison as above. When there was a significant interaction between a categorical (i.e., range status) and a continuous variable (i.e., May mean temperature), we ran separate regressions for each level of the categorical variable. Cumulative abundance was log transformed to meet the assumption of normality.

### RESULTS

#### 3.1 Climate cues affecting flowering time in the host plant-community

One model including May mean and summer maximum temperatures best explained day of first flowering (ΔAIC < 2; Table S3). Flowering onset was predicted by both May mean temperature ($R^2 = 261.30, p < .0001$) and summer maximum temperature ($R^2 = 22.37, p < .0001$) (Table 2). May mean temperature accounted for 11.7% of the variance in flowering onset with summer maximum temperatures explaining an additional 1.1% (Table 2). Essentially, when May temperatures are warmer, flowering begins earlier (Figure 1a).

Day of peak flowering was best explained by one model (Table S3) that included winter precipitation ($F = 28.28, p < .0001, R^2 = 2.2%$), May mean temperature ($F = 33.89, p < .0001, R^2 = 2.8%$) and summer maximum temperature ($F = 20.16, p < .0001, R^2 = 1.6%$). While all climate factors and the interaction between winter precipitation and summer maximum temperature ($F = 7.16, p < .0001, R^2 = 2.3%$) influenced the peak flowering day (Table 2), they together explained only 8.9% of the variation in total, compared to 57.2% of the variation attributed to first flowering day ($F = 901.07, p < .0001$). Results indicate that flowering schedules of alpine bumble bee host plants are cued by average temperatures in May (Figure S3).

Cumulative flower density over the season was influenced by flowering phenology. Flower density decreased with later onset of flowering ($F_{1,764} = 67.32, p < .0001, R^2 = 4.9%$; Figure S4a) and increased with later peak flowering ($F_{1,764} = 57.28, p < .0001, R^2 = 4.1%$; Figure S4b). These results show that patches of plants initiating flowering early and taking longer to reach peak flowering produced more flowers over the season.

| Model                        | Estimate | Partial $R^2$ | $\chi^2$ or $F$ | $p$   |
|------------------------------|----------|---------------|-----------------|-------|
| Day of first flowering       |          |               |                 |       |
| May mean temperature         | -4.35    | 0.117         | 261.30          | <.0001|
| Summer maximum temperature   | -2.55    | 0.011         | 22.37           | <.0001|
| Day of peak flowering        |          |               |                 |       |
| Day of first flowering        | 0.70     | 0.572         | 901.07          | <.0001|
| May mean temperature         | -1.67    | 0.028         | 33.89           | <.0001|
| Winter precipitation          | -4.79    | 0.022         | 28.28           | <.0001|
| Summer maximum temperature   | -7.06    | 0.016         | 20.16           | <.0001|
| Summer precipitation          | -0.06    | 0.000         | 0.33            | .56   |
| Winter precipitation: summer maximum temperature | 0.29 | 0.023 | 7.16 | <.0001 |

Cumulative flower density

| Model                        | Estimate | Partial $R^2$ | $\chi^2$ or $F$ | $p$   |
|------------------------------|----------|---------------|-----------------|-------|
| Day of first flowering       | -0.070   | 0.049         | 67.32           | <.0001|
| Day of peak flowering        | 0.060    | 0.041         | 57.28           | <.0001|

#### 3.2 Cues driving foraging phenology of colonizing versus resident bumble bee species

Timing of queen emergence was best described by one model that included range status, May mean temperature, winter precipitation, and one-way interactions of climate factors with range status (Table S4). Neither range status nor mean May temperature influenced queen emergence schedule (Table 3). Instead, emergence of both resident and colonizing bumble bee queens was delayed by heavy winter precipitation ($F = 6.60, p = .014$; Table 3; Figure 1b), explaining 12.3% of the variation and indicating that snowmelt timing drives queen emergence schedule in these alpine sites. Thus, bumble bee colony initiation is shaped by different climate cues than first flowering of bumble bee host plants.

Worker emergence was best explained by one model that included range status, summer maximum temperature, summer precipitation, and one-way interactions of climate factors with range status (Table S4). Both interaction terms were marginally statistically significant (Table 3), each accounting for ~3% of the variation (Table S4). Resident bumble bee workers emerged earlier than those of colonizing species ($F = 6.84, p = .040, R^2 = 7.6%$; Figure S5a). However, this trend was weaker in warmer and wetter summers (Table 3; Figure 1c,d). Summer precipitation significantly advanced day of worker emergence, independent of its interaction with range status ($F = 7.79, p = .0068, R^2 = 8.4%$).

