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RESEARCH ARTICLE

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Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb

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Abstract

1. Despite a global footprint of shifts in flowering phenology in response to climate change, the reproductive consequences of these shifts are poorly understood. Furthermore, it is unknown whether altered flowering times affect plant population viability.
2. We examine whether climate change-induced earlier flowering has consequences for population persistence by incorporating reproductive losses from frost damage (a risk of early flowering) into population models of a subalpine sunflower (*Helianthella quinquenervis*). Using long-term demographic data for three populations that span the species' elevation range (8–15 years, depending on the population), we first examine how snowmelt date affects plant vital rates. To verify vital rate responses to snowmelt date experimentally, we manipulate snowmelt date with a snow removal experiment at one population. Finally, we construct stochastic population projection models and Life Table Response Experiments for each population.
3. We find that populations decline ($\lambda_s < 1$) as snowmelt dates become earlier. Frost damage to flower buds, a consequence of climate change-induced earlier flowering, does not contribute strongly to population declines. Instead, we find evidence that negative effects on survival, likely due to increased drought risk during longer growing seasons, drive projected population declines under earlier snowmelt dates.
4. *Synthesis*. Shifts in flowering phenology are a conspicuous and important aspect of biological responses to climate change, but here we show that the phenology of reproductive events can be unreliable measures of threats to population persistence, even when earlier flowering is associated with substantial reproductive losses. Evidence for shifts in reproductive phenology, along with scarcer evidence that these shifts actually influence reproductive success, are valuable but can

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paint an incomplete and even misleading picture of plant population responses to climate change.

KEYWORDS
demography, drought, earlier flowering, environmental driver, matrix model, phenological shift, population dynamics, snowmelt

1 | INTRODUCTION

Phenology is important for survival and reproduction but is rarely included in models of population dynamics (Elzinga et al., 2007; Forrest & Miller-Rushing, 2010). As a result, very little is known about the role that phenology plays in population viability (McLean, Lawson, Leech, & Pol, 2016), which is especially relevant given anthropogenic climate change and its effect on phenological events in a diversity of taxa (Parmesan & Yohe, 2003; Root et al., 2003; Thackeray et al., 2016). Correlational evidence from long-term studies suggests that phenology could influence population dynamics, because species whose phenological events are unresponsive to climate change exhibit decreases in abundance (Møller, Rubolini, & Lehikoinen, 2008; Willis, Ruhfel, Primack, Miller-Rushing, & Davis, 2008). Specifically, species that fail to shift their phenological events may be exposed to novel abiotic or biotic environments that negatively affect their performance, because they are not tracking preferred environmental conditions (Cleland et al., 2012). However, species that do shift their phenological events in response to climate change can also be exposed to novel environments, such as drought or increased frost risk, which can negatively affect survival and reproduction (Franks, Sim, & Weis, 2007; Inouye, 2008). Whether a phenological shift results in exposure to novel environmental conditions or not will depend on both the degree to which different aspects of climate are changing and the degree to which phenology is responsive to changing environmental cues.

Climate change-induced phenological shifts could therefore impose a combination of positive and negative effects on various aspects of species' life cycles, making it difficult to intuit the consequences for population persistence. Indeed, the few studies that develop more nuanced models of population dynamics find evidence for population growth, decline or no change in response to phenological shifts under climate change (Boggs & Inouye, 2012; Ozgul et al., 2010; Reed, Grotan, Jenouvrier, Saether, & Visser, 2013). It is often assumed that effects of phenological shifts on demographic vital rates—survival, growth and reproduction—will affect population persistence, but this assumption is rarely tested (McLean et al., 2016). It is important to test this assumption because changes in demographic vital rates often affect population growth rate unequally (i.e. finite rate of increase, λ; Caswell, 2001). The sensitivity of population growth rate to changes in each vital rate and the sensitivity of each vital rate to phenological cues will collectively determine the overall effect on population persistence. This common demographic property helps to explain the diversity of responses of animal populations to phenological shifts. For example, a direct positive effect of a phenological shift on a high-sensitivity vital rate leads to substantial increases in population size (Ozgul et al., 2010).

Shifts in flowering phenology are widely documented biological responses to global climate change (CaraDonna, Iler, & Inouye, 2014; Parmesan, 2006) and have been hypothesized to affect plant population persistence because the timing of flowering can influence reproductive success (Elzinga et al., 2007). However, phenological shifts have typically been studied in isolation from the rest of the plant life cycle because of a shortage of data (Miller-Rushing, Hoye, Inouye, & Post, 2010), leaving open the question of whether shifted flowering times under climate change actually have consequences for population persistence. Furthermore, there are surprisingly few known cases of reproductive consequences of shifted flowering times (Rafferty, CaraDonna, Burkle, Iler, & Bronstein, 2013). Even if reproductive consequences exist, a reproductive loss may not necessarily translate to an effect on population growth rate. First, plant species with certain life-history traits should generally be buffered from reproductive losses; for example, population growth rates in iteroparous perennial plant species tend to be more sensitive to perturbations in survival and growth rather than reproduction (Franco & Silvertown, 2004; Silvertown, Franco, Pisanty, & Mendoza, 1993). Second, climate change may have positive effects on other vital rates, which could compensate for reproductive losses to buffer against population decline (Doak & Morris, 2010).

Here, we investigate the extent to which climate change-induced earlier flowering can threaten population viability in three populations of a subalpine perennial sunflower, *Helianthella quinquenervis* (hereafter *Helianthella*). Earlier spring snowmelt is an important dimension of climate change in high-elevation and high-latitude ecosystems, areas that are experiencing rapid climate change (Høye, Post, Meltofte, Schmidt, & Forchhammer, 2007; Inouye & Wielgolaski, 2013; Steltzer, Landry, Painter, Anderson, & Ayres, 2009). Many plant species flower earlier as spring snowmelt dates become earlier (Høye et al., 2007; Iler, Hoye, Inouye, & Schmidt, 2013), and early initiation of flower buds can increase susceptibility to damage by frost in some species. In *Helianthella*, early flowering can result in total reproductive failure in some years (Figure 1a,b; Inouye, 2008). Therefore, we examine the effect of flowering phenology on population persistence by incorporating this well-documented consequence of early snowmelt and early flowering for *Helianthella*—frost damage—into projections of reproductive success.

