Received: 21 April 2022 | Accepted: 19 September 2022

DOI: 10.1111/1365-2656.13825

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

The shifting importance of abiotic and biotic factors across the life cycles of wild pollinators

Jane E. Ogilvie[1,2] | Paul J. CaraDonna[1,2,3]

[1]Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA

[2]Chicago Botanic Garden, Glencoe, Illinois, USA

[3]Plant Biology and Conservation, Northwestern University, Evanston, Illinois, USA

Correspondence
Jane E. Ogilvie
Email: janeeogilvie@gmail.com

Paul J. CaraDonna
Email: pcaradonna@chicagobotanic.org

Funding information
Chicago Botanic Garden; National Science Foundation, Grant/Award Number: DEB-1754518; Northwestern University; Rocky Mountain Biological Laboratory, Grant/Award Number: Research Fellowship for Scientists; Western North American Naturalist, Grant/Award Number: Grant Supporting Natural History Research

Handling Editor: Ainhoa Magrach

Abstract

1. Organisms living in seasonal environments are exposed to different environmental conditions as they transition from one life stage to the next across their life cycle. How different life stages respond to these varying conditions, and the extent to which different life stages are linked, are fundamental components of the ecology of an organism. Nevertheless, the influence of abiotic and biotic factors on different parts of an organism's life cycle is often not accounted for, which limits our understanding of the ecological consequences of environmental change.
2. We investigated the relative importance of climate conditions, food availability, and previous life-stage abundance in an assemblage of seven wild bumble bee species, asking: how do these three factors directly influence bee abundance at each life stage? To do so, we used a 7-year dataset where we monitored climate conditions, floral resources, and abundances of bees in each life stage across the active colony life cycle in a highly seasonal subalpine ecosystem in the Colorado Rocky Mountains, USA.
3. Bee abundance at different life stages responded to abiotic and biotic conditions in a broadly consistent manner across the seven species: the survival and recruitment stage of the life cycle (overwintered queens) responded negatively to longer winters; the growth stage (workers) responded positively to floral resource availability; and the reproductive stage (males) was positively related to the abundance of the previous life stage (workers). Most species also exhibited some idiosyncratic responses.
4. Our long-term examination of annual bumble bees reveals a general set of responses in the abundance of each life stage to climate conditions, floral resource availability, and previous life stage. Across species, these three factors each directly influenced a distinct life stage, illustrating how their relative importance can shift throughout the life cycle. The life-cycle approach that we have taken highlights that important details about demography can be overlooked without considering life-stage-specific responses. Ultimately, it is these life-stage-specific responses that shape population outcomes, not only for animal pollinators but also for many organisms living in seasonal environments.

KEYWORDS
Bombus, bumble bee, climate change, floral resources, long-term data, pollinator community, pollinator decline, population ecology

1 | INTRODUCTION

An organism needs suitable environmental conditions to survive, grow, and reproduce. In turn, the response of an organism to its abiotic and biotic environment over its life cycle should shape its population dynamics (Caswell, 2001; Ehrlén et al., 2016; White, 2008). In seasonal environments, abiotic and biotic conditions can change dramatically such that different parts of an organism's life cycle can be exposed to very different environmental factors (Cordes et al., 2020; Elton, 1927; Fretwell, 1972; Radchuk et al., 2013). Whether or not the relative importance of abiotic and biotic factors shift across an organism's life cycle has a variety of ecological and evolutionary implications, particularly in the context of rapid environmental change (e.g. Boyce et al., 2006; Radchuk et al., 2013). For example, abiotic factors, such as short winters or hot summers, might exert stronger effects on certain parts of an organism's life cycle compared with other stages, where biotic factors, such as food resources, may prevail instead (e.g. Johnston et al., 2021; Radchuk et al., 2013). Nevertheless, the effects of abiotic and biotic factors on different parts of an organism's life cycle are often not accounted for, which limits our understanding of the effects of environmental variation on populations (e.g. Crone et al., 2013; Griffith et al., 2016; Radchuk et al., 2013).

The extent to which different stages of an organism's life cycle are linked can also have strong population-level effects (Caswell, 2001; Iles et al., 2019). Temporal covariation among demographic parameters, such as survival, growth, and reproduction, is important because it can exacerbate or diminish the consequences of environmental variation (Iles et al., 2019). For example, positive covariation among demographic parameters can amplify the effects of environmental variation, whereas negative covariation, or a lack of covariation, can buffer against such variation, since the responses of each life stage exhibit opposing effects or are decoupled. Temporal covariation among demographic parameters appears to be common, but our understanding of the direction and magnitude of such relationships is still relatively limited (Fay et al., 2022).

How environmental variation influences different stages of an organism's life cycle and to what extent successive stages of the life cycle are linked are critical for predicting population and community responses to environmental change. This is especially the case for wild pollinators because we currently know relatively little about the factors driving their demography and thus population dynamics (Roulston & Goodell, 2011; but see Boggs & Inouye, 2012; Crone & Williams, 2016; Wong & Forrest, 2021). Animal pollinators are ecologically and economically important (Klein et al., 2007; Ollerton et al., 2011), but many populations are undergoing declines worldwide (Cameron & Sadd, 2020; Potts et al., 2016). Theoretically, the abundance of different pollinator life stages can be influenced by the climate conditions directly experienced, the availability of floral food resources, and the success of previous life stages (i.e. temporal demographic correlations). Indeed, two major hypothesised mechanisms underlying observed global pollinator declines are reduced food resources (Potts et al., 2016; Woodard & Jha, 2017), and changing climate conditions (Crossley et al., 2021; Soroye et al., 2020), which can have both direct effects on pollinator survival and indirect effects on floral resource availability (Ogilvie et al., 2017; Thomson, 2016). Although climate and resource conditions define the most basic requirements for pollinator populations, these two factors are often studied in isolation (but see Ogilvie et al., 2017; Wong & Forrest, 2021) and their effects across different life stages in pollinator life cycles are poorly understood.

To address these knowledge gaps, we evaluate the relative importance of the direct effects of abiotic and biotic factors across the life cycles of seven wild bumble bee species that coexist within the same ecological community. Specifically, we ask: how does the abundance of each life stage respond to the climate conditions they directly experience, the availability of food resources, and the abundance of previous life stages? To do so, we used a unique long-term study where we have monitored climate conditions, floral resource abundance, and bee abundance across the active bumble bee colony life cycle over 7 years in a subalpine ecosystem in the Colorado Rocky Mountains, USA. Bumble bees are quintessential generalist foragers that can tolerate a wide range of climate conditions. Although the abundance of each life stage can be influenced by climate, floral resources, and the success of the previous life stage, we predict that it is unlikely that each will respond to such factors similarly because each life stage performs a different function, is active during a different time of the year and, therefore, directly experiences different abiotic and biotic environments (Figure 1). By examining wild pollinator populations across their life cycles over multiple years, our work helps to clarify how the relative importance of environmental and demographic factors may shift across organisms' life cycles, which is crucial for predicting population and community responses to environmental change.

