

RESEARCH ARTICLE

Comparative impacts of long-term trends in snowmelt and species interactions on plant population dynamics

Diane R. Campbell^{1,2}  | Mary V. Price^{2,3}  | Nickolas M. Waser^{2,3}  |
Rebecca E. Irwin^{2,4}  | Alison K. Brody^{2,5} 

¹Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA

²Rocky Mountain Biological Laboratory, Crested Butte, CO, USA

³Department of Biology, University of California, Riverside, CA, USA

⁴Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

⁵Department of Biology, University of Vermont, Burlington, VT, USA

Correspondence

Diane R. Campbell

Email: drcampbe@uci.edu

Funding information

Division of Environmental Biology, Grant/Award Number: 0089643, 0455348, 1654655 and 9805034

Handling Editor: Ryan Phillips

Abstract

1. Climate change can impact plant fitness and population persistence directly through changing abiotic conditions and indirectly through its effects on species interactions. Pollination and seed predation are important biotic interactions that can impact plant fitness, but their impact on population growth rates relative to the role of direct climatic effects is unknown.
2. We combined 13 years of experiments on pollen limitation of seed set and pre-dispersal seed predation in *Ipomopsis aggregata*, a subalpine wildflower, with a long-term demographic study that has documented declining population growth with earlier spring snowmelt date. We determined how pollen limitation and seed predation changed with snowmelt date over 21 years and incorporated those effects into an integral projection model to assess relative impacts of biotic factors on population growth.
3. Both pollen limitation and the difference in stigma pollen load between pollen-supplemented and control plants declined over years. Neither pollen limitation nor seed predation changed detectably with snowmelt date, suggesting an absence of indirect effects of that specific abiotic factor on these indices of biotic interactions. The projected biotic impacts of pollen limitation and seed predation on population growth rate were small compared to factors associated with snowmelt date. Providing full pollination would delay the projected date when earlier snowmelt will cause populations to fall below replacement by only 14 years.
4. *Synthesis.* Full pollination and elimination of seed predation would not compensate for the strong detrimental effects of early snowmelt on population growth rate, which in *I. aggregata* appears driven largely by abiotic environmental factors. The reduction over two decades in pollen limitation also suggests that natural selection on floral traits may weaken with continued climate change. These results highlight the value of studying both abiotic factors and biotic interactions to understand how climate change will influence plant populations.

KEYWORDS

biotic interaction, integral projection model, *Ipomopsis*, plant-climate interactions, pollen limitation, population growth, precipitation, seed predation

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Changing environmental conditions, including those due to anthropogenic climate change (IPCC, 2014), can endanger populations through direct effects of abiotic conditions on vital rates such as survival and reproduction (Doak & Morris, 2010). Because individual species are embedded in communities of interacting species, vital rates may also respond to biotic interactions that are altered by climate change (Maron et al., 2014). Little is known about the relative strengths of direct abiotic effects and indirect effects of climate change mediated through species interactions. In situations where both occur, it is also unclear whether climate change will alter species interactions in ways that reinforce or compensate for abiotic effects on population growth rates. Thus, it is unclear whether ignoring the impacts of biotic interactions in models for population growth will fundamentally alter conclusions about the impacts of climate change.

Consider two examples of biotic interactions that can influence the population growth of plants. The first is pollination by animals, a critical ecosystem service (Kremen et al., 2007) on which over 85% of all flowering plant species depend (Ollerton et al., 2011). Hundreds of studies have documented increased seed production with experimental supplementation of pollination level, providing evidence for pollen limitation of seed production (reviewed in Bennett et al., 2018; Knight et al., 2005). The second interaction is pre-dispersal seed predation, which, like pollen limitation, can severely reduce seed production (e.g. Gomez, 2008; Irwin & Brody, 2011). Seed predation and pollen limitation can also occur together (Cariveau et al., 2004). In only a few of those cases of pollination or seed consumption do we understand whether and how the changes in seed production impact population growth (e.g. Baer & Maron, 2018; Ehrlén et al., 2006; Price et al., 2008).

The study of population responses to both abiotic and biotic conditions is not new (Nicholson & Bailey, 1935). But the impacts of species interactions and climate are rarely measured in a way that allows direct comparison of their effects on population growth. A recent meta-analysis involving 208 plant species provided a valuable step forward, suggesting comparable impacts of abiotic and biotic drivers on population growth rate (λ ; Morris et al., 2020). However, most of the studies included in Morris et al. (2020) examined only a single type of driver, either abiotic or biotic. A complementary approach is to compare multiple factors within the same plant species, and to do so over a term long enough to capture a range of climatic conditions similar to that either experienced or forecast over the short term.