We use long-term records of snowmelt date and demographic vital rates, in addition to a snow removal experiment, to determine



FIGURE 1 (a, b) Early initiation of *Helianthella quinquenervis* flower buds in years with early snowmelt can result in frost damage and (c) an example of the range of plant size. (a) Frost damage occurs when flower buds are relatively small and (b) results in zero seed production. (c) Above-ground meristems, or rosettes, are counted to represent plant size. Photos by D. Inouye [Colour figure can be viewed at wileyonlinelibrary.com]

how *Helianthella* vital rates respond to earlier spring snowmelt. We test four primary hypotheses related to the potential effects of early snowmelt on plant vital rates: (a) increased water stress, (b) longer growing seasons, (c) increased frost damage and (d) demographic compensation. One reason for earlier snowmelt is less winter snowfall (Inouye, Morales, & Dodge, 2002), resulting in lower water availability during the growing season when snowmelt is early compared to when snowmelt is late (Sloat, Henderson, Lamanna, & Enquist, 2015). Under the water stress hypothesis, all vital rates (survival, growth and reproduction) may decrease as a direct response to early snowmelt. Alternatively, longer growing seasons under early snowmelt conditions (Ernakovich et al., 2014) may lead to increased vegetative growth because there are more days over which plants can photosynthesize and grow. As outlined above, we expect early snowmelt to lead to increased frost damage to developing flower buds, negatively affecting reproduction. Finally, compensatory responses in reproduction are common in perennial plants (Villellas, Doak, García, & Morris, 2015), so that there may also be more flowering plants and increased investment in flowers the year following early snowmelt. After resolving these vital rate responses to earlier snowmelt, we ask: (a) does earlier snowmelt affect population growth rates in *Helianthella*? If so, (b) through which vital rates does earlier snowmelt most strongly affect population growth rate?

2 | MATERIALS AND METHODS

2.1 | Study sites and species

This study was conducted in the Elk Range of the Colorado Rocky Mountains in habitats ranging from subalpine to alpine. The mean temperature for this study region during the growing season (June–August) is 12.7°C, with a mean minimum temperature of 2.5°C, a mean maximum temperature of 23.0°C and mean total precipitation of 4.6 cm (averages are from 1910 through 2012, the final year of the study). Climate data come from an NOAA (National Oceanic & Atmospheric Administration, USA) weather station in Crested Butte, Colorado, USA, which is the nearest NOAA weather station to our study populations.

Helianthella quinquenervis (Asteraceae) is a long-lived, iteroparous perennial sunflower (Inouye & Taylor, 1979). Its range spans western North America (*ca*. 2,700–3,500 m a.s.l.), with southern-most populations in northern Mexico and northern-most populations in the northern USA (Weber, 1952). *Helianthella* reproduces by seed and produces vegetative meristems from existing roots (rosettes; Figure 1c). A rosette contains 2–8 leaves and is our unit of plant size; an individual can include many rosettes (up to 104; Figure 1c).

The demographic vital rates of three populations of *Helianthella* that span its elevation range in the Elk Range of the Colorado Rockies have been studied for 14–15 years in permanent plots (low: 1999–2012; mid: 1998–2012; high: 1999–2012). All *Helianthella* plants within plots were tagged with a unique identification number and mapped. There were two 1.5 m × 10 m study plots at the low-elevation population that contained on average 700 plants per year (Horse Ranch Park; 2,703 m a.s.l.; 38°51.774′N; 107°09.556′W), six 1.5 m × 5 m plots at the mid-elevation population that contained on average 752 plants per year (Rocky Mountain Biological Laboratory; 2,886 m a.s.l.; 38°57.5′N, 106°59.3′W), and four 1.0 m × 5 m plots at the high-elevation population that contained on average 254 plants per year (Virginia Basin; 3,407 m a.s.l.; 38°58.612′N; 106°58.690′W). Pocket gophers destroyed virtually all plant ID tags in the high-elevation population in 2003 and 2004, so we used data from 2005–2012 for this population. We refer to the populations as low, mid, and high but cannot draw inferences about effects of elevation because there was one study population at each elevation.

Snowmelt date has been measured with HOBO data loggers (Onset Computer Corporation, Massachusetts, USA) at the low- and high-elevation populations since 2008 and at the mid-elevation population since 2007. Spikes in light level and temperature in the spring defined snowmelt date. Snowmelt date has also been recorded in a 5 m × 5 m plot *ca*. 1.5 km from the study site of the mid-elevation population from 1975 to present, and was defined as the first date of bare ground in the spring. We used this long-term snowmelt dataset

for all analyses because it overlaps with the initial years of the demographic datasets, and because annual snowmelt date at each site was highly correlated with the long-term dataset (low: $r = 0.97$; mid: $r = 0.99$; high: $r = 0.97$). Snowmelt date as measured from the long-term dataset is advancing as the climate changes (Anderson, Inouye, McKinney, Colautti, & Mitchell-Olds, 2012). Earlier snowmelt dates were correlated with longer growing seasons ($r = -0.82$; $p < 0.0001$; $n = 39$ years), defined as the number of days between snowmelt and the first day on which temperature drops below 25°F at a NOAA weather station *ca*. 9 km from the mid-elevation population (Crested Butte, CO, USA). However, snowmelt date was also strongly positively correlated with total winter snowfall ($r = 0.90$, $p < 0.0001$, $n = 40$ years), so that there was less water available during the growing season under early snowmelt.

2.2 | Long-term demographic study

The size (rosette number) and reproductive status of all individuals in each plot were assessed annually. Connections among rosettes can be felt just below the soil surface and were excavated with fingers to assign connected rosettes to a single individual. Following a previous study (Inouye, 2008), we counted the number of flowering stalks that were aborted because of frost, the number of flowering stalks that were undamaged, and the number of capitula on each undamaged stalk. Typically, the entire flower stalk was aborted in the event of frost damage, sometimes when the stalks were only a few cm tall. Plants were considered dead if they were missing for at least 2 years (e.g. if a plant was missing in 2010 and 2011, then it was scored as dead in 2010). Seedlings were distinct as small two-leafed plants, often with visible cotyledons, and were counted each year. Patterns of recruitment strongly suggested the absence of a seed bank; high seedling densities followed years of high flower production, and almost no new seedlings were observed following years of high frost damage and low flower production (e.g. there were zero seedlings following years of zero seed production in four of five plot-years). In 2011, we collected 150 capitula from 74 individual plants of various sizes (1–34 rosettes) at the mid-elevation population and counted the number of seeds per capitulum. This average value of seed production was used to estimate recruitment rates for all populations. Previous research found no evidence that *Helianthella* seed production per capitulum varied across a similar elevation gradient that included two of the same sites as the current study (Davis, 2001).