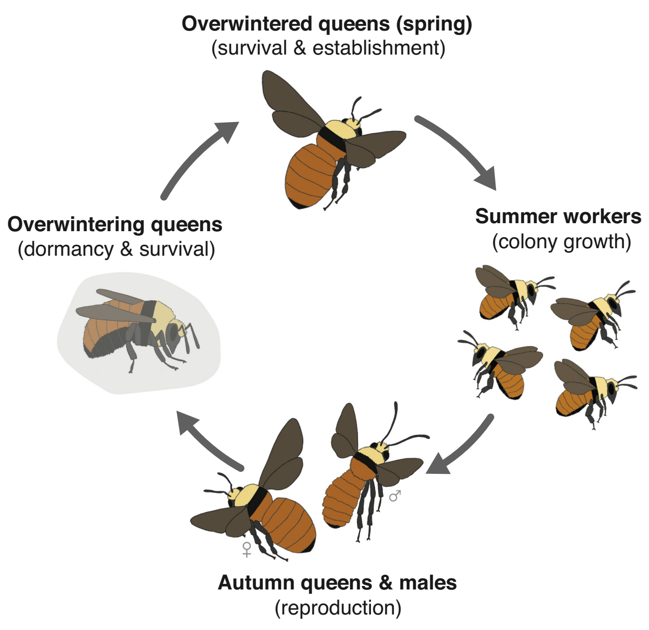

FIGURE 1 Annual life cycle of a bumble bee colony illustrating each life stage and its corresponding demographic parameter.

2 | MATERIALS AND METHODS

2.1 | Study system

We monitored climate conditions, floral resources, and the abundance of seven wild bumble bee species across seven growing seasons (2015–2021) in subalpine habitats near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA (2900 m a.s.l.). In this system, winter conditions, including snowpack and snowmelt timing, are important for many ecosystem processes. The short season of pollinator activity and flowering begins when the snow melts in spring (April–June) and ends when temperatures cool in autumn (September–October). Furthermore, over four decades, the timing of spring snowmelt influences the abundance of flowers (CaraDonna et al., 2014; Ogilvie et al., 2017; Figure S1); although we note that over the 7-year period of our study, this trend is not apparent (Table S1). Thus, the study area typifies high-elevation and high-latitude locations with extreme seasonal climates, which are experiencing especially rapid anthropogenic climate change (IPCC, 2007; Nogués-Bravo et al., 2007).

We established six study sites spread over 8 km within the East River Valley near the RMBL, each separated from the others by at least 1 km (from edge to edge), and each approximately 500 m in diameter (196,349 m^2)—a scale that reflects typical bumble bee foraging distances observed in Colorado montane meadows (Elliott, 2009; Geib et al., 2015). Mark-recapture data from 2 years of study at these sites suggests that our focal bumble bee species do not travel between sites (there were no site transfers from 2012 marked bees). Each site includes the three major habitats where bumble bees are observed foraging or searching for nests in the area: wet meadow, dry meadow, and aspen forest. Across the six sites there are 153 non-graminoid herbaceous and shrub flowering plant species from 40 plant families, 96 species of which we have observed bumble bees to visit, although 99% of bumble bee visits are to 48 plant species. Five of the plant species visited by bumble bees are introduced (the common *Taraxacum officinale*, and rarer *Trifolium pratense*, *Trifolium repens*, *Linaria vulgaris* and *Cirsium arvense*). Non-native bees, including the honey bee, *Apis mellifera*, are absent in this area. Our research did not require animal ethics approval. We had permission to carry out field work in the Gunnison National Forest with U. S. Department of Agriculture Forest Service Special Use Permit GUN1120 and on private land from the RMBL and the Town of Mt. Crested Butte.

2.2 | Bumble bees

Our observations focused on the seven most common bumble bee species: *Bombus appositus*, *Bombus bifarius*, *Bombus flavifrons*, *Bombus insularis*, *Bombus mixtus*, *Bombus occidentalis* and *Bombus rufocinctus*. *B. insularis* is a nest parasite of other bumble bees and does not have workers. These seven species coexist in our study system and belong to the same ecological community.

Globally, bumble bees are a rich group of approximately 260 species in mostly temperate and montane ecosystems, though many species are experiencing contractions in their distribution and relative abundance (Cameron & Sadd, 2020). Bumble bee species, including those within our study assemblage, vary in life-history traits, including diet breadth, phenology, and body size—all of which may influence their response to changes in the abiotic and biotic environment (Martinet et al., 2021; Ogilvie & Forrest, 2017). Their floral resource needs extend across most of the growing season as they transition from one life stage to the next, and each life stage is exposed to a new set of abiotic conditions (Figure 1). In the context of the bumble bee life cycle in temperate and montane ecosystems, we have several hypotheses for the relative importance of biotic and abiotic conditions on each life stage. In spring, overwintered queens that mated the previous autumn and have survived winter diapause emerge to search for nests and establish colonies. The abundance of overwintered queens in spring should be related to floral resources and colony reproductive output during the previous growing season when they were produced (Carvell et al., 2017; Inari et al., 2012), as well as the winter conditions they directly experience during diapause (Vesterlund & Sorvari, 2014). If surviving overwintered queens are successful in colony establishment, their colonies grow in the number of foraging workers over the summer and eventually produce reproductive bees toward the end of the season (autumn queens and males). Both colony growth and reproductive output may be influenced by the availability of floral resources during summer (Crone & Williams, 2016), the prevailing climate conditions directly experienced (Iserbyt & Rasmont, 2012), and the abundance of the previous life stage (Inari et al., 2012).

2.3 | Quantifying bumble bee abundance

We monitored the abundance of bumble bees of each species and life stage at weekly intervals across the entire season of aboveground activity (16–22 weeks, late April to late September). During each weekly census we systematically searched the three habitats at each study site (dry meadow, wet meadow, aspen forest) for 20 min each, moving steadily through the site, not revisiting areas, and recording all bumble bees seen. For each bee, we recorded the following: (i) species identity, (ii) life stage (overwintered queen, worker, male), (iii) whether the bee was foraging, searching for a nest, both, or flying through, and (iv) the plant species visited if the bee was foraging. Bees were typically identified to species on the fly based on distinctive colour patterns and body size following Williams et al. (2014), but if the identity was uncertain, we netted the bee for closer inspection and quickly released it.

To estimate the abundances of each species and life stage at each site for each year, we summed the abundances of bees seen in each weekly observation (number of bees per hour for all weeks observed). We standardised bee counts in each week to express them as the number of bees per hour, to accommodate rare instances where our weekly censuses at a given site were longer or shorter than 1 h. Our visual assessments of abundance are estimates of population size, and by summing abundances across weeks we may recount some individual bees. Nevertheless, resighting rates from week-to-week within our sites are low (on average, across species, we resight only 2.5 bees per site per season), thus recounts likely contribute minimally to our abundance estimates. Furthermore, by summing abundances across weeks, our measure of abundance is robust to random variation in bee abundances in any one week (e.g. unusually low or high abundances in one week).

2.4 | Quantifying the effect of previous life stage

To understand the extent to which demographic responses are linked across the bumble bee life cycle (i.e. temporal covariation), we examined how each life stage is influenced by the abundance of the previous life stage. For overwintered queens this was males observed in the previous season ($t-1$), which we use as an estimate of reproductive output; for workers this was overwintered queens in the current season; and for males this was workers in the current season (Figure 1). For overwintered queens, we also considered the abundance of workers in the previous season ($t-1$), since this is the most common life stage measured in other bumble bee population studies and has been shown to relate to the production of both males and new queens (e.g. Crone & Williams, 2016; Pelletier & McNeil, 2003; Spiesman et al., 2017); our results are qualitatively similar when we use either workers or males as a predictor of overwintered queen abundance (Figure S2). We were unable to include autumn queens as a distinct life stage or include them in reproductive output because the observation of new, autumn queens is rare in our study system (Table S2). Thus, although reproductive output is represented only by male abundance, the production of males is correlated with autumn queens at both colony and population levels (Pelletier & McNeil, 2003; Rundlöf et al., 2014).