A few studies have compared the impacts of a climate variable and a biotic interaction on projected population growth in the same system. In one example, population growth of a Hawaiian shrub responded more strongly to variation in wet season precipitation than to mollusc herbivory (Bialic-Murphy & Gaoue, 2018), but how herbivory itself responded to variable precipitation was not explored. In a second example, the population dynamics of a butterfly species was influenced by how its nectar source responded to the climatic variable of snowmelt timing (Boggs & Inouye, 2012), but the direct

effect of climate on butterfly vital rates was not incorporated into the model. A third study applied population models to long-term data on grassland plants to simulate removal of climate effects on competing species, and found stronger direct than indirect effects of competition in four of five communities (Chu et al., 2015). We still lack, however, experimental manipulation of interactions that provides information for a single plant species and locale on whether and how climate change affects demographic parameters both in total, and indirectly as mediated through species interactions.

Here we assemble such information for the subalpine wildflower *Ipomopsis aggregata* in the Rocky Mountains of North America. In this system, climate change is causing earlier snowmelt in the spring (Wadgymar et al., 2018), which leads to lower population growth for *I. aggregata*. Populations are expected to drop below replacement within four decades, primarily due to lower seedling establishment and lower seed production with earlier snowmelt, although survival is also affected (Campbell, 2019). Earlier spring snowmelt is one of the clearest signals of climate change in mountainous areas of North America (Clow, 2010; Pederson et al., 2011). For some plant species, it can lead to longer periods of drought stress (Sloat et al., 2015), increase vulnerability to post-snowmelt frost (Inouye, 2008), or cause earlier blooming (CaraDonna et al., 2014). At sites where *I. aggregata* grows, early snowmelt usually reduces soil moisture during the early part of the summer and lengthens the period of time between input of snowmelt water and onset of summer monsoon rains (Sloat et al., 2015). Experimental manipulations of snowmelt and summer precipitation have shown that the associated drought lowers carbon gain through photosynthesis and also some aspects of reproduction in *I. aggregata* (Campbell & Wendlandt, 2013; Powers et al., 2022). As *I. aggregata* generally forms buds after spring frost and does not start blooming until weeks after snowmelt, frost events have little impact on its reproduction. Impacts on phenology are generally smaller for summer blooming species like *I. aggregata* than for earlier blooming ones (CaraDonna et al., 2014) and were not observed for *I. aggregata* in one study using experimental warming (Price & Waser, 1998). We consider it likely that effects of snowmelt timing are mediated mostly through drought stress.

The association of population growth rate with snowmelt timing might, however, involve not only direct impacts of abiotic conditions but also potential changes in biotic interactions that influence seed production. Both pollination and seed predation do impact population growth in *I. aggregata* (Irwin & Brody, 2011; Price et al., 2008). To separate out the impacts of these biotic interactions on population responses to climate, we combined studies of pollen limitation and pre-dispersal seed predation over an exceptionally long time period (13 flowering seasons spread over 21 years) with a long-term demographic study (Campbell, 2019).

We address the following questions:

Question 1: Do biotic interactions vary with a climate variable?

Specifically, how much do pollen limitation and seed predation vary across years in their effects on seed production, and to what extent is variation in those biotic interactions explained by the timing of spring snowmelt?

Question 2: How much do biotic interactions contribute to the overall impact of a climate variable on population growth? Specifically, how do the impacts of pollination level and seed predation on population growth rate compare with the overall impact of snowmelt timing, as assessed by an integral projection model? Our general approach was to simulate the absence of pollen limitation and seed predation and assess whether the increased fecundity rescued populations from the negative population growth projected with climate change. A large effect of eliminating those biotic sources of seed loss would suggest a relatively large indirect impact of those biotic interactions on how population growth responds to a climate variable, whereas a small effect would suggest that direct abiotic effects are more important.