2.3 | Vital rate estimation

Methods for vital rate estimation and population modelling closely followed our previous study (Compagnoni et al., 2016). We used the long-term demographic data to fit statistical models for six individual-level processes ("vital rates") that collectively determined population dynamics: (a) survival, (b) growth, (c) flowering (yes or no), (d) fertility of flowering plants (total # flowering stalks), (e) flower stalk abortion rate (flower viability), and (f) seedling recruitment (detailed methods are available in Appendix S1). The first four vital rates were size-dependent. For the size-dependent vital rates, we used the natural logarithm of rosette number as the predictor variable, which facilitated model convergence and fit. Models included random year effects to accommodate temporal environmental stochasticity. There was enough interannual variation in snowmelt date, included in the models as a fixed effect (below), so that random year effects represented interannual variability that was unrelated to snowmelt. In preliminary analyses, one-rosette seedlings had different growth and survival rates than older one-rosette plants. We therefore modelled seedling vital rates separately from the rest of the size distribution.

2.4 | Model selection

All models were fit in a hierarchical Bayesian framework in Stan using R package 'RStan' (Stan Development Team, 2017). We fit models that included site (low-, mid- and high-elevation populations) and snowmelt date as predictor variables. Candidate models included all combinations of additive and interactive effects of these two variables, including two- and three-way interactions with size for the size-dependent vital rates (Table S1). Candidate models included two alternatives for snowmelt timing: given demographic data collected in year $t + 1$, we considered the timing of snowmelt in years t and $t + 1$ as exclusive alternatives to examine lagged effects of climate on vital rates (Dalgleish, Koons, Hooten, Moffet, & Adler, 2011). This allowed us to consider different biological hypotheses for how snowmelt may affect vital rates. For example, if snowmelt timing affected plant size via the length of the growing season, we would expect the best-fitting vegetative growth model (change in size from year t to $t + 1$) to include timing of snowmelt in year t and not year $t + 1$. Site was not included as a factor for seedling survival because of too few data points at the high-elevation population. We therefore assumed a shared seedling survival function across populations (three candidate models testing for snowmelt effects; Table S1). Neither site nor snowmelt date were included in the analysis of recruitment because of poor model convergence when these factors were included (there were fewer data points to estimate recruitment vs. other vital rates).

We ran four 5,000-iteration Markov Chain Monte Carlo simulations, discarding the initial 1,000 iterations, which was sufficient to reach convergence for the vital rate parameters. Models were considered as converged if the Brooks and Gelman's potential scale reduction factor of each parameter was <1.1 (Brooks & Gelman, 1998). We used uninformative ('flat') prior probability distributions for all parameters. We assumed that random year effects were independent across vital rates, based on our previous findings that accounting for vital rate correlations in this and other perennial plant species does not modify prediction for population dynamics (Compagnoni et al., 2016).

We used the information criterion WAIC to quantify support for the candidate models (Hooten & Hobbs, 2015; Watanabe, 2010) using the loo package v.0.1.3 in R (Vehtari, Gelman, & Gabry, 2016). For all vital rates except survival, we used the statistical model with

the lowest WAIC score in population models. The snowmelt effect in the model with the lowest WAIC score for survival was inconsistent with our a priori hypotheses, predicting *higher* survival to year $t + 1$ under earlier snowmelt in year $t + 1$. It is unclear why more days from snowmelt to early July (the time of the census) compared to a year with later snowmelt—when there are fewer days between snowmelt and the census—would increase survival of plants from the previous year. In contrast, under the water stress hypothesis we expected to see *reduced* survival to year $t + 1$ in response to early snowmelt in year t. One post hoc explanation for a positive effect of early snowmelt on survival is that negative autocorrelation in snowmelt dates across years may drive this unexpected positive effect on survival because snowmelt in year t and $t + 1$ are negatively correlated ($r = -0.47$, $p = 0.074$). We therefore use the model with the second-lowest WAIC score for survival (ΔWAIC = 2.98; Table S1), in which earlier snowmelt in year t is associated with *reduced* survival to $t + 1$. This effect is also consistent with a 1-year lag effect of snowmelt on all other size-dependent vital rates (Results). Our snow removal experiment (Section 2.7) provides evidence that negative autocorrelation in snowmelt dates is unlikely to affect other vital rates, because all vital rate responses from the long-term observational study are consistent with vital rate responses to experimental snow removal (Figures 2 and 3).

To further address this uncertainty in model selection for adult survival, we examined survival data from a watering experiment that was conducted at the mid-elevation population in 2012. The year 2012 was dry, with the earliest snowmelt date and second-lowest annual precipitation (19 cm below average, from an NOAA weather station in Crested Butte, CO) from 1975–2012 (time span of long-term snowmelt record). We added 36 L (4.8 mm) of water per plot, twice per week during the dry period (4–27 June) to half of the long-term demography plots ($n = 3$ plots). Plots were also watered twice in July (12 and 27 July) for a total of 48 mm additional water per plot. Water was applied with watering cans, using water from a mountain spring that was the source of water for the Rocky Mountain Biological Laboratory, the location of the mid-elevation population. Water was added slowly so that water infiltrated the soil and did not visibly run off of the plot. We applied water in the evening to minimize evaporation. We focus on survival in the context of this watering experiment because our goal is to examine evidence to either support or refute our choice of survival model for use in population modelling; we can examine additional support for the other vital rates in our snow removal experiment (see Section 2.7 below). Treatment plots were paired with a control plot so that each pair was in a similar location within the meadow. The demographic census continued until present (2018) as described above, allowing us to use data from 2014 to confirm that plants missing in 2013 were dead. If early snowmelt reduces survival via drought effects, we expected to find higher survival in the watered versus the control plots in 2013. We used a generalized linear mixed effects model with treatment as a predictor and plot as a random intercept term to analyse survival rates to 2013. Watering in 2012 did not affect vital rates in 2012 (Table S2).

To compare the magnitude of snowmelt effects across vital rates, we estimated vital rate values for median-sized plants (three rosettes) at mean snowmelt date and at 1 week earlier than mean snowmelt date, in each population. We then calculated the proportional change in each vital rate [(early value – mean value)/mean value]. To estimate uncertainty around this value, proportional change was calculated 100 times across samples from the posterior distribution of vital rate coefficients from the best statistical model for each vital rate. This allowed us to compare more directly differences in the effects of snowmelt timing across vital rates, especially for the size-independent rate of flower stalk abortion.

2.5 | Stochastic population model

We built stochastic matrix population projection models, which are appropriate for a discrete size variable (# rosettes). The projection matrix was populated with generalized linear models (detailed methods are in Appendix S1). Because we found strong statistical support for population differences in the vital rates (Table S1), and because the size range differed across populations, we built separate models for each population (max size 104, 43 and 55 rosettes for low, mid and high populations, respectively) and thus a projection matrix of different dimensions. We truncated the maximum size distribution at the 0.99th percentile of observed plant sizes to keep the rare but largest plants from having undue influence on model projections. It is more conservative to use slightly smaller versus slightly larger than observed sizes because there were few data points to fit functions in the range of largest plants. We simulated population dynamics for 1,000 years to estimate the stochastic population growth rate (λ_S) and repeated the estimation of λ_S over a range of snowmelt dates; for λ_S at each snowmelt date, we then calculated 95% credible intervals, which incorporate stochasticity from the simulated population trajectories and parameter uncertainties from our fitted models (Appendix S1).