2.5 | Quantifying floral resource abundance

In the same weekly censuses, we also recorded floral abundance. At each site we counted the flowers of plant species visited by bumble bees in 15 permanent 20 × 0.5 m belt transects, five distributed throughout each of the three habitats (i.e. 50 m^2 of transect area per habitat, 150 m^2 total transect area per site). We counted individual flowers of most species, but instead counted the number of flowering stalks for *Castilleja* spp., *Eriogonum* spp., *Valeriana occidentalis* and *Haeckelia floribunda* as well as members of the Apiaceae and Lamiaceae; similarly, we counted the number of capitula for all Asteraceae and the number of catkins for *Salix* spp.

We quantified the abundance of floral resources for bumble bees by first generating a list of all flower species visited by each species and life stage across the 7 years. This list was used to create a floral preference index by dividing the number of visits to each plant species by the number to the most-visited species (following Pleasants, 1981). Rescaling the flower counts by this index prevents rarely visited species from representing an inappropriate share of a bee diet. For example, *B. bifarius* rarely visits the early spring flowering *Claytonia lanceolata*, so this plant species should be scored as a minor element of their diet even though the flowers are abundant.

The rescaled flower counts then allowed us to estimate those resources that had the potential to influence the abundance of each bumble bee life stage. For overwintered queens (produced toward the end of each growing season but observed the following spring; Figure 1), our estimate of resource abundance includes all flowers visited across the entire previous growing season ($t-1$). For workers, our estimate includes all flowers visited from the start of the growing season through the end of observed worker activity. For males, our estimate includes all flowers visited from the start of the growing season through the end of observed male activity.

2.6 | Quantifying climate conditions

We selected climate variables that each life stage directly experiences and that are hypothesised to influence the abundance of each life stage most strongly. Although climate can have indirect effects on bee abundance through its effects on floral resource availability (e.g. Ogilvie et al., 2017; Thomson, 2016), here we focus our analyses on the climate variation that each life stage experiences. For overwintered queens, our climate variable is spring snowmelt date—the date when bare ground appears and emergence from underground winter hibernacula is possible. In our system, earlier spring snowmelt indicates a shorter winter with less snowpack (Inouye, 2008). Shorter winters may be more favourable for winter survival, compared to longer winters, since overwintering queens spend less time in diapause using stored energy reserves (Beekman et al., 1998). For workers and males, our climate variable is the ratio of temperature to precipitation (mean daily maximum temperature divided by the sum of precipitation) which captures variation in both summer temperature and precipitation when the bees are active. For this ratio, lower values indicate cooler and wetter conditions, whereas higher values indicate warmer and drier conditions. If these climate conditions are within tolerable limits, then warmer and drier years may be more favourable for foraging, survival and reproduction (Zaragoza-Trello et al., 2021); alternatively, if these same conditions push beyond tolerable limits, they may be less favourable and reduce bee abundances (Iserbyt & Rasmont, 2012). For workers, the temperature: precipitation ratio includes June and July conditions, and for males, it includes July and August conditions—these are times when the two life stages are mostly active. None of the hypothesised climate variables are correlated with one another (confidence intervals for each pairwise correlation overlapped with zero).

Climate conditions were measured by local resident billy barr at a central site at the RMBL, 0.5–4.5 km from the six study sites. Snowmelt date was the day of year that a permanent 5 × 5 m plot was first free of snow, while temperature minima and maxima (in °C) and precipitation (in mm) were measured daily using a Davis Instruments temperature sensor and a standard US National Weather Service rain gauge, respectively.

2.7 | Data analysis

We analysed how climate conditions, floral food resources, and previous life stage were related to bee abundance for each bumble bee species and life stage by constructing generalised linear mixed effects models with each of these factors as additive predictor variables. Study site was included in all models as a random intercept term. The bee counts are overdispersed, so we used a negative binomial error distribution. We checked all models to ensure there was no multicollinearity among predictor variables (i.e. variance inflation factors were all much less than 2.5). Analyses were conducted in a Bayesian statistical framework. All models used weakly informative priors (using the 'stan_glmer.nb' function) and were created in the Stan computational framework (http://mc-stan.org/) accessed with the RSTANARM package in R (Goodrich et al., 2022). Model estimates (i.e. the effect of each factor) from our negative binomial models are expressed as the change in the log count of bees per 1 unit change in the predictor variable (except for flowers, which for simplicity are shown as the change in the log count of bees per 100 flowers). Bayesian R^2 values were calculated for each full model using residual variance following Gelman et al. (2019). The Bayesian statistical framework places an emphasis on the uncertainty of predictions produced from a given model (i.e. the parameter estimates) as opposed to a single point estimate (Ellison, 2004). Evidence for a hypothesis can be expressed as the probability of a given parameter estimate (i.e. the posterior distribution of the model estimates; Ellison, 2004). We consider strong evidence for a non-zero model parameter estimate when the 89% Bayesian credible interval from the posterior distribution does not include zero; in other words, this means that at a minimum 89% of the predictions from a model are consistent with the hypothesis of a non-zero effect. All analyses were conducted in R version 4.2.1 (R Core Team, 2022).

3 | RESULTS

Seven years of season-long censuses yielded counts of 30,236 bees, 1,004,241 flowers, and 700 unique interactions between flowers and life stages of the different bumble bee species. Over this time, we detected no clear directional trends in the abundance of bumble bee species and life stages (Figure 2; Figure S3). Climate conditions varied considerably from 2015 to 2021: spring snowmelt dates varied by 1 month (May 5–June 6); the summer average high temperature spanned almost 3.0°C (19.9–22.7°C, June–August); summer precipitation varied more than 3-fold (78–272 mm, June–August); and the ratio of temperature: precipitation varied 5-fold (0.1–0.5). Likewise, floral resource abundance for all flowers visited by bumble bees varied 7-fold across years and study sites (959–6966 flowers/m^2, summed over each season).

Across bumble bee species, our full additive models relating the abundance of different life stages to putative environmental and demographic drivers explained 32%–68% of the variation for overwintered queens; 43%–59% for workers; and 40%–77% for males (range of values represents median Bayesian R^2 values across species; Figure 3; Table S3). The life stages responded to variation in climate, floral resources, and abundance of the previous life stage in some consistent ways across species, but most species also exhibited some idiosyncratic responses (Figures 3 and 4; Figures S4–S8). We can illustrate both patterns using the examples of the two most common species, *B. bifarius* and *B. flavifrons* (Figure 4).

For the abundance of overwintered queens, our models revealed broadly consistent evidence of a negative response to winter climate conditions (quantified as the timing of spring snowmelt) across species (five out of seven species; Figure 3; Table S3). That is, more queens were observed in years with earlier snowmelt dates. For

FIGURE 2 Mean abundance of seven bumble bee species (*Bombus* spp.) and life stages over 7 years. Bee abundances are averaged across the six study sites in each year. Note the different abundance scales for each life stage; *Bombus insularis* is a bumblebee nest parasite without a worker life stage. Bee abundance values standardised by average abundance are included in Figure S3.