2 | MATERIALS AND METHODS

2.1 | Study system

Ipomopsis aggregata subsp. *aggregata* (Polemoniaceae) is a sub-alpine herb that is distributed widely throughout the Rocky Mountains (Grant & Wilken, 1986). We studied populations within or near (<1 km) the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, CO (38°57'27"N 106°59'19"W), with the exception of one site, Lower Loop, 8 km distant. Permission to use the Lower Loop site was granted by the Crested Butte Land Trust. For all other sites, permission was granted by RMBL, with use at Copper Creek governed by an agreement between RMBL and the US Forest Service. Between 1935 and 2021, in areas near RMBL, spring snowmelt has occurred 1.4 ± 0.5 days per decade earlier on average (data = $411.21 - 0.1361 \times \text{Year}$; $R^2 = 0.08$, $p = 0.007$, Powers et al., 2022), with considerable variation around the trend line as well (Campbell, 2019). Seeds germinate in the late spring, and the plant spends 2 to 10 years or more as a vegetative rosette before flowering (Campbell, 1997). It then blooms, producing on average about 80 hermaphroditic flowers across the summer season, sets seed and dies after that single flowering episode in >96% of cases (Campbell, 1997). There is virtually no seed bank, with nearly all plants that germinate doing so the first year (Campbell, 1997). Plants are highly self-sterile due to prezygotic ovule degeneration, a form of late-acting incompatibility (Sage et al., 2006; Waser & Price, 1991), and the main pollinators are Broad-tailed and Rufous Hummingbirds (*Selasphorus platycircus* and *Selasphorus rufus*), which account for an estimated 94% of flower visits by pollinators near our study sites (Price et al., 2005). Fruits are often attacked by a pre-dispersal seed predator, the Anthomyiid fly *Delia* sp. (formerly *Hylemya* sp.). Female flies usually lay a single egg on the inside of the sepals of an elongated flower bud or young flower, and the hatched larva typically consumes all of the seeds in the developing fruit (Brody, 1992). These flies have been reported to attack and eat seeds in between 10% and 30% of fruits near our sites (Brody & Irwin, 2012; Brody et al., 2008; Price et al., 2021). Much more rarely, an unidentified

caterpillar (Noctuidae) destroys a fruit by chewing it (Juenger & Bergelson, 1998). Population growth is strongly influenced by seed production, as shown by experiments manipulating input of seeds into populations (Price et al., 2008).

2.2 | Field experiments

We used supplemental hand-pollinations in the field to assess the degree to which seed production was pollen limited in the years of 1995 through 2003, 2005 and 2007. We combined those 11 years of new data with previously published data from two other years, 1987 (Campbell, 1991) and 1990 (Campbell & Halama, 1993). In most years, treatments were replicated across multiple sites as well as multiple plants per site (Table S1). In total, we compared seed production from 329 supplementally hand-pollinated plants and 345 unmanipulated plants from 32 site-year combinations over 13 years. We refer to supplementally hand-pollinated plants hereafter as 'hand-pollinated' for simplicity.

In 1987 and 1990, pollen was added from two donor plants 3–10 m away from each hand-pollinated plant to all its receptive flowers three to four times per week (Campbell, 1991; Campbell & Halama, 1993). In other years, pollen was added three times per week except in 1996 and 2003, when pollen was added twice per week. A single pollen donor was used for each recipient flower in 1995–2002. In 2003, 2005 and 2007, anthers from three to five plants were mixed together in an Eppendorf tube, but a single anther was then removed to add pollen to a stigma. As each flower lasts two or more days, most or all flowers should have received supplemental pollen, but the slight differences in frequency of hand-pollinations may have meant that hand-pollinated plants were most fully pollinated in 1987, 1990, 2005 and 2007. Moreover, the use of multiple pollen donors may have done a better job at ensuring pollinations between compatible mates in some years. Hand-pollinations were performed either using a wooden toothpick or by brushing anthers across the stigma. We always attempted to saturate the stigmatic surface with pollen.

Each flower produced by a plant usually experiences one of three fates: aborted (i.e. no fruit capsule formed because the ovary does not expand), expanded fruit with mature seeds, or expanded fruit attacked by the fly *Delia* or the rare caterpillar. It is possible that *Delia* oviposits under the sepals of some flowers that subsequently abort, but in that case there are no seeds to be destroyed. Like abortions, expanded fruits attacked by the fly or caterpillar typically release zero seeds, as the seeds are eaten first. Fruits were collected every few days just prior to dehiscence of the capsule. In cases where expanded fruits dehisced and released seeds before we were able to collect them, we substituted the average number of seeds made by an unattacked expanded fruit on that plant. For each plant, we determined the following measures of reproductive success: actual seeds per flower, percent fruits destroyed by a seed predator and an estimate of seeds per flower whether eaten or not (hereafter 'seeds initiated per flower'). Seeds initiated per flower

is the average seeds per flower that a plant would have produced in the absence of seed predators (Abdala-Roberts et al., 2014; Campbell, 1991; Campbell et al., 2022; Price et al., 2021). Actual seeds per flower was calculated by dividing total seeds produced by a plant by total flower number. Seeds initiated per flower was estimated by dividing actual seeds per flower by the proportion of fruits that were not destroyed by seed predators. This calculation may slightly underestimate seed losses to predators because it makes the unrealistic, but necessary, assumption that oviposition is uncoupled to probability of abortion (Brody & Morita, 2000; Price et al., 2021). Per-plant measures were then averaged across all plants in a given treatment, site and year. For analyses employing a year as the unit of replication, those site-specific values were then averaged across sites to obtain estimates for control plants and supplementally hand-pollinated plants in each year of the study.