2.6 | Life table response experiment

We used regression-style life table response experiments (LTREs) to decompose the response of λ_S to snowmelt date into the contributions from each of the snowmelt-sensitive vital rates (Caswell, 2001, 2010). LTREs approximate the total demographic effect of snowmelt timing by weighting the response of each vital rate to snowmelt by the response of fitness to the vital rate (i.e. its sensitivity) and summing over vital rates. We fit snowmelt effects separately from random year effects, therefore assuming that environmental stochasticity was consistent across snowmelt dates (detailed methods are in Appendix S1).

2.7 | Snow removal experiment

Combinations of observational and experimental approaches to study the role of *any* environmental factor in plant demographic studies are surprisingly rare but are a powerful approach for understanding environmental drivers of population dynamics [e.g. 6

of 136 studies (Ehrlén, Morris, von Euler, & Dahlgren, 2016)]. In 2014, we conducted a snow removal experiment at the mid-elevation population to manipulate snowmelt date. Total snowpack was removed from six 2.5 m × 1.5 m plots, including a 0.25 m buffer around each plot, on the 9th and 10th of May when snow was *ca.* 1 m deep. The removal plots were directly adjacent to the long-term demography plots, which served as controls. We used data from half of the control plots so that all study plots were the same size. We followed the demographic census protocol in these plots in 2014 and 2015 as described above, with the exception that new seedlings and 2-year old plants were excluded due to time constraints. Nonetheless, experimental data captured the range of size variation present in the long-term demographic data. Our snow removal treatment resulted in a 10-day earlier snowmelt date compared to controls: first date of bare ground occurred on the 14 May in the snow removal treatment and the 24 May in the controls. For context, snowmelt date in the removal treatment was very similar to the mean snowmelt date over the timeframe of the demographic study: 14 versus 15 May, respectively (1998–2012), and the control treatment was similar to the long-term average snowmelt date: 24 versus 21 May respectively (1975–2012). For frost damage to occur in either treatment, night-time temperatures needed to dip below the threshold at which we observe frost damage (−2.5°C) when flower buds are developing (June). In June 2014, night-time temperatures fell below −2.5°C on four different nights. Thus, we expected to see a high rate of flower stalk abortion overall, but a higher rate in the snow removal compared to the control.

To control for individual variation in responses to snowmelt, we limited statistical analysis to plants that were present in both years of the experiment (235 plants in controls and 271 plants in removals). We analysed vital rate responses to the snow removal experiment in both 2014 (*t*) and 2015 (*t* + 1), to consider 1-year lag effects of snowmelt as above. We were able to test explicitly for lagged effects of snowmelt date in three of the reproductive vital rates: flower stalk abortion rate, flowering and fertility. Growth was analysed as the change in plant size (number of rosettes) from 2014 to 2015 and therefore was not included as a response in 2014, because we did not have plant size data for 2013 (i.e. the year before the experiment was conducted). We do not test for effects of snow removal on survival because plants must be missing for 2 years before they are declared dead, and we did not follow the fates of individuals beyond year *t* + 1. Flower stalk abortion rate, growth, probability of flowering and fertility (the number of flowering stalks in which a plant invests regardless of frost damage) were response variables in separate linear mixed models with treatment as a fixed categorical variable, size as a continuous covariate (for size-dependent vital rates), and plot as a categorical random variable (Bates, Mächler, Bolker, & Walker, 2015). A binomial error structure was used for abortion rate and flowering probability, and a Poisson error structure for fertility. We estimated p-values using package "lmerTest" (Kuznetsova, Brockhoff, & Christensen, 2017). Analyses and population modeling were performed in R v. 3.3.1 (R Core Team, 2016).

3 | RESULTS

Both our observational and experimental results illustrate that snowmelt timing can elicit positive and negative responses in *Helianthella*

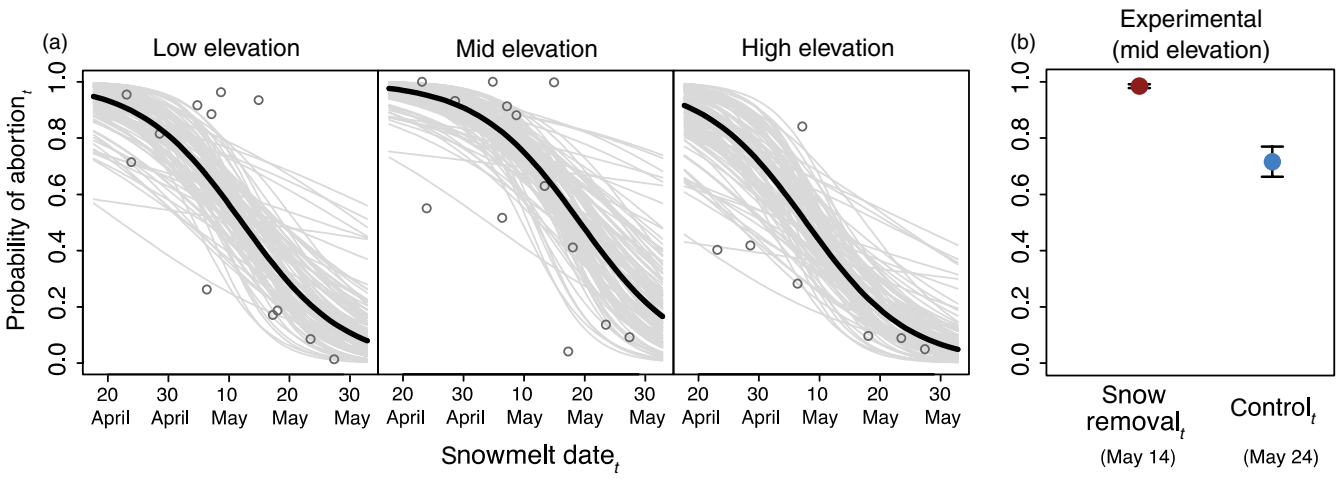

FIGURE 2 Flower stalk abortion rate for three populations of *Helianthella quinquenervis* (aspen sunflower) spanning the elevation range of the species in the Colorado Rocky Mountains, USA (*ca.* 2,700–3,400 m a.s.l.), as a function of spring snowmelt date. Probability of abortion is calculated as the total number of stalks that were aborted due to frost damage divided by the total number of flowering stalks initiated. The subscript *t* indicates year *t*. (a) Abortion is shown as a mean probability across individual plants in the long-term demographic data (1998–2012; open grey circles) and (b) as a mean across plots for the snow removal experiment, ±1 *SEM* (*n* = 6 plots per treatment). Black lines are predicted values from mixed models that include year as a random intercept term, and grey lines represent 100 posterior samples to show the uncertainty in expected abortion rate that is incorporated into our population models (see main text and Appendix S1 for details) [Colour figure can be viewed at wileyonlinelibrary.com]