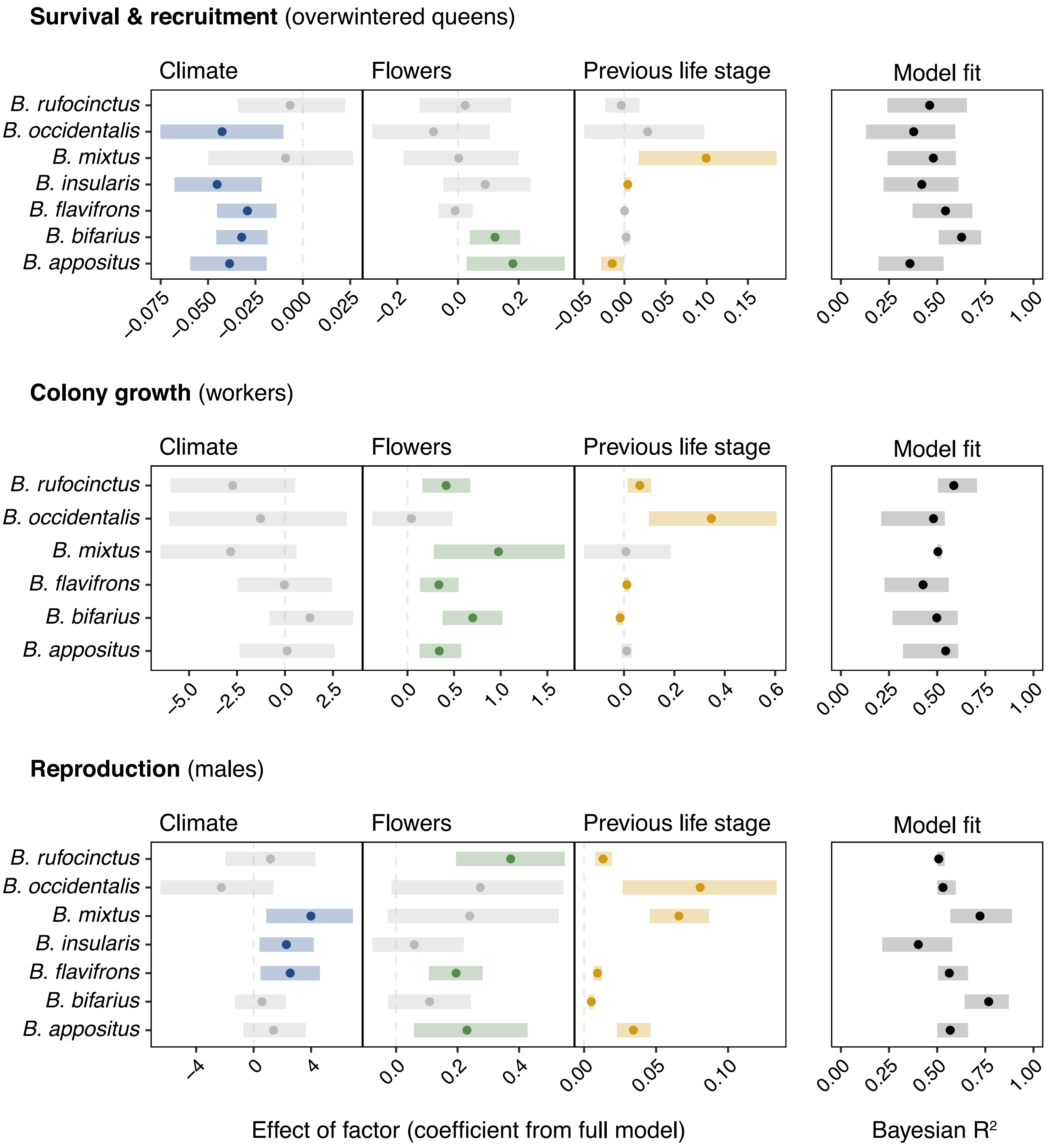

FIGURE 3 The effect of climate conditions, floral abundance, and previous life stage on the abundance of bees in different life stages in the seven bumble bee species. Dots represent the median estimate (i.e. effect) of the posterior distribution from negative binomial mixed effects models including all three factors; error bars represent 89% Bayesian credible intervals. Coloured dots and error bars represent model factors with evidence in support of a non-zero effect (e.g. 89% credible interval does not include zero). The effect of each factor (coefficients from the full model) can be interpreted as follows: For every one-unit change in the predictor variable, the expected log count of bees changes by the corresponding coefficient estimate (with the other predictor variables in the model held constant); for flowers, coefficients are shown as change for every 100 flowers. Model fits represent the median and 89% credible interval for Bayesian R^2 values. The climate variable for overwintered queens is spring snowmelt date; for workers is the June and July temperature: precipitation ratio; and for males is the July and August temperature: precipitation ratio. Floral abundance is specific to each bumble bee species and life stage and includes all flowers that could affect the production of a life stage (see Section 2 for details). Abundance of the previous life stage for overwintered queens is the abundance of males in the previous year ($t-1$); for workers is overwintered queens in the current year (t), and for males is workers in the current year (t).

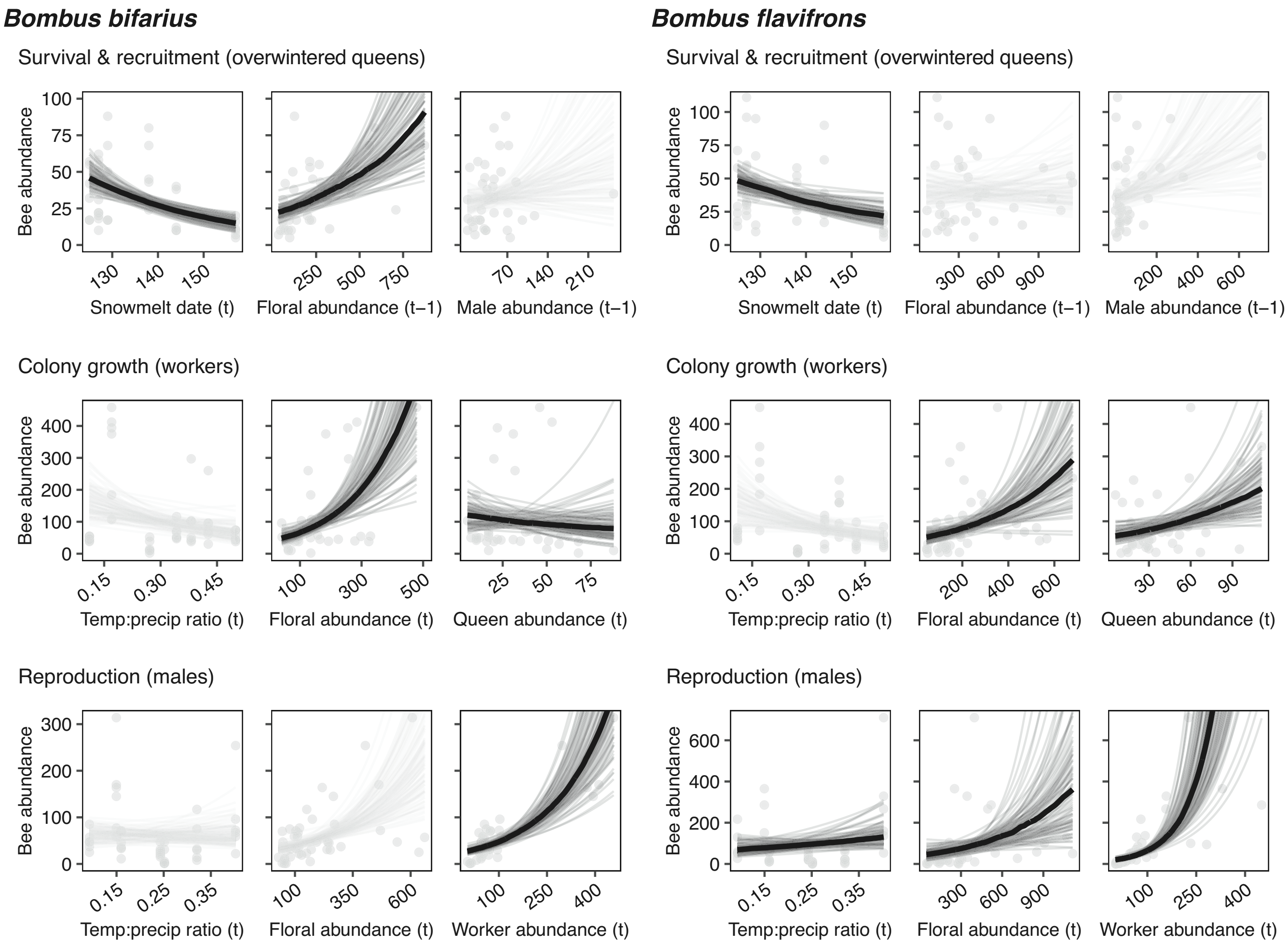

FIGURE 4 Examples of the effects of climate conditions, floral resources, and previous life stage on the abundance of different life stages for *Bombus bifarius* and *Bombus flavifrons*. Model fit lines represent 100 draws from the posterior distribution from a bivariate negative binomial model of each predictor variable on each response variable. Darker lines indicate evidence of a non-zero effect from the full additive model (see Figure 3 and Materials and Methods for details), and the thick solid line represents the median estimate from the posterior distribution. Each dot represents a year-site abundance value; $n = 36$ for overwintered queens; $n = 42$ for workers and males. Similar bivariate plots for all other species are included in Figures S4–S8. Note that the coefficients from the full models (Figure 3) represent effects when the other predictor variables are held constant and therefore may differ somewhat from the bivariate relationships shown here for illustrative purposes.