We analysed effects of supplemental hand-pollination on seeds per flower but did not do so separately for its components of fruits per flower (i.e. proportion not aborted) and seeds per fruit, because previous studies show that the two latter indices respond to the same extent to pollination level (Campbell & Halama, 1993). Thus, separating them would not aid in distinguishing impacts of pollen limitation from other causes of low seed production.

In 6 of the 13 years, we also estimated pollen loads on stigmas of control and hand-pollinated plants (Table S1), using previously published data from a total of 1,608 stigmas during 1995 to 1998 (Price et al., 2005) combined with two new years of data (2003 and 2005). In 2003 and 2005 we collected approximately 20% of stigmas on each plant. In all years, stigmas were collected from flowers whose corollas had withered and thus were finished blooming. We stained the stigmas in basic fuchsin dye (Kearns & Inouye, 1993) and examined them under a light microscope to count *I. aggregata* pollen grains. For each treatment group, values were averaged across plants and sites to obtain yearly mean pollen loads. We did not emasculate plants by removing anthers because doing so interferes with the mechanics of pollen deposition (Price & Waser, 1982) and artificially decreases geitonogamy, thus influencing pollen quality (de Jong et al., 1992). As a result, we could not distinguish between self-pollen, which would not lead to seed formation in this self-sterile species, and outcross pollen, but visitation rate by pollinators is positively related to total pollen receipt when comparing plants within a year (Price et al., 2005).

To explore causes of variation in pollen limitation and seed predation, we also examined rates of pollinator visitation and oviposition by *Delia* sp. flies. Pollinator visitation rates to *I. aggregata* were previously estimated at these same sites in seven summers, from 1996 to 2002, as described in (Price et al., 2005). Visitation rate was expressed as the number of probes by flower visitors per open flower per hour of observation at a plot or plant, using sums of values across the entire season. Values were then averaged across sites in a given year to yield a yearly estimate of visitation. For 6 years, we obtained estimates of egg oviposition by *Delia* sp. on calyces of unmanipulated plants, by carefully lifting sepals with fine forceps, at

sites within 1 km of RMBL (Table S1). Data from 2000 were previously published (Brody & Morita, 2000). For each year, we summed the number of flowers checked for an egg over the season and the number of eggs found. Oviposition rate was calculated as sum of eggs divided by sum of flowers. In total we examined over 30,000 flowers for eggs under the sepals.

2.3 | Analysis

2.3.1 | Question 1: Do biotic interactions vary with a climate variable?

To answer this question, we analysed temporal patterns of pollen limitation and seed predation impact in several steps. First, we tested for variation across years in these biotic interactions using sites as replicates. Second, we tested for a systematic trend, linear or nonlinear, with year. Third, we tested for correlations with the particular climate variable of snowmelt timing. Fourth, we explored mechanisms behind these patterns by examining correlations of pollen limitation with pollinator visit rate and pollen load on stigmas, as well as the correlation of seed predation impact with oviposition rate.

For each of the 32 site-year combinations we estimated pollen limitation as the proportional increase in seed set due to hand-pollination: hereafter the pollen limitation index $\frac{HP-C}{C}$, where HP = mean actual seeds per flower of hand-pollinated plants and C = mean actual seeds per flower of control plants. We based our analyses on measures of proportional increase in seed set, rather than effect sizes used in meta-analysis, because proportional increases could easily be incorporated into integral projection models (IPMs). To test for average pollen limitation across the 13 years of study, these values were then compared with the null hypothesis of zero effect using a one-sample *t*-test. We then tested if the estimate of pollen limitation varied across years using one-way ANOVA with sites as replicates in each year.

For each of the site-year combinations, we estimated the impact of seed predation as the proportional increase in seed set in the absence of seed predation using data from control plants only (hereafter the seed predation index) as: $\frac{C_i - C}{C}$, where C_i = mean seeds initiated per flower by control plants. Since seeds initiated cannot by definition be less than actual seeds, the effect was always positive and thus differed from zero. As for pollen limitation, we tested if the seed predation index varied across years using one-way ANOVA with sites as replicates in each year.