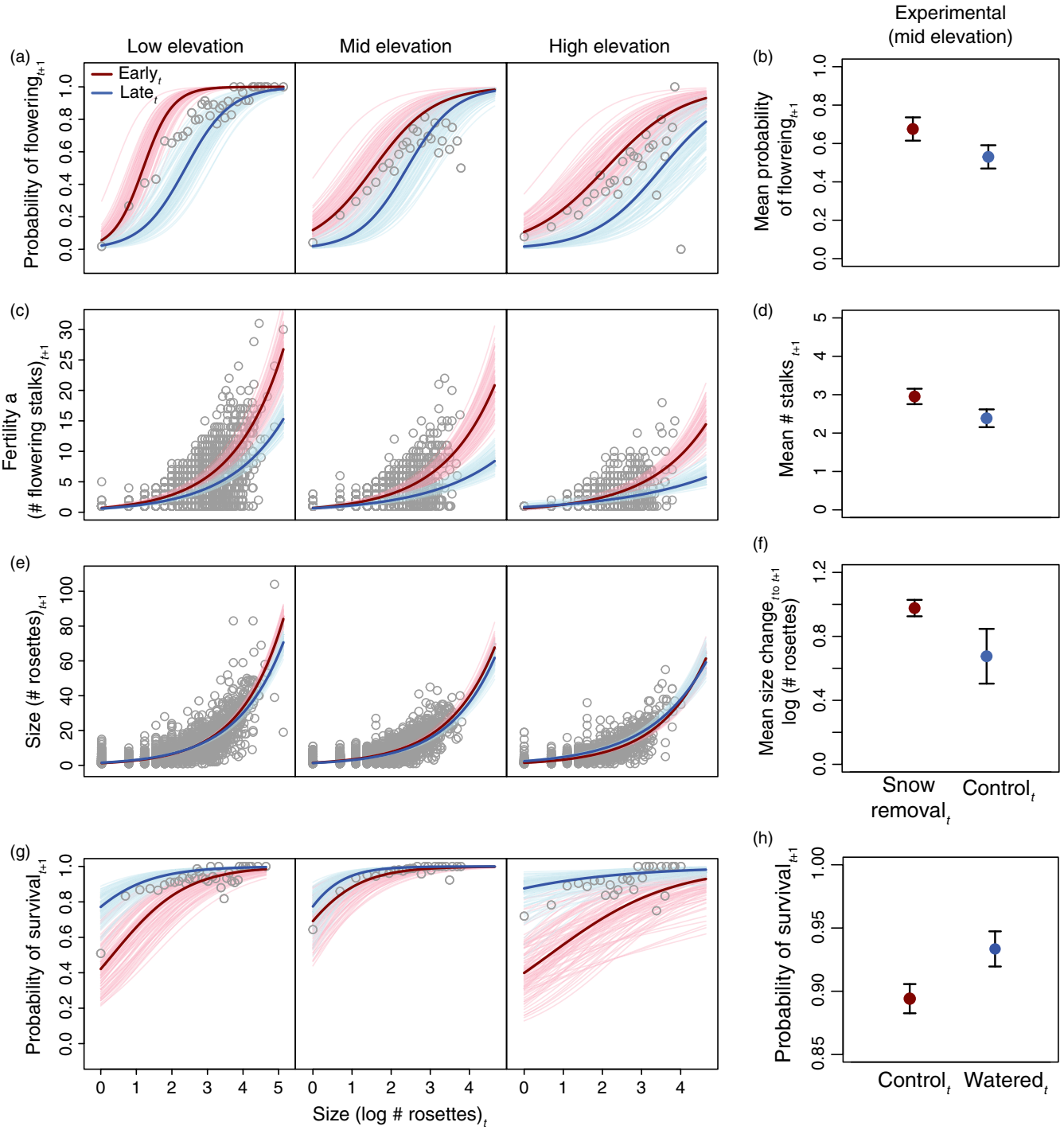

FIGURE 3 Size-dependent vital rate responses to the timing of snowmelt in *Helianthella* for (a, c, e, g) three observational populations, (b, d, f) a snow removal experiment and (h) a water addition experiment (survival only). Lines are predicted values from mixed models that include snowmelt × size interactions and correspond to the earliest and latest snowmelt dates on record during the timeframe of the observational study (1998–2012). Lighter coloured lines in the background represent 100 posterior samples based on the earliest and latest snowmelt dates, which represent uncertainty that is incorporated into population models. (a, c, e, g) Points show raw data (binned means for survival and flowering) over all years, and (b, d, f, h) plot-level means are shown for the experiments, ±1 *SEM* (snow removal: $n = 6$ plots per treatment; see Table 1 for statistical results; watering: $n = 3$ plots per treatment). Note the scale of the *y*-axis differs for observational versus experimental panels for some vital rates because (c, d) means are shown instead of raw values, and (h) because survival was high overall in the experiment, making data difficult to see if plotted from 0 to 1. Subscript *t* indicates year *t* (vs. year *t* + 1) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 *Helianthella* vital rate responses to experimental snow removal at the mid-elevation population. Results are from mixed models with plot as a random intercept term, plant size as a continuous predictor (for size-dependent vital rates), and treatment (control vs. snow removal) as a categorical predictor. The removal treatment was applied in 2014, and treatment effects in 2015 represent a lagged response to earlier snowmelt. Size change is not shown in 2014 because data on plant size are unavailable prior to the snow removal. The test statistics for size change are *t*-values and for flower stalk abortion rate, flowering probability, and flowering stalks are *z*-values (binomial, binomial and Poisson error structures respectively)

Year	Vital rate response	Predictor	Estimate ± 1 *SE*	Test statistic	Estimated *p* value
2015	Flower stalk abortion$_{t+1}$	Treatment	−0.04 ± 0.65	−0.055	0.96
2015	Size change$_{t+1}$	Size$_t$	0.027 ± 0.027	1.01	0.32
		Treatment	0.37 ± 0.21	1.77	0.077
2015	pr (flowering)$_{t+1}$	Size$_{t+1}$	0.70 ± 0.071	9.76	<0.0001
		Treatment	0.80 ± 0.38	2.12	0.034
2015	Flowering stalks$_{t+1}$	Size$_{t+1}$	0.069 ± 0.0039	17.48	<0.0001
		Treatment	0.13 ± 0.073	1.74	0.083
2014	Flower stalk abortion$_t$	Treatment	2.58 ± 0.39	6.62	<0.0001
2014	pr (flowering)$_t$	Size$_t$	0.33 ± 0.039	8.27	<0.0001
		Treatment	0.42 ± 0.24	1.74	0.083
2014	Flowering stalks$_t$	Size$_t$	0.061 ± 0.0071	8.65	<0.0001
		Treatment	0.025 ± 0.099	0.25	0.80

demographic vital rates. Across all study populations, early snowmelt in year *t* is associated with increases in flower stalk abortion due to frost damage in year *t* (Figure 2a). Similarly, experimental snow removal leads to significantly higher rates of flower stalk abortion compared to controls in year *t* (Table 1; Figure 2b). As expected, there is no difference in floral abortion rate between snow removals and control plots in year *t* + 1, the year following snow removal (Table 1).