One model, including day of worker emergence, range status, maximum summer temperature, and the interaction between...
range status and maximum summer temperature best explained variance in the timing of peak worker activity (Table S4). When workers emerged earlier, they reached peak activity earlier (F = 31.23, p < .0001, partial R² = 50%; Table 3; Figure S5b; y = 48.44 + 0.81x) indicating that for both resident and colonizing species, peak worker activity is primarily constrained by emergence time.

Variance in the timing of worker accrual was greater for colonizing bumble bee species than for residents (Figure 2; for unadjusted density curves, see Figure S6). Resident species tended to have lower kurtosis than colonizing species (W = 1.00, p = .071; Figure S7). Colonizers exhibited shallower peak abundance with more worker activity earlier and later in the summer (Figure 2a; Figure S7). Resident worker numbers accumulated and declined more abruptly as the season progressed. Kurtosis in worker activity schedules changed from negative (platykurtotic) to increasingly positive as the mean elevation at which a species was collected historically increased (F₁,₆ = 10.32, p = .018, R² = 63%; Figure 2b), indicating that greater canalisation in phenology was favored in higher-elevation species.

FIGURE 1 Relationships of climate factors to phenology for (a) host-plant flowering and (b, c) life history events of resident and colonizing bumble bee species. (a) First flowering date (day of year, here and elsewhere) advances with may mean temperature (χ² = 261.30, p < .0001; y = 212.18 − 6.01x). (b) Day of queen emergence is delayed with heavier winter precipitation for both resident and colonizing species (F₁,₃⁹ = 6.60, p = .014, y = 5.15 + 0.0012x). (c) Emergence timing of workers in resident and colonizing bumble bees tended to differ in response to mean maximum summer temperature (F₁,₆₈ = 2.87, p = .095; resident: F₁,₂₅ = 2.27, p = .15; colonizing: F₁,₄₅ = 3.22, p = .079, y = 227.12 − 1.87x) and summer precipitation (d; F₁,₆₈ = 3.02, p = .087; resident: F₁,₂₅ = 0.017, p = .90; colonizing: F₁,₄₅ = 7.67, p = .0081, y = 221.08 − 1.14x), resulting in decreasing overlap in emergence under cool, dry conditions. Plant species are denoted as follows, CAOC, Castilleja occidentalis; ME, Mertensia spp.; PEGR, Pedicularis groenlandica; PEWH, Penstemon whippleanus; POVI, Polemonium viscosum; RHRH, Rhodiola rhodantha; TRDA, Trifolium dasyphyllum; TRNA, Trifolium nanum, TRPA, Trifolium parryi. Solid lines denote statistically significant relationships (p < .05). Marginally significant relationships (.05 < p < .10) are denoted by dashed lines. To clarify differential responses between colonizing and resident bees, dotted lines are used to indicate non-significant patterns (p > .10) when only one group had a significant response.
### 3.3 | Impacts of climate cues on synchrony of colonizers and residents with floral resources

The mismatch between peak worker density and peak flowering was predicted by one model (Table S4) with significant effects of May mean temperature ($F = 11.93, p = .0024$), summer precipitation ($F = 5.06, p = .035$), and their interaction ($F = 8.68, p = .0077$; Table 3; Figure 3). Respectively, each term explained 22%, 14%, and 0.9% of the variance. Overall, warmer May temperatures led to greater phenological mismatch between peak forager and resource abundances regardless of range status (Figure 3).

### 3.4 | Relationship of phenological mismatch to abundances of resident and colonizing species

Differences in phenological mismatch for colonizing and resident bumble bees did not affect cumulative worker abundances and were not included in the best model (Table S6). Instead, cumulative worker abundance was best explained by a model including statistically significant one-way interactions of range status with summer maximum temperature ($F = 9.72, p = .0027$) and summer precipitation ($F = 8.50, p = .0048$; Table 4), indicating that workers of resident and colonizing bumble bee species responded differently to climate factors. Relative abundance also was best explained by a model that included statistically significant interactions of range status with summer maximum temperature ($F = 18.54, p = .0001$) and summer precipitation ($F = 5.92, p = .018$; Table 4). Resident worker abundance (both relative and absolute) decreased, whereas colonizing worker abundance increased, with summer maximum temperature, resulting in comparable densities and representation under warmer conditions (Figure 4a,c).