species with evidence of a non-zero response, we observed on average a 2.2-fold decrease in bee abundance across the observed range of snowmelt dates. For *B. bifarius* and *B. appositus*, the abundance of overwintered queens also responded positively to the abundance of floral resources in the year before queens emerged from winter diapause ($t-1$) (Figures 3 and 4). For these two species, there was on average a 2.0-fold increase in bee abundance across the observed range of floral resources. Three species (*B. mixtus*, *B. insularis* and *B. appositus*) also exhibited an effect of abundance of the previous life stage (reproductive output in year $t-1$ predicting overwintered queen abundance in year t; note that using worker abundance in year $t-1$ as the predictor variable provided similar results, Figure S2). For *B. mixtus* and *B. insularis*, this relationship was positive, whereas for *B. appositus*, it was negative. For these three species, there was on average a 2.5-fold increase in bee abundance across the observed range of males in the previous season.

The abundance of workers responded most consistently to floral resource availability, with a positive effect in five out of six species, including in *B. bifarius* and *B. flavifrons* (Figure 4); only for *B. occidentalis* was this effect not evident (Figure 3; Table S3; recall that *B. insularis*, a bumble bee nest parasite, lacks a worker life stage). For the species with evidence of a non-zero response, there was on average a 4.2-fold increase in bee abundance across the range of observed floral resources. We also observed a positive effect of the abundance of the previous life stage (overwintered queens) on worker abundance for *B. flavifrons*, *B. occidentalis* and *B. rufocinctus* and a negative effect for *B. bifarius*. Across these four species, there was on average a 3.1-fold increase in bee abundance across the observed range of overwintered queens. Summer climate conditions (temperature: precipitation ratio for June and July) did not obviously relate to worker abundance for any species.

The abundance of males (representing reproductive output), responded most consistently to the abundance of the previous life stage: worker and male numbers were positively related for all six species (again *B. insularis* is not included since it lacks a worker life stage), including in *B. bifarius* and *B. flavifrons* (Figures 3 and 4; Table S3). Across these six species there was on average a 5.0-fold increase in the abundance of bees across the observed range of workers. Additionally, in all but two of these species, other factors also played a role in affecting male abundance. We observed positive effects of floral resource abundance on male abundance (three of seven species; on average a 3.1-fold increase in bees across the range of observed floral resources), and positive effects of climate conditions (three of seven species; on average a 8.7-fold increase across the range of climate conditions)—that is, we observed more males when it was warmer and drier. Both factors were positively related to male abundance in *B. flavifrons* (Figure 4).

4 | DISCUSSION

Organisms living in seasonal environments are exposed to different sets of abiotic and biotic conditions as they transition from one life stage to the next across their life cycle. How different parts of an organism's life cycle respond to these varying conditions is a basic feature of their population ecology and life history and is critical for understanding how they will respond to environmental change. In our long-term examination of annual bumble bees, we observed broadly consistent responses in the abundance of each life stage to climate conditions, floral resource availability, and previous life-stage abundance. Across the seven species we studied, these three factors each directly influenced a distinct life stage, illustrating how the relative importance of different ecological and environmental factors can shift throughout the life cycle (Figure 3). The general consistency of responses across species and their life stages emerges despite interspecific variation in emergence timing, body size and other aspects of morphology, behaviour, and natural history, suggesting common underlying mechanisms.

The shifting importance of different abiotic and biotic factors through the bumble bee life cycle provides insight into the demographic mechanisms that may underlie how populations of wild pollinators are responding to environmental change. Recognising this complexity is especially relevant in an era of climate change and biodiversity loss. Changing climate and reductions in floral food resources are two hypothesised mechanisms predicted to have strong, negative effects on many wild pollinator species (Cameron & Sadd, 2020; Potts et al., 2016; Roulston & Goodell, 2011; Woodard & Jha, 2017). Our results illustrate that changes in these two factors do not necessarily influence each part of the life cycle in the same manner. We find that certain life stages can respond more strongly to the direct effects of important climate conditions they experience compared with other life stages. Similarly, although floral food resources are at the core of the plant–pollinator mutualism, we find their strongest effects on only some parts of the life cycle, and much less so for others. These findings provide evidence that pollinator population declines are unlikely to be driven by factors affecting only a single life stage—indeed, our understanding of population dynamics should be contingent on how each life stage is influenced by different abiotic and biotic factors.

Across the bumble bee life cycle, we observed consistent temporal covariation in growth and reproduction, but other successive life stages were inconsistently related. The positive covariation we observed among the growth and reproductive stages of the life cycle suggests that the positive effects of floral food resources on worker abundance also translate into positive effects on reproductive output. Although positive relationships were most common when we observed temporal covariation between successive life stages (consistent with other empirical work on animals; Fay et al., 2022), we also observed instances where life stages were inconsistently related across species. For example, the abundance of the recruitment stage of the life cycle (overwintered queens) was positively related to reproductive output in the previous year for only two species and negatively related for another; similarly, colony growth (workers) was positively related to the abundance of recruits (overwintered queens) for three species and negatively related for another (Figure 3). Such variation means that the direct effects of abiotic and biotic factors can be either amplified *or* buffered depending on the species and life stage in question (e.g. Boyce et al., 2006; Iles et al., 2019). Yet, at the same time, the lack of covariation between successive life stages for other species means that the effects of environmental factors can also operate at least somewhat independently.

The abundance of overwintered queens, who establish colonies after surviving diapause, responded most consistently to variation in winter climate conditions and less consistently to floral resources or the abundance of the previous life stage. That is, we observed more queens with earlier snowmelt. In our subalpine ecosystem queens spend 8–9 months underground in winter diapause, which is at the longer end of the known range for bumble bees (6–9 months; Alford, 1969). Earlier springs occur after shorter winters of lower snowfall, meaning that diapausing queens spend less time dependent on their macronutrient stores, which should improve overwintering survival (Beekman et al., 1998). Critically, this survival effect may override any positive effect of floral food resources or reproductive output in the previous year. On the other hand, survival of queens in laboratory settings was strongly related to nutrient acquisition before diapause (Treanore & Amsalem, 2020; Woodard et al., 2019), and overwintered queen abundance was related to floral resources in the preceding season in some field studies (Carvell et al., 2017; Inari et al., 2012). Consistent with this, overwintering success was positively related to previous-year resource availability—in addition to snowmelt timing—for two of our study species (*B. appositus* and *B. bifarius*). Nevertheless, in ecosystems with long and harsh winters, such conditions are likely to be a dominant driver of animal overwintering survival and thus may be particularly important for understanding population trends (e.g. Ozgul et al., 2010). For example, in other snow-dominated mountain ecosystems, population abundance of small mammals was most strongly affected by winter conditions compared with other alternative mechanisms, including resource availability and phenology (Johnston et al., 2021).