In contrast to the immediate effects on floral damage in year *t*, model selection indicates that size-dependent vital rates respond to snowmelt timing with a 1-year lag: snowmelt in year *t* affects the vital rate in year *t* + 1 (Table S1). Vital rate responses in the snow removal experiment are consistent with these lagged responses in the observational data (Table 1; Figure 3). Early snowmelt in year *t* leads to increased flowering (Figure 3a) and fertility (Figure 3c) in year *t* + 1, especially in larger plants. Although we also find a higher probability of flowering in year *t* in snow removal plots compared to controls, this response is stronger in year *t* + 1 (Table 1). As expected, we find higher fertility in year *t* + 1 in the removals compared to the controls and no difference between treatments in year *t* (Table 1).

Effects of snowmelt on vegetative growth (size in *t* + 1) vary by population (Figure 3e). At the low-elevation population, early snowmelt is associated with decreased growth in small plants and increased growth in large plants. At mid-elevation, early snowmelt is associated with increased growth, and growth is higher in snow removals compared to controls (Table 1). At the high-elevation population, early snowmelt is associated with decreased growth.

Across all three populations, early snowmelt decreases the probability that an individual survives to the following year, especially in smaller plants (Figure 3g). We are unable to directly compare survival in the snow removal experiment to the long-term data because plants must be missing for at least 2 years before they can be declared dead, and we did not assess vital rates in year *t* + 2. However, consistent with the hypothesis that reduced survival occurs because of increased water stress when snowmelt is early, we find lower volumetric soil moisture content and increased leaf water potential (an instantaneous measure of plant water stress) in snow removal plots compared to controls during parts of the growing season (Figure S1). Additionally, we find that water addition increases the proportion of plants surviving to year *t* + 1 by 5.4% ± 3.5% ($z = 1.5$, $p = 0.12$; Figure 3h). Although the effect of watering is not statistically significant, the direction of the effect supports the water stress hypothesis. Seedling survival is unaffected by snowmelt date (Table S1).

After calculating proportional responses of each vital rate to a 1-week earlier snowmelt date (for median-sized plants), the magnitude of responses to snowmelt date can be more directly compared across vital rates. We find that some vital rates respond more strongly than others to earlier snowmelt (Figure 4). A 1-week earlier snowmelt date generally has a larger effect on reproductive vital rates compared to survival and growth (except fertility; Figure 4). For example, the effect of snowmelt on flower stalk abortion rate (flower viability) is nine times stronger than on survival in the high-elevation population and 25 times stronger in the low-elevation population.

Across all populations, λ_S declines with advancing snowmelt dates (Figure 5a–c). Population declines are most pronounced in the low- and high-elevation populations, where extinction ($\lambda_S < 1$) is predicted with 95% certainty in the high-elevation population even at current snowmelt dates and predicted in the low-elevation population if the early snowmelt dates observed in our study become more frequent. In these two populations most strongly threatened by early snowmelt, the most important vital rate through which earlier snowmelt leads to population declines is survival, with much weaker contributions from floral abortion (Figure 5d,f; survival is top

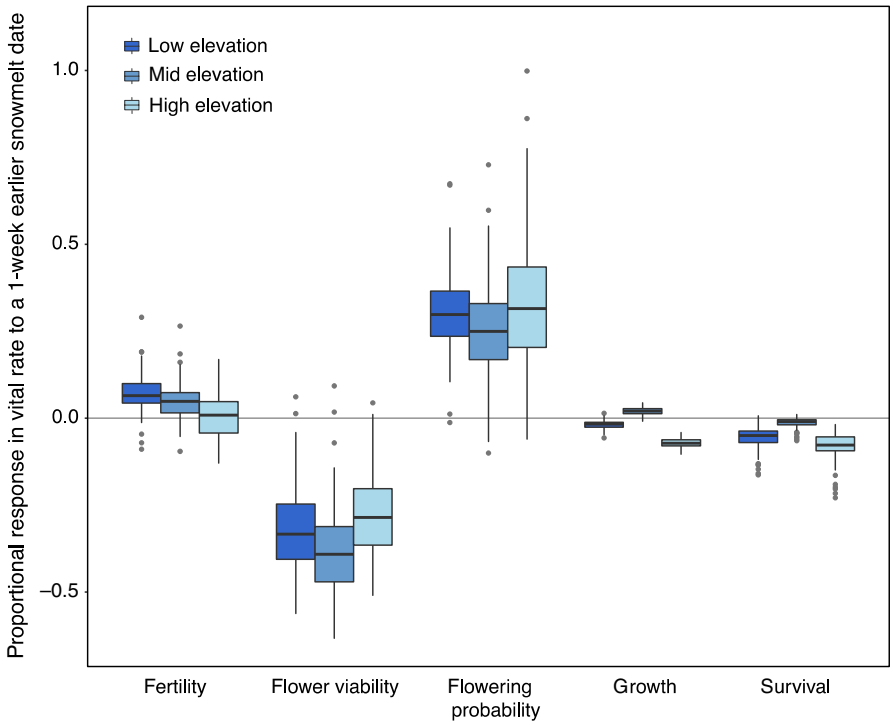

FIGURE 4 Vital rate responses to a one-week earlier spring snowmelt date in median-sized plants (three rosettes) in three populations of *Helianthella quinquenervis*. Box plots represent proportional change in each vital rate [(early value − mean value)/mean value], which was calculated 100 times across samples from the posterior distribution of each vital rate coefficient. Flower viability is the probability that a flower stalk will not be aborted in response to frost damage (1-abortion rate), to standardize interpretation of effect sizes across vital rates: a negative value has a negative effect on population growth rate [Colour figure can be viewed at wileyonlinelibrary.com]

line in all panels). Additionally, at the high-elevation population, negative effects of snowmelt on vegetative growth also contribute to population decline (Figure 5f). We also find that the extent to which the probability of survival drives effects of snowmelt on population persistence varies across populations (Figure 5). The mid-elevation population is comparatively stable across the observed range of snowmelt dates (Figure 5b), where survival and floral abortion contribute relatively equally to weak negative effects of snowmelt on λ_S (Figure 5e). Across all populations, the positive effects of snowmelt on flowering and fertility are insufficient to compensate for negative effects on other vital rates (Figure 5d,e,f).