### 4 | DISCUSSION

Under climate change, high-elevation communities may reach novel states due to colonization by species pre-adapted to warmer conditions, as well as loss of resident species lacking the plasticity or adaptive potential to adjust to changing regimes. Predicting outcomes of these combined processes is challenging since warming may have multiple synergistic pathways of impact on organisms. Our results shed light on ongoing impacts of climate change for high-elevation bumble bee communities of the Rocky Mountains. Bumble bees expanding their ranges upward from lower elevations appear to cope better with warming than high-elevation residents, although, on average, they are no better matched to phenological

| Table 3 | Parameter estimates for the model best explaining the effects of climate variables and range status on bumble bee phenology and the phenological mismatch between bumble bee forager activity and host-plant flowering. A single model best explained the timing of each life history event (Table S4) and the phenological mismatch between day of peak worker activity and day peak flowering (Table S5). Therefore, model averaging was not required. |
| --- | --- | --- | --- | --- |
| Day of queen emergence |
| Range status | 0.048 | 0.016 | 0.79 | .44 |
| May mean temperature | 0.0045 | 0.005 | 0.22 | .64 |
| Winter precipitation | 0.0017 | 0.123 | 6.60 | .014 |
| Range status: may mean temperature | −0.017 | 0.040 | 1.96 | .17 |
| Range status: winter precipitation | −0.00096 | 0.024 | 1.18 | .29 |
| Day of worker emergence |
| Range status | −67.98 | 0.076 | 6.84 | .040 |
| Summer maximum temperature | −1.26 | 0.025 | 2.08 | .15 |
| Summer precipitation | −1.02 | 0.084 | 7.79 | .0068 |
| Range status: summer maximum temperature | 2.51 | 0.033 | 2.87 | .095 |
| Range status: summer precipitation | 0.95 | 0.034 | 3.02 | .087 |
| Day of peak worker activity |
| Day of worker emergence | 0.76 | 0.50 | 31.23 | <.0001 |
| Range status | −22.92 | 0.019 | 0.60 | .47 |
| Summer maximum temperature | −1.05 | 0.018 | 0.56 | .46 |
| Range status: summer maximum temperature | 1.44 | 0.021 | 0.70 | .42 |
| Phenological mismatch: day of peak worker activity—day of peak flowering |
| Range status | 2.18 | 0.28 | 0.27 | .62 |
| May mean temperature | 29.87 | 0.22 | 11.93 | .0024 |
| Summer precipitation | 1.78 | 0.14 | 5.06 | .035 |
| May mean temperature: summer precipitation | −1.05 | 0.009 | 8.68 | .0077 |
advancement in host flowering. While neither colonizing nor resident species exhibit mechanisms to synchronize foraging activity with earlier flowering under warm conditions, low-elevation bees have a more generalized strategy of seasonal resource use (Figure 2) that may allow them to take advantage of the richer floral resources available over the season in locations with longer flowering intervals. Our findings, while based on observational rather than experimental data, concur with the prediction that phenotypic plasticity of generalist species buffers them from the disruptive effects of climate change (Herbertsson et al., 2021; Schweiger et al., 2010; Sponsler et al., 2022). Results support the view that a legacy of strong selection for survival and reproduction in a cold environment constrains the performance of resident alpine bumble bees under warming, and favors colonizing species with more generalized phenology and greater heat tolerance (Martinet et al., 2015; Oyen et al., 2016).

Unique climate drivers cue timing of key life cycle events in alpine flowering plants and their bumble bee pollinators. As reported elsewhere (Iler et al., 2013; Kudo & Cooper, 2019; Menzel et al., 2006), temperature before flowering is a strong driver of flowering phenology. Specifically, temperatures in May, weeks before the onset of the growing season at our high-elevation field sites, most strongly affect the timing of onset and peak flowering in preferred bumble bee food resources (Figure 1a). Pronounced spatial variance in micro-climate characterizes alpine ecosystems (Kudo, 2020; Ohler et al., 2020) and this, as well as variation among host species in phenological response (Figure 1a), likely weakened but did not overwhelm these community level effects. For every degree of warming, onset of flowering advanced by 6 days and peak flowering by 5 days (Figure 1a; Figure S3, respectively). Conversely, bumble bee queen emergence in snowy environments is primarily cued by snowmelt schedule rather than temperature (Kudo et al., 2008; Kudo & Cooper, 2019; Pawlikowski et al., 2020; Stemkovski et al., 2020). While winter snowpack and May temperature regimes are correlated (Table S6), the coupling is so weak ($R^2 < .05$) as to play little role in synchronizing queen and flower appearance. Weak coupling between the snowpack and early spring temperature likely reflects the importance of exposure in alpine habitats, where extreme cold temperatures characterize both wind-swept ridges and snow-packed slopes (Zwinger & Willard, 1996). Byron (1980) postulated that bumble bee emergence at snowmelt optimizes nest site selection by queens of ground nesting alpine species and that nest site availability and quality rather than food limits colony success at high elevations (see also Sarro et al., 2022).
Worker emergence schedules were similarly insensitive to summer temperature and precipitation regimes (for temperature, see Pawlikowski et al., 2020), but consistent with historical (mid-20th century) differences in climate between low and high elevations (Table S1). Colonizers tended to emerge later than residents under all but the warmest summer temperatures (Figure 1c) and exhibited greater variation in timing of worker accrual than their alpine congeners (Figure 2). Such life history differences between low- and high-elevation species are predicted under a model of counter-gradient selection on life history traits at high elevations (Berven et al., 1979). According to this hypothesis, historically shorter growing seasons in alpine environments favor early growth onset and rapid development for poikilothermic organisms, while the longer growing season of lower elevations favors plasticity in the growth phase (Berven et al., 1979; Laugen et al., 2003). The establishment of colonizing species from lower elevations, thus appears to expand the range of alpine species, research probing physiological responses to extreme temperature stress in bumble bees suggests that the two resident alpine species, B. lapponicus and B. kirbiellus are more cold tolerant and heat sensitive than their low-elevation congeners (respectively, Martinet et al., 2015; Oyen et al., 2016). Such phenotypic differences in temperature tolerance could have allowed high-elevation bumble bees to begin foraging earlier under historically cooler temperatures (Figure 1c), while incurring a cost in adaptability as temperatures have warmed (e.g., an evolutionary trap, Schlaepfer et al., 2002).