To determine if there were systematic temporal patterns, which could result from any environmental variable related to climate change, we treated each year as the unit of replication. For these analyses, we used four indices for how species interactions influence seed production. The first index was the pollen limitation index as defined above: $\frac{HP-C}{C}$. Second, we determined the extent of pollen limitation in the absence of pre-dispersal seed predators in similar fashion, except using values for seeds expanded whether eaten or

not: $\frac{HP_i - C_i}{C_i}$, where HP_i = mean seeds initiated per flower by hand-pollinated plants and C_i = mean seeds initiated per flower by control plants. The third index was the seed predation index as defined above: $\frac{C_i - C}{C}$. Finally, we examined the combined influence of pollen limitation and seed predators as: $\frac{HP_i - C}{C}$, that is, as (mean seeds initiated per flower by hand-pollinated plants – mean actual seeds per flower of control plants) / mean actual seeds per flower of control plants. Regression analysis was used to examine how these indices changed with year. The linear regression coefficient expressing slope of an index on year was estimated from simple regression, with the effect of the quadratic coefficient determined from a regression model with both linear and quadratic terms. Yearly trends could be due to a variety of factors, including a systematic change in the key climate variable of snowmelt date, change in other climate variables such as summer precipitation, or change in abundances of interacting organisms.

Pollen limitation, but not the seed predation index, changed systematically with year (see Section 3). So to determine if degree of pollen limitation was related to the key climate variable of snowmelt date, we performed linear and quadratic regression on the Julian date the snow melted in the spring (the first date with zero snow on the ground at RMBL; www.gothicwx.org.) Date of snowmelt was highly correlated with total winter water content of the snow in cm ($r = 0.93$, $N = 13$ years, $p < 0.0001$; data from www.gothicwx.org), so we did not consider it possible to separate the effects of those two aspects of snowpack. At this site, the date of snowmelt has advanced 1.4 days per decade over the years of 1935–2021 (Powers et al., 2022). We examined the correlation coefficients between the pollen limitation index, pollinator visitation rate and an index of the proportional increase in pollen on stigmas of hand-pollinated plants compared to control plants. We used a one-tailed test for the association of the pollen limitation index with the increase in pollen added to the stigmas. Lastly we examined the correlation coefficient between the seed predation index and the oviposition rate for seed predators.

2.3.2 | Question 2: How much do biotic interactions contribute to the overall impact of a climate variable on population growth?

To examine the effects of pollen limitation and seed predation on demography of *I. aggregata* populations, we employed IPMs (Ellner et al., 2016). In a size-structured IPM, vital rates are influenced by a continuous measure of individual size, in our case the ln-transformed length of the longest leaf. The previous model (Campbell, 2019), based on 16 years of data, included probability of seedling establishment from seed, size-dependent survival, growth, size-dependent probability of flowering and size-dependent seed production (see Appendix S1). The Campbell (2019) model followed that for a monocarpic plant with a time delay; size for reproductive individuals was measured one time step before reproduction (Kuss et al., 2008). In this case, the kernel describing all possible transitions from size z to

size z' is composed of two parts describing (1) the transitions in size due to growth and survival, and (2) the production of size z' offspring by size z parents in the preceding year (Appendix S1). Seedling establishment, growth and seed production all depended on the day of snowmelt in spring, whereas survival and probability a plant flowered depended on the day of snowmelt in the previous year (see vital rate functions used in Table S2). Our general approach here was to modify the model (which was constructed for a different *I. aggregata* population) by altering total seed production by the proportion change estimated due to pollen limitation alone (i.e. increasing it by the average pollen limitation index), by seed predators alone, and by the combined effects of pollen limitation and seed predation.

In the original demographic model, total seed production was reduced in years when the snow melted earlier (Campbell, 2019), as were seedling establishment, vegetative growth and probabilities of surviving or flowering in the next year. These patterns led to a reduced finite rate of increase (λ) for the population. Here, finding no correlation between the extent of pollen limitation and snowmelt date (see Section 3), we examined how λ for each snowmelt date would change if seed production were increased by a proportion defined by our pollen limitation index: $\frac{HP - C}{C}$. To examine the impact of seed predators alone we repeated the modelling using the seed predation index: $\frac{C_i - C}{C}$. Lastly, to examine the impacts of both pollen limitation and seed predation, we used the percentage increase in seeds initiated per flower in hand-pollinated plants compared with actual seeds per flower in control plants: $\frac{HP_i - C}{C}$. We then examined the relationship of λ to snowmelt date using analysis of covariance with the factor of scenario (control, pollen limitation eliminated, seed predation eliminated, both eliminated), linear coefficient for snowmelt, quadratic coefficient for snowmelt and interactions between scenario and the linear and quadratic coefficients.