4 | DISCUSSION

Even in the presence of substantial reproductive losses, climate-induced shifts in flowering phenology may not translate into consequences for population persistence. Although it seems intuitive that shifts in flowering phenology should affect population growth rates because the timing of flowering influences reproductive success (Elzinga et al., 2007), this perspective does not take the full plant life cycle into consideration. By placing the consequences of earlier flowering induced by climate change in the context of the entire plant life cycle, we find evidence that early snowmelt threatens population extinction primarily via reductions in survival, and less so because of earlier flowering and the associated increase in floral abortion risk (Figure 5). Reproductive losses following a phenological shift may occur because of exposure to novel abiotic conditions (as in our study), decreased synchrony with mutualists or food resources (Kudo & Ida, 2013; Reed et al., 2013), or increased synchrony with antagonists (Liu, Reich, Li, & Sun, 2011). Regardless of the mechanism, populations of iteroparous and longer lived species generally should be buffered from reproductive losses, in part because they have multiple opportunities for reproduction over their lifetimes (Dalgleish, Koons, & Adler, 2010; Morris et al., 2008; Reed et al., 2013).

To understand the effects of any environmental change on population persistence, it is important to consider both the *magnitude* of the climate effect on a vital rate and the *sensitivity* of λ_S (stochastic population growth rate) to changes in that vital rate. A large vital rate response to a climatic change can have negligible effects on λ_S if λ_S is insensitive to changes in that vital rate, as we find here for floral abortion rate. In the high- and low-elevation populations, the high sensitivity of λ_S to changes in survival makes changes to reproduction relatively unimportant for population persistence, even though the effects of snowmelt on floral abortion rate are much stronger than on survival. Our results are consistent with demographic life-history theory, which predicts that changes in reproduction should have relatively weak effects on population viability in long-lived iteroparous species (Franco & Silvertown, 2004; Pfister, 1998; Silvertown et al., 1993). It is important to confront these predictions with empirical data, because perturbation analyses rely on small changes in fitness components that may not reflect the actual magnitude of vital rate responses to environmental changes. At the mid-elevation population, floral abortion contributes slightly to a weak trend towards population decline (Figure 5b,e), but this negative effect on λ_S is driven in equal part by a reduction in survival. Survival in the mid-elevation population exhibits the weakest response to early snowmelt, which explains why there is not a strong projected population decline at mid-elevation. Additionally, in