The abundance of workers, representing colony growth, was positively associated with floral resource abundance in all but one of our study species, as also reported for other bumble bees (e.g. Crone & Williams, 2016; Herrmann et al., 2017; Mola et al., 2020). More resources allow colonies to produce more workers, thereby increasing their potential to produce more reproductive bees. Furthermore, the absence of any relationship between summer climate conditions (temperature and precipitation) and worker abundance suggests that the variation experienced over our study is within tolerable limits for colony growth. Most of our study species nest below-ground (Williams et al., 2014), which should buffer colonies from extreme summer temperatures. That the previous life stage predicts worker abundance in only half of our species suggests that the survival and establishment of queens need not be related to worker production. Successful colony establishment by overwintered bumble bee queens appears to be low in the wild (Goulson, 2010), which may decouple the recruitment stage from colony growth later in the more favourable parts of the growing season. Nevertheless, for three species (*B. flavifrons*, *B. occidentalis*, and *B. rufocinctus*) we observed positive covariation of workers with the abundance of overwintered queens, suggesting that when conditions are favourable for queens they can also translate into positive effects on colony growth. In contrast, for one species (*B. bifarius*), we observed a negative relationship between queen and worker abundance, illustrating that at least for some species, when conditions are favourable for queens they are not so favourable for colony growth.

Reproductive output (represented as the abundance of male bees) exhibited consistent and positive covariation with the abundance of workers in all species. This agrees with the intuitive premise that resource-dependent growth and size predict eventual reproductive output (e.g. Crone & Williams, 2016; Kingsolver & Huey, 2008). Indeed, we observed that reproductive output was also positively affected by food resource abundance for three species, *B. appositus*, *B. flavifrons*, and *B. rufocinctus*. Reproductive output also increased with warmer and drier summer conditions for *B. flavifrons*, *B. insularis*, and *B. mixtus*—a pattern reported for another bumble bee species (*B. terrestris*; Zaragoza-Trello et al., 2021; but see Holland & Bourke, 2015), as well as other animals (e.g. Kingsolver & Huey, 2008; Wells et al., 2022). Although extreme temperatures associated with climate change may adversely affect animals in a variety of ways (CaraDonna et al., 2018; Martinet et al., 2021; Pörtner & Farrell, 2008; Spooner et al., 2018), the temperatures experienced in our system were likely within a favourable range for bumble bee foraging activity (Kenna et al., 2021). We also note that our estimate of reproductive output does not incorporate autumn queens—a life stage for which we have sparse data (Table S2). However, the increased abundance of male bees with higher worker abundance suggests an increased investment in reproduction which should also increase the production of autumn queens, at least to some extent (e.g. Crone & Williams, 2016; Herrmann et al., 2017). Nevertheless, for many species, reproductive output tended not to influence the abundance of queens in the following season; this lack of a relationship indicates that favourable conditions for reproduction do not necessarily translate into meaningful effects on recruitment, although the ultimate consequence for population dynamics remains an open question.

Although our 7-year study encompassed considerable variation in abiotic and biotic conditions, more years of data are necessary to clarify some relationships, and indeed, some patterns may shift qualitatively with a longer temporal perspective (e.g. Thomson, 2019). For example, we suspect the negative relationship between the abundance of *B. appositus* overwintered queens and reproductive output in the previous year to become positive or disappear with more years of study, because the inclusion of 2021 data reversed a previously weakly positive relationship (2021 had the highest queen numbers for *B. appositus* while reproductive output was especially low in 2020). We do expect most relationships reported here to remain qualitatively (if not quantitatively) similar, so long as climate conditions remain within the range of variation we witnessed (which approximates that of the last 50 years, e.g. Cordes et al., 2020). But this is far from certain: the coming decades in our study region are predicted to become increasingly warmer and drier, with less winter snow and a greater frequency of extreme events (IPCC, 2021). As such, nonlinear or threshold responses (Iler et al., 2013; Kingsolver & Huey, 2008) might occur as organisms encounter conditions outside the historical range (e.g. CaraDonna et al., 2018; Martinet et al., 2021).

Predicting population outcomes under environmental change requires not only an understanding of how different factors influence each part of an organism's life cycle but also which life stages—and thus vital rates—most strongly influence population growth (e.g. Caswell, 2001; Crouse et al., 1987; McLean et al., 2016). Long-term climate change in our study region is resulting in less winter snowpack and earlier spring snowmelt timing, which on average, leads to shorter winters and fewer floral resources produced during the growing season (Figure S1; Cordes et al., 2020; Ogilvie et al., 2017). Because shorter winters appear to favour the survival of overwintered queens (Figure 3), we hypothesise that these same conditions are likely unfavourable for colony growth and reproduction over the long-term because lower input of snowmelt water and longer growing seasons can reduce densities of floral food resources (Figure S1; CaraDonna et al., 2014; Ogilvie et al., 2017). However, despite these potentially contrasting effects, the lack of covariation between the abundance of workers and queens for many species, as well as the lack of covariation between queens and reproductive output in the previous year, suggests that the positive and negative effects experienced by each life stage under climate change will often remain isolated to that stage. Although successful establishment of colonies by overwintered queens in spring is hypothesised to be a critical event for bumble bee population dynamics (Woodard et al., 2019), it remains unclear whether the benefits of warmer and shorter winters for queen survival will compensate for the expected negative effects of reduced floral resources on colony growth and reproduction. Indeed, successful reproduction and recruitment for shorter-lived organisms (animals and plants) is an important life stage for population dynamics (Franco & Silvertown, 2004; McLean et al., 2016).

Many bumble bee species are declining world-wide (Cameron & Sadd, 2020), and our study provides insight on drivers that may contribute to their population declines. Among our focal species, *B. occidentalis* is of greatest conservation concern because it was once common and widespread but has declined rapidly across its range in recent decades (Cameron et al., 2011; Graves et al., 2020). At broad geographic scales, declines in *B. occidentalis* populations are potentially driven by a combination of climate change, parasites, pesticides, and habitat loss. In our montane study system, which is mostly unaffected by these stressors except for climate change, *B. occidentalis* abundance was affected by climate conditions and the abundance of previous life stages across its life cycle (Figure 3; Figure S7). Given that two of the sequential life stages covary for this species (overwintered queens and workers, and workers and males), effects during specific life stages can precipitate to others, highlighting that conservation efforts should consider how multiple factors affect each life stage across the life cycle.

Our long-term study demonstrates that different demographic parameters throughout the bumble bee life cycle show distinct responses to variation in the abiotic and biotic environment. The life-cycle approach we have taken with an assemblage of coexisting bumble bees illustrates that important details about demography can be overlooked without consideration of life-stage-specific responses. Our findings also provide evidence that pollinator population declines are unlikely to be driven by factors affecting only a single life stage, although more research is needed to understand which life stages have the strongest effects on population growth rates. Ultimately, it is life-stage-specific responses that shape population outcomes, not only for bumble bees and other animal pollinators, but for many other organisms living in seasonal environments.

AUTHOR CONTRIBUTIONS

Jane E. Ogilvie and Paul J. CaraDonna collected the data; Jane E. Ogilvie established the long-term monitoring project; Jane E. Ogilvie and Paul J. CaraDonna conceived the study, analysed the data, wrote the manuscript and gave their approval for publication.