Phenology describes the temporal pattern of resource and consumer abundance, not the abundances themselves. For this reason, we assessed how forager abundances in resident and colonizing species relate to climate change. Results suggest that while mismatches between the timing of peak floral resource availability and bumble bee foraging are exacerbated by warming (Figure 3a,b), they are less likely to drive changes in bumble bee abundance or community composition than other climate effects (Tables 4 and S6; but see Ogilvie et al., 2017). This conclusion is consistent with observed shifts in traits promoting resource generalization in alpine bumble bees (e.g., shorter proboscis length; Miller-Struttmann et al., 2015). Specifically, the capacity for diet breadth to expand to less-preferred late-season flowers (e.g., Solidago, Sedum) may buffer impacts of phenological mismatches with historically favored resources (Sponsler et al., 2022), but do little to ameliorate other, more detrimental aspects of climate change.

We are aware that gaps in our knowledge could temper these findings. Our sampling schedule for bumble bee forager density precluded observation of reproductives and thus of sensitivity of recruitment to warming. While variation in worker numbers is known to affect reproductive output (Muller & Schmid-Hempel, 1992), direct observations on new queen production (Tables 4 and S6) consistent with negative impacts of warming in alpine ecosystems.

| Model                                      | Estimate | Partial R² | F      | p         |
|--------------------------------------------|----------|------------|--------|-----------|
| Cumulative worker abundance                |          |            |        |           |
| Range status                               | 5.05     | 0.21       | 22.96  | .003      |
| Summer maximum temperature                 | 0.081    | 0.059      | 5.17   | .026      |
| Summer precipitation                        | 0.013    | 0.009      | 0.81   | .37       |
| Range status: may mean temperature         | -0.19    | 0.10       | 9.72   | .0027     |
| Range status: summer precipitation          | -0.064   | 0.087      | 8.50   | .0048     |
| Relative worker abundance                  |          |            |        |           |
| Range status                               | 2.39     | 0.26       | 32.89  | .0012     |
| Summer maximum temperature                 | 0.040    | 0.082      | 7.94   | .0063     |
| Summer precipitation                        | 0.012    | 0.041      | 4.12   | .046      |
| Range status: may mean temperature         | -0.10    | 0.17       | 18.54  | .0001     |
| Range status: summer precipitation          | -0.021   | 0.058      | 5.92   | .018      |
5 | CONCLUSIONS

As range-stable and range-expanding bumble bee species respond to climate change, novel communities are generated with discouraging implications for long-term persistence of alpine resident species. Our study suggests that effects of climate change favor colonizing bumble bee species in historically cold environments, to the detriment of resident species. How differences in their responses to climate change affect competition between resident and colonizing species or their pollination services remains to be seen. However, prior work in this system suggests that colonizing taxa are not morphologically equivalent to resident species (Miller-Struttmann et al., 2015) and may behave differently within the community. Future research exploring the effects of rapid changes in community composition on network structure could clarify the knock-on effects of displacement for community stability and pollination.

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CONFLICT OF INTEREST
There are no conflicts of interest to report.

DATA AVAILABILITY STATEMENT
The data and R scripts that support the findings in this article are openly available in Dryad at https://doi.org/10.5061/dryad.6q573n61q.

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