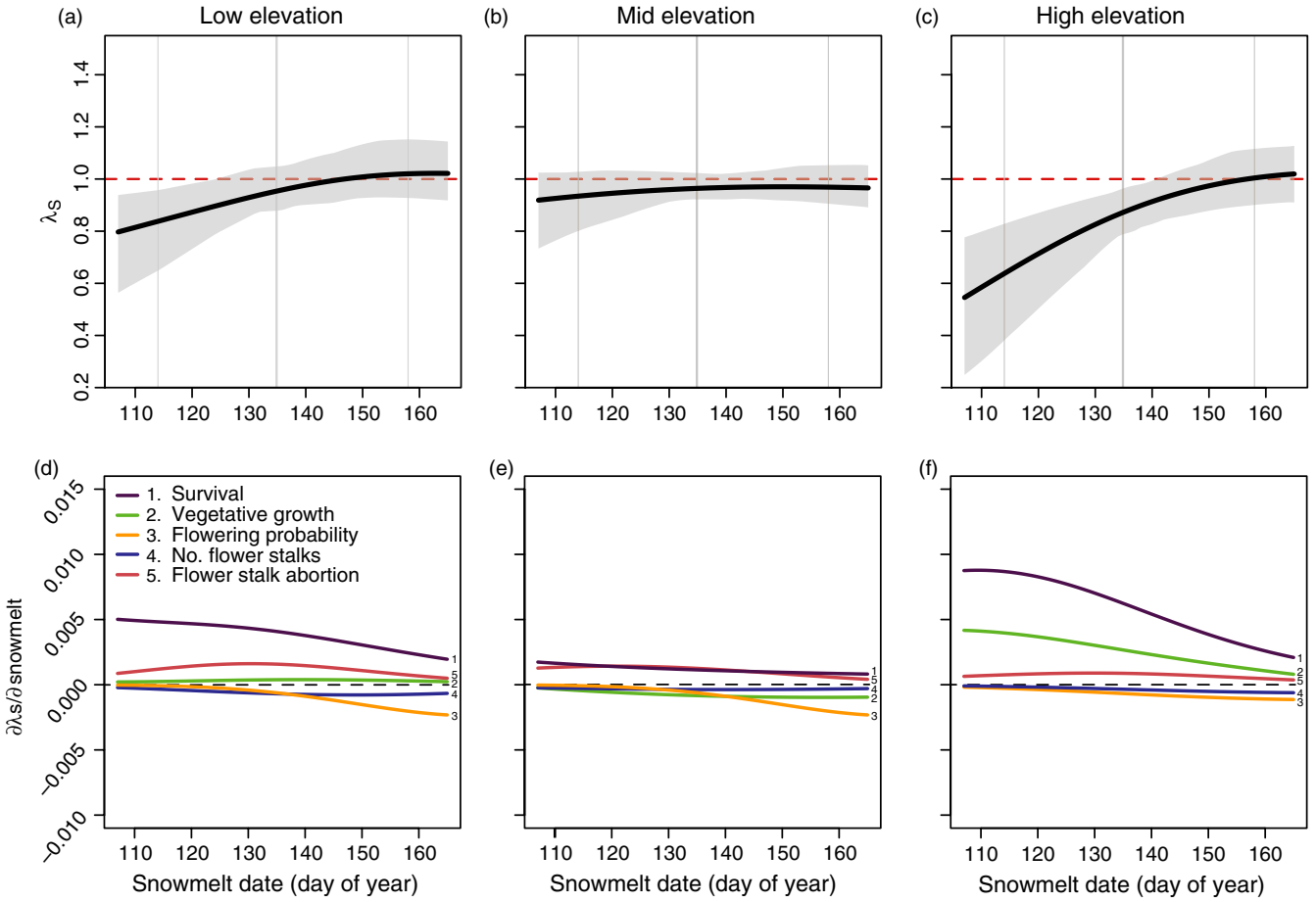

FIGURE 5 (a–c) Stochastic population growth rate (λ_S) and (d–f) the magnitude by which the effect of snowmelt on each vital rate influences the response of λ_S to snowmelt date ($\partial\lambda_S/\partial$ snowmelt) for three study populations of *Helianthella*, as a function of the timing of spring snowmelt date. (a–c) Grey shading represents the 95% credible intervals for λ_S, and the solid black lines represent the mean; dashed red lines indicate a stable population growth rate ($\lambda_S = 1$): values below this represent a population decline. Vertical grey lines indicate the average (thick line) and earliest and latest (thin lines) snowmelt dates observed over the timeframe of the longest demographic dataset (mid-elevation, 1998–2012). (d–f) Each coloured line represents the contribution of the response of λ_S to snowmelt date from each snowmelt-responsive vital rate, from a regression-style LTRE. Positive LTRE values (d–f) indicate that the vital rate response caused λ_S to increase with later snowmelt date (later is better), whereas negative values caused λ_S to decrease with later snowmelt date (earlier is better). Values near zero (dashed line) indicate that the vital rate response contributes little to the overall realized response of λ_S (a–c), which is the sum of the vital-rate specific contributions [Colour figure can be viewed at wileyonlinelibrary.com]

the high-elevation population, negative effects of snowmelt on growth influence λ_S despite being comparatively small in magnitude, emphasizing the opposite extreme: a relatively weak vital rate response in a high-sensitivity vital rate can influence λ_S. Thus, just as we should avoid the assumption that a large demographic response to an environmental change is likely to affect population growth rate, we should also not assume that a demographic response is unlikely to affect population growth rate just because it is relatively small in magnitude.

In addition to different magnitudes of negative responses to early snowmelt, some vital rates responded in the opposite direction to interannual variation in snowmelt date. The lagged positive effects of early snowmelt on flowering and fertility are an example of demographic compensation within all three populations. In the year following early snowmelt (year $t + 1$), more plants flower within each population, and those flowering plants invest in a higher number of flower stalks, both in the experiment and the observational data. Consistent with the lag response, field observations suggest that *Helianthella* pre-forms flower buds, probably one year in advance because small flower buds are present by the end of the summer (D.W. Inouye, personal observation). Two ecological phenomena may explain increased flowering and fertility in year $t + 1$: early snowmelt in year t is associated with both a longer growing season and an increased risk of frost damage. During longer growing seasons, *Helianthella* plants likely gain more photosynthate that could be allocated to future reproduction, and in the event of frost damage, *Helianthella* plants may allocate resources that otherwise would have gone into current reproduction to future reproduction (or some combination of both). Compensatory demographic responses are likely to be a common response to climate change, both within and across plant populations (Villellas et al., 2015). Whether compensation buffers populations from decline depends in part on whether it occurs in

a high- or low-sensitivity vital rate. In *Helianthella*, the positive effect of increased future reproduction is insufficient to buffer populations from the negative effects of early snowmelt on other vital rates.

In particular, reduced survival under early snowmelt conditions contributes to population decline in all three populations. Reduced survival under earlier snowmelt dates is consistent with the hypothesis that plant water stress increases as snowmelt dates become earlier. In our study area, earlier snowmelt leads to longer growing seasons with an extended dry period that can increase plant water stress (Sloat et al., 2015). We find reduced soil moisture and evidence of increased water stress in *Helianthell*a in snow removal plots compared to controls during parts of this dry period (Figure S1). Consistent with this, we find that experimental water additions during the dry period increase survival to year $t + 1$. Although the effect of watering was not statistically significant, we had only three plots per treatment, and the effect size is consistent with the long-term survival response to early snowmelt at the mid-elevation population, which was smaller than the other two populations (Figures 3g, 4). Drought conditions are likely to intensify in the future because climate models predict both earlier snowmelt and less snowfall throughout western North America as the climate continues to change (Diffenbaugh, 2012; Fyfe et al., 2017; Higgins & Shi, 2001; IPCC, 2013), suggesting that further climate change will exacerbate any drought-mediated negative effects of early snowmelt on survival.

Although our study shows that frost damage to reproductive structures does not necessarily threaten plant population persistence, frost events can still have various ecological and economic consequences (CaraDonna & Bain, 2016; Inouye, 2000). Non-lethal frost effects on flowers, such as reductions in flower size and number, can affect pollinator behaviour (Pardee, Inouye, & Irwin, 2017). Frost damage to flower buds and flowers can also reduce the availability of floral resources within a community and has been linked to reduced population size in insect pollinators (Boggs & Inouye, 2012; Ogilvie et al., 2017). Insect seed predators (tephritid and agromyzid flies that are host-specific to *Helianthella*) and mutualist ants that collect extrafloral nectar from buds (Inouye & Taylor, 1979) may also be affected by loss of flower buds to frost. Furthermore, frost events are expected to increase in frequency under continued climate change (Ellwood, Temple, Primack, Bradley, & Davis, 2013; Labe, Ault, & Zurita-Milla, 2016), emphasizing the importance of further study on the ecological effects of frost in the context of climate change.

Studying the effects of climate change on all components of an organism's life cycle allowed us to tease apart the complex effects of a single climate driver on population dynamics. Ultimately, multiple abiotic and biotic factors will influence how population dynamics respond to climate change (Ehrlén et al., 2016). For example, *Helianthella* requires animal pollination to produce seed, experiences predispersal seed predation (Inouye & Taylor, 1979), and is susceptible to fungal rust infections. All these factors may directly affect demographic vital rates and may interact with snowmelt timing to affect *Helianthella* populations. Such ecological complexity highlights what remains to be learned about the combined effects of multiple environmental drivers on population dynamics, an especially relevant challenge as the climate continues to change. Nevertheless, we show that the phenology of reproductive events can be unreliable measures of threats to population persistence, even when earlier flowering is associated with substantial reproductive losses. Instead, other less conspicuous demographic effects of climate change may elevate extinction risk in plant populations. Ample evidence for shifts in reproductive phenology, along with scarcer evidence that these shifts actually influence reproductive success, are valuable but can paint an incomplete and even misleading picture of population responses to climate change.

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AUTHORS' CONTRIBUTIONS

D.W.I. initiated the long-term demographic study. D.W.I., A.M.I., J.L.W., P.J.C., A.A., and T.E.X.M. all collected long-term demographic data. A.M.I., P.J.C., and A.A. performed the snow removal experiment. A.C., A.M.I., J.L.W., and T.E.X.M. analysed the data and constructed population models. A.M.I. wrote the manuscript and all authors edited drafts.

DATA ACCESSIBILITY

The data used in this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.863c8sk (Iler, 2019), and the transition matrices in this study are archived in the Compadre Database (http://www.compadre-db.org).

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SUPPORTING INFORMATION

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

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