3 | RESULTS

3.1 | Question 1: Do biotic interactions vary with a climate variable?

Averaged over the 32 site-year combinations, supplemental hand-pollination increased mean seeds per flower by 24%, a value significantly different from zero (one-sample $t_{31} = 2.25$, $p = 0.0314$). Using those site-years as replicates, the pollen limitation index ranged from -0.29 to $+2.81$ (Table S1) and varied significantly across years (one-way ANOVA, $F_{12,19} = 13.37$, $p < 0.0001$). Averaged over the site-year combinations, eliminating the impact of seed predation increased mean seeds per flower by 46% (range = 10% to 177%). Unlike pollen limitation, the seed predation index did not change detectably across years ($F_{12,19} = 1.57$, $p = 0.18$).

The yearly magnitude of pollen limitation has declined over years since 1987 ($F_{1,11} = 8.43$, $p = 0.0143$ for linear coefficient) in a decelerating fashion (quadratic coefficient $F_{1,10} = 10.92$, $p = 0.0080$ in regression with both linear and quadratic terms; Figure 1a). When we used a yearly mean as the unit of replication (Table 1), the pollen

FIGURE 1 Relationship between indices of biotic interactions and year of measurement. (a) Pollen limitation index. (b) Pollen limitation index assuming seed predators are absent. (c) Seed predation index. (d) Combined index expressing proportion increase in seed production due to supplemental pollination and removal of seed predators. Curves indicate quadratic regression fits and 95% confidence intervals. Dashed line indicates zero effect

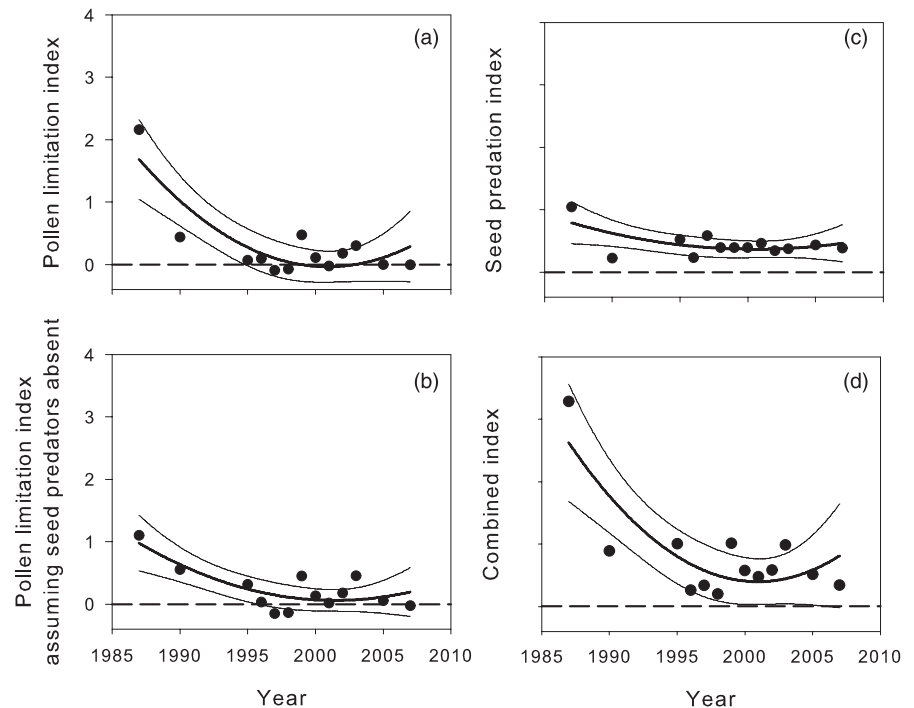


TABLE 1 Yearly estimates of pollen limitation index (PL index), seed predation index (Pred index) and potentially explanatory variables. Pollen load on HP: Mean stigmatic pollen load on supplementally hand-pollinated plants. Pollen load on C: Mean stigmatic pollen load on control plants. Visitation rate by all pollinators: Mean visits/flower/h. oviposition rate: Fly eggs/flower