ACKNOWLEDGEMENTS

We thank the many people who have assisted with flower counting over the years, especially Justin Bain, Alyssum Cohen, Jackie Fitzgerald, Kaitlin Griffith, Gwen Kirschke, Kyle Spells, and Daniele Wiley. We thank Will Petry and Amy Iler for advice on statistical analyses, and Nick Waser, Amy Iler, John Mola, the Iler and CaraDonna Lab Group, and two reviewers for constructive feedback on the manuscript. We thank billy barr for collection of long-term climate data and Jennie Reithel for logistical support at the RMBL. Funding was provided in part by the RMBL, the Chicago Botanic Garden, Northwestern University, the Western North American Naturalist, and the National Science Foundation (DEB-1754518 to P.J.C.). We acknowledge that our field research was conducted on the ancestral and unceded land of the Tabeguache band of the Núu-agha-tuvu-pu (Ute) people.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on the Open Science Framework https://doi.org/10.17605/OSF.IO/JB7ZP (Ogilvie & CaraDonna, 2022).

ORCID

Jane E. Ogilvie https://orcid.org/0000-0001-8546-0417
Paul J. CaraDonna https://orcid.org/0000-0003-3517-9090

REFERENCES

Alford, D. V. (1969). A study of the hibernation of bumblebees (Hymenoptera: Bombidae) in southern England. *Journal of Animal Ecology*, *38*(1), 149–170. https://doi.org/10.2307/2743

Beekman, M., Stratum, P., & Lingeman, R. (1998). Diapause survival and post-diapause performance in bumblebee queens (*Bombus terrestris*). *Entomologia Experimentalis et Applicata*, *89*(3), 207–214. https://doi.org/10.1046/j.1570-7458.1998.00401.x

Boggs, C. L., & Inouye, D. W. (2012). A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters*, *15*(5), 502–508. https://doi.org/10.1111/j.1461-0248.2012.01766.x

Boyce, M. S., Haridas, C. V., Lee, C. T., & NCEAS Stochastic Demography Working Group. (2006). Demography in an increasingly variable world. *Trends in Ecology & Evolution*, *21*(3), 141–148. https://doi.org/10.1016/j.tree.2005.11.018

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in north American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 662–667. https://doi.org/10.1073/pnas.1014743108

Cameron, S. A., & Sadd, B. M. (2020). Global trends in bumble bee health. *Annual Review of Entomology*, *65*(1), 209–232. https://doi.org/10.1146/annurev-ento-011118-111847

CaraDonna, P. J., Cunningham, J. L., & Iler, A. M. (2018). Experimental warming in the field delays phenology and reduces body mass, fat content and survival: Implications for the persistence of a pollinator under climate change. *Functional Ecology*, *32*(10), 2345–2356. https://doi.org/10.1111/1365-2435.13151

CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(13), 4916–4921. https://doi.org/10.1073/pnas.1323073111

Carvell, C., Bourke, A. F. G., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., Redhead, J. W., Sumner, S., Wang, J., & Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*, 547–549. https://doi.org/10.1038/nature21709

Caswell, H. (2001). *Matrix population models. Construction, analysis, and interpretation* (2nd ed.). Sinauer.

Cordes, L. S., Blumstein, D. T., Armitage, K. B., CaraDonna, P. J., Childs, D. Z., Gerber, B. D., Martin, J. G. A., Oli, M. K., & Ozgul, A. (2020). Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(30), 18119–18126. https://doi.org/10.1073/pnas.1918584117

Crone, E. E., Ellis, M. M., Morris, W. F., Stanley, A., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T. N., Knight, T. M., Lesica, P., Oostermeijer, G., Quintana-Ascencio, P. F., Ticktin, T., Valverde, T., Williams, J. L., Doak, D. F., Ganesan, R., Mceachern, K., Thorpe, A. S., & Menges, E. S. (2013). Ability of matrix models to explain the past and predict the future of plant populations. *Conservation Biology*, *27*(5), 968–978. https://doi.org/10.1111/cobi.12049

Crone, E. E., & Williams, N. M. (2016). Bumble bee colony dynamics: Quantifying the importance of land use and floral resources for colony growth and queen production. *Ecology Letters*, *19*(4), 460–468. https://doi.org/10.1111/ele.12581

Crossley, M. S., Smith, O. M., Berry, L. L., Phillips-Cosio, R., Glassberg, J., Holman, K. M., Holmquest, J. G., Meier, A. R., Varriano, S. A., McClung, M. R., Moran, M. D., & Snyder, W. E. (2021). Recent climate change is creating hotspots of butterfly increase and decline across North America. *Global Change Biology*, *27*(12), 2702–2714. https://doi.org/10.1111/gcb.15582

Crouse, D., Crowder, L., & Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, *68*(5), 1412–1423. https://doi.org/10.2307/1939225

Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, *104*(2), 292–305. https://doi.org/10.1111/1365-2745.12523

Elliott, S. E. (2009). Subalpine bumble bee foraging distances and densities in relation to flower availability. *Environmental Entomology*, *38*(3), 748–756. https://doi.org/10.1603/022.038.0327

Ellison, A. M. (2004). Bayesian inference in ecology. *Ecology Letters*, *7*(6), 509–520. https://doi.org/10.1111/j.1461-0248.2004.00603.x

Elton, C. (1927). *Animal ecology*. Macmillan Company.

Fay, R., Hamel, S., van de Pol, M., Gaillard, J. M., Yoccoz, N. G., Acker, P., Authier, M., Larue, B., Le Coeur, C., Macdonald, K. R., Nicol-Harper, A., Barbraud, C., Bonenfant, C., Van Vuren, D. H., Cam, E., Delord, K., Gamelon, M., Moiron, M., Pelletier, F., … Sæther, B. E. (2022). Temporal correlations among demographic parameters are ubiquitous but highly variable across species. *Ecology Letters*, *25*(7), 1640–1654. https://doi.org/10.1111/ele.14026

Franco, M., & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, *85*(2), 531–538. https://doi.org/10.1890/02-0651

Fretwell, S. D. (1972). *Populations in a seasonal environment*. Princeton University Press.

Geib, J. C., Strange, J. P., & Galen, C. (2015). Bumble bee nest abundance, foraging distance, and host-plant reproduction: Implications for management and conservation. *Ecological Applications*, *25*(3), 768–778. https://doi.org/10.1890/14-0151.1

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. *The American Statistician*, *73*(3), 307–309. https://doi.org/10.1080/00031305.2018.1549100

Goodrich, B., Gabry, J., Ali, I., & Brilleman, S. (2022). *Rstanarm: Bayesian applied regression modeling via Stan*. R package version 2.21.3. https://mc-stan.org/rstanarm/

Goulson, D. (2010). *Bumblebees: Behaviour, ecology, and conservation* (2nd ed.). Oxford University Press.

Graves, T. A., Janousek, W. M., Gaulke, S. M., Nicholas, A. C., Keinath, D. A., Bell, C. M., Cannings, S., Hatfield, R. G., Heron, J. M., Koch, J. B., Loffland, H. L., Richardson, L. L., Rohde, A. T., Rykken, J., Strange, J. P., Tronstad, L. M., & Sheffield, C. S. (2020). Western bumble bee: Declines in the continental United States and range-wide information gaps. *Ecosphere*, *11*(6), e03141. https://doi.org/10.1002/ecs2.3141

Griffith, A. B., Salguero-Gómez, R., Merow, C., & McMahon, S. (2016). Demography beyond the population. *Journal of Ecology*, *104*(2), 271–280. https://doi.org/10.1111/1365-2745.12547

Herrmann, J. D., Haddad, N. M., & Levey, D. J. (2017). Testing the relative importance of local resources and landscape connectivity on *Bombus impatiens* (Hymenoptera, Apidae) colonies. *Apidologie*, *48*(4), 545–555. https://doi.org/10.1007/s13592-017-0499-1

Holland, J. G., & Bourke, A. F. G. (2015). Colony and individual life-history responses to temperature in a social insect pollinator. *Functional Ecology*, *29*(9), 1209–1217. https://doi.org/10.1111/1365-2435.12480

Iler, A. M., Høye, T. T., Inouye, D. W., & Schmidt, N. M. (2013). Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120489. https://doi.org/10.1098/rstb.2012.0489

Iles, D. T., Rockwell, R. F., & Koons, D. N. (2019). Shifting vital rate correlations alter predicted population responses to increasingly variable environments. *The American Naturalist*, *193*(3), E57–E64.