Year	Snowmelt day	PL index	Pred index	Pollen load on HP	Pollen load on C	Pollen load index	Visitation rate	Oviposition rate
1987	132	2.16	1.04	—	—	—	—	—
1990	138	0.44	0.22	—	—	—	—	—
1995	170	0.066	0.52	135.28	124.05	0.090	—	—
1996	141	0.093	0.23	158.33	146.45	0.081	0.0250	—
1997	152	-0.094	0.58	180.49	166.58	0.083	0.0158	0.397
1998	140	-0.075	0.39	167.97	148.89	0.128	0.0164	—
1999	145	0.473	0.39	—	—	—	0.0171	0.459
2000	131	0.109	0.39	—	—	—	0.0541	0.429
2001	134	-0.027	0.46	—	—	—	0.0224	0.435
2002	115	0.179	0.34	—	—	—	0.0590	0.454
2003	143	0.301	0.37	167.44	107.14	0.563	—	0.256
2005	146	-0.002	0.43	137.46	142.87	-0.038	—	—
2007	121	-0.007	0.38	—	—	—	—	—

limitation index averaged 0.28 across the 13 years, a value that differs slightly from the average of 0.24 given above because of variation in number of sites measured per year. Similar trends were seen when we removed the effect of seed predators on seed set from the estimates of pollen limitation. Specifically, the effect of supplemental hand-pollination on seeds initiated per flower (whether eaten or not) also declined over years ($F_{1,11} = 7.42$, $p = 0.0198$ for linear coefficient) in a decelerating way (quadratic coefficient $F_{1,10} = 5.56$, $p = 0.0401$; Figure 1b). Eliminating the impact of seed predation

increased seeds per flower by 44% on average in these yearly analyses, but, unlike for hand-pollination, the index of seed predation did not change detectably with year ($F_{1,11} = 2.79$, $p = 0.1233$ for the negative linear coefficient and $F_{1,10} = 2.68$, $p = 0.1325$ for quadratic coefficient; Figure 1c). Simulating the removal of both pollen limitation and seed predation increased seed set by 80% on average, and that impact declined with year ($r = -0.64$, $p = 0.0192$), in decelerating fashion (quadratic coefficient $F_{1,10} = 8.36$, $p = 0.0161$; Figure 1d), just as had the effect of hand-pollination alone.

Neither index of pollen limitation changed detectably with the climate variable of snowmelt date (linear coefficient for pollen limitation index $F_{1,11} = 0.29$, $p = 0.5999$, quadratic coefficient $F_{1,10} = 0.19$, $p = 0.6736$). The year with the latest snowmelt in our dataset was 1995 and the earliest was 2002, and those 2 years had reasonably similar values for the pollen limitation index (0.066 and 0.179 respectively). Nor did the seed predation index change with snowmelt date (linear coefficient $F_{1,11} = 0.29$, $p = 0.7733$, quadratic coefficient $F_{1,10} = 0.01$, $p = 0.9063$). Thus we saw no evidence for an indirect effect of snowmelt date on the extent of pollen limitation or impact of seed predation on seed production in *I. aggregata*.

Although the pollen limitation index was unrelated to the date of snowmelt, it did correlate positively with the amount by which hand-pollination increased pollen deposition on stigmas of the same plants (Pearson correlation $r = 0.81$, $N = 6$ years, one-tailed $p = 0.0255$; Table 1). Perhaps surprisingly, the effect of supplemental hand-pollination on seeds per flower was not higher in years of lower pollinator visitation ($r = 0.18$, $N = 7$ years, $p = 0.71$). The seed predation index also did not correlate with oviposition rate ($r = 0.03$, $p = 0.94$), but the sample size of 6 years was small for this test, especially given that the two indices were estimated from different sets of sites.

3.2 | Question 2: How much do biotic interactions contribute to the overall impact of a climate variable on population growth?

We investigated the effects of average pollen limitation and seed predation by altering seed production in IPM models by the 28% increase in seeds per flower with hand-pollination (i.e. the absence of pollen limitation), 44% increase in seeds per flower in the absence of seed predation, and 80% increase in the absence of both pollen limitation and seed predation. These figures are not additive because they each represent a proportional increase and because the effect of seed predation was calculated from control plants alone and not hand-pollinated plants. Differences in the finite rate of increase (λ) among those scenarios and the control scenario (seed production as in the original IPM model (Campbell, 2019) varied with snowmelt date ($p < 0.0001$ for interactions of linear and quadratic coefficients). If all vital rates are allowed to vary to the extent observed with snowmelt date (Campbell, 2019), the control curve intersects the stable population with zero population growth ($\lambda = 1$) at day 130 (10 May; Figure 2a). That date is the expected snowmelt date forecasting 45 years into the future, although several past years have already had earlier snowmelts that are predicted to lead to negative population growth. Full pollination would only change the expected day when $\lambda = 1$ to day 128 (yielding a difference of 1.9 days), staving off consistent population decline only for an additional 14 years. Even eliminating both pollen limitation and seed predation would only change the expected day when $\lambda = 1$ to day 126 (Figure 2a), a difference of 4.2 days in snowmelt from the natural situation. We also considered the case for which seed production is assumed to be the