Inari, N., Hiura, T., Toda, M. J., & Kudo, G. (2012). Pollination linkage between canopy flowering, bumble bee abundance and seed production of understorey plants in a cool temperate forest. *Journal of Ecology*, *100*(6), 1534–1543. https://doi.org/10.1111/j.1365-2745.2012.02021.x

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, *89*(2), 353–362. https://doi.org/10.1890/06-2128.1

IPCC (2007). *Climate change 2007: Synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change* [Core Writing Team, R. K. Pachauri, & A. Reisinger (Eds.)]. IPCC.

IPCC (2021). *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* [V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.)]. Cambridge University Press.

Iserbyt, S., & Rasmont, P. (2012). The effect of climatic variation on abundance and diversity of bumblebees: A ten years survey in a mountain hotspot. *Annales de La Société Entomologique de France (N.S.)*, *48*(3–4), 261–273. https://doi.org/10.1080/00379271.2012.10697775

Johnston, A. N., Christophersen, R. G., Beever, E. A., & Ransom, J. I. (2021). Freezing in a warming climate: Marked declines of a subnivean hibernator after a snow drought. *Ecology and Evolution*, *11*(3), 1264–1279. https://doi.org/10.1002/ece3.7126

Kenna, D., Pawar, S., & Gill, R. J. (2021). Thermal flight performance reveals impact of warming on bumblebee foraging potential. *Functional Ecology*, *35*(11), 2508–2522. https://doi.org/10.1111/1365-2435.13887

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, *10*(2), 251–268.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Martinet, B., Dellicour, S., Ghisbain, G., Przybyla, K., Zambra, E., Lecocq, T., Boustani, M., Baghirov, R., Michez, D., & Rasmont, P. (2021). Global effects of extreme temperatures on wild bumblebees. *Conservation Biology*, *35*(5), 1507–1518. https://doi.org/10.1111/cobi.13685

McLean, N., Lawson, C. R., Leech, D. I., & van de Pol, M. (2016). Predicting when climate-driven phenotypic change affects population dynamics. *Ecology Letters*, *19*(6), 595–608. https://doi.org/10.1111/ele.12599

Mola, J. M., Miller, M. R., O'Rourke, S. M., & Williams, N. M. (2020). Wildfire reveals transient changes to individual traits and population responses of a native bumble bee *Bombus vosnesenskii*. *Journal of Animal Ecology*, *89*(8), 1799–1810. https://doi.org/10.1111/1365-2656.13244

Nogués-Bravo, D., Araújo, M. B., Errea, M. P., & Martínez-Rica, J. P. (2007). Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change*, *17*(3–4), 420–428. https://doi.org/10.1016/j.gloenvcha.2006.11.007

Ogilvie, J. E., & CaraDonna, P. J. (2022). Data from: The shifting importance of abiotic and biotic factors across the life cycles of wild

pollinators. *Open Science Framework*. https://doi.org/10.17605/OSF.IO/JB7ZP
Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, *21*, 75–82. https://doi.org/10.1016/j.cois.2017.05.015
Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., & Irwin, R. E. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecology Letters*, *20*(12), 1507–1515. https://doi.org/10.1111/ele.12854
Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x
Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*(7305), 482–485. https://doi.org/10.1038/nature09210
Pelletier, L., & McNeil, J. N. (2003). The effect of food supplementation on reproductive success in bumblebee field colonies. *Oikos*, *103*(3), 688–694. https://doi.org/10.1034/j.1600-0706.2003.12592.x
Pleasants, J. M. (1981). Bumblebee response to variation in nectar availability. *Ecology*, *62*(6), 1648–1661. https://doi.org/10.2307/1941519
Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, *322*(5902), 690–692. https://doi.org/10.1126/science.1163156
Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588
R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/
Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, *82*(1), 275–285. https://doi.org/10.1111/j.1365-2656.2012.02029.x
Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, *56*(1), 293–312. https://doi.org/10.1146/annurev-ento-120709-144802
Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, *172*, 138–145. https://doi.org/10.1016/j.biocon.2014.02.027
Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, *367*(6478), 685–688. https://doi.org/10.1126/science.aax8591
Spiesman, B. J., Bennett, A., Isaacs, R., & Gratton, C. (2017). Bumble bee colony growth and reproduction depend on local flower dominance and natural habitat area in the surrounding landscape. *Biological Conservation*, *206*, 217–223. https://doi.org/10.1016/j.biocon.2016.12.008
Spooner, F. E., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*, *24*(10), 4521–4531. https://doi.org/10.1111/gcb.14361
Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, *19*(10), 1247–1255. https://doi.org/10.1111/ele.12659
Thomson, J. D. (2019). Progressive deterioration of pollination service detected in a 17-year study vanishes in a 26-year study. *New Phytologist*, *224*(3), 1151–1159. https://doi.org/10.1111/nph.16078
Treanore, E., & Amsalem, E. (2020). The effect of intrinsic physiological traits on diapause survival and their underlying mechanisms in an annual bee species *Bombus impatiens*. *Conservation Physiology*, *8*(1), coaa103. https://doi.org/10.1093/conphys/coaa103
Vesterlund, S.-R., & Sorvari, J. (2014). Longevity of starved bumblebee queens (Hymenoptera: Apidae) is shorter at high than low temperatures. *European Journal of Entomology*, *111*(2), 217–220. https://doi.org/10.14411/eje.2014.035
Wells, C. P., Barbier, R., Nelson, S., Kanaziz, R., & Aubry, L. M. (2022). Life history consequences of climate change in hibernating mammals: A review. *Ecography*, *2022*(6), e06056. https://doi.org/10.1111/ecog.06056
White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*, *83*(3), 227–248. https://doi.org/10.1111/j.1469-185X.2008.00041.x
Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). *Bumble bees of North America: An identification guide*. Princeton University Press. https://doi.org/10.1515/9781400851188
Wong, L. H., & Forrest, J. R. K. (2021). The earlier the better? Nesting timing and reproductive success in subalpine cavity-nesting bees. *Journal of Animal Ecology*, *90*(5), 1353–1366. https://doi.org/10.1111/1365-2656.13460
Woodard, S. H., Duennes, M. A., Watrous, K. M., & Jha, S. (2019). Diet and nutritional status during early adult life have immediate and persistent effects on queen bumble bees. *Conservation Physiology*, *7*(1), coz048. https://doi.org/10.1093/conphys/coz048
Woodard, S. H., & Jha, S. (2017). Wild bee nutritional ecology: Predicting pollinator population dynamics, movement, and services from floral resources. *Current Opinion in Insect Science*, *21*, 83–90. https://doi.org/10.1016/j.cois.2017.05.011
Zaragoza-Trello, C., Vilà, M., Botías, C., & Bartomeus, I. (2021). Interactions among global change pressures act in a non-additive way on bumblebee individuals and colonies. *Functional Ecology*, *35*(2), 420–434. https://doi.org/10.1111/1365-2435.13703

SUPPORTING INFORMATION

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

How to cite this article: Ogilvie, J. E., & CaraDonna, P. J. (2022). The shifting importance of abiotic and biotic factors across the life cycles of wild pollinators. *Journal of Animal Ecology*, *91*, 2412–2423. https://doi.org/10.1111/1365-2656.13825