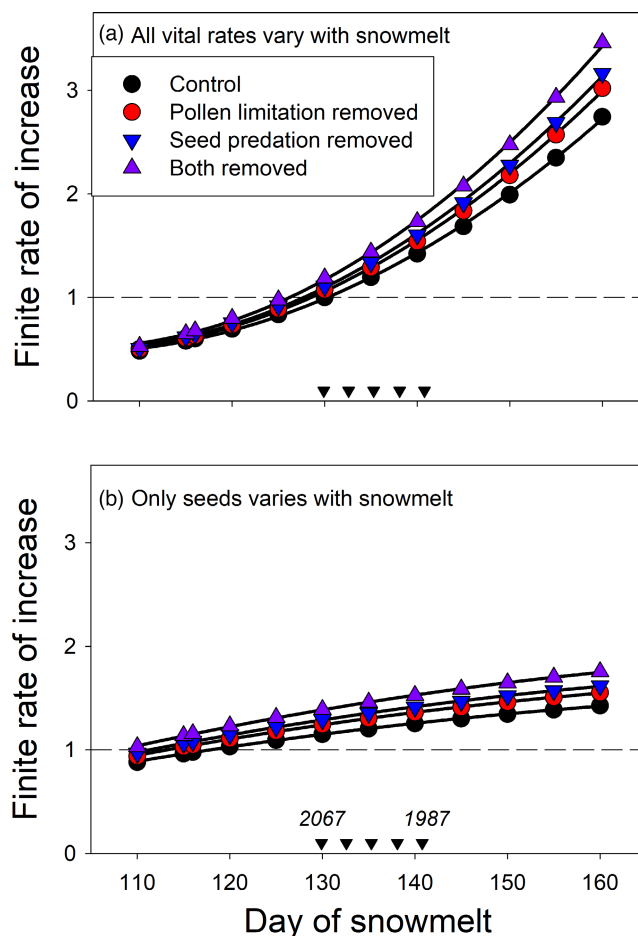


FIGURE 2 Relationships between finite rate of increase (λ) and snowmelt date in integral projection models for four scenarios: Control, pollen limitation removed, seed predation removed and both removed. Quadratic regression fits are shown. Small black triangles indicate predicted days of snowmelt at 20 year intervals from 1987 to 2067 based on data from (Powers et al., 2022). Note that time is proceeding from right to left along the X-axis. (a) all vital rates allowed to vary with snowmelt date to the extent observed. (b) Only seed production allowed to vary with snowmelt date

only vital rate changed by snowmelt date (Figure 2b). In that case the effect of supplemental pollination was equivalent to a 4.7 day later snowmelt rather than 1.9 day later, but that is because the general effect of snowmelt date on λ is greatly underestimated in that case. All effects of eliminating pollen limitation or seed predation were larger for later snowmelt dates, when seed production was higher and impacts of snowmelt on vital rates were amplified (Figure 2). Thus, the population level impact of those biotic interactions is expected to shrink as snowmelt gets earlier and earlier with climate change (Figure 2a).

4 | DISCUSSION

Ecologists increasingly recognize the critical need to incorporate biotic interactions into an understanding of how climate change

will alter population dynamics (e.g. Alexander et al., 2015; Gilman et al., 2010). In theory, climate-driven responses of organisms at a higher trophic level can have strong impacts on dynamics at a lower trophic level (Gilman et al., 2010), suggesting that plants might often be influenced by indirect impacts mediated through interactions with consumers. Although biotic and abiotic impacts on population growth are similar on average for plants (Morris et al., 2020), there are relatively few empirical studies comparing direct and indirect impacts of climate variables in the same plant species (Chu et al., 2015). Here, eliminating certain indirect effects of biotic interactions through supplemental full pollination and removal of seed predation could not compensate for the strong overall effects of early snowmelt on population growth in *I. aggregata*. Averaged over a 21-year period (1987–2007), both pollen limitation and seed predation had large effects on seed production, but impacts on population growth rate were nevertheless small in the context of how all vital rates change with snowmelt timing. Furthermore, neither pollen limitation nor seed predation correlated detectably with snowmelt timing, as would be expected if plant–animal interactions mediated indirect effects on that climate variable on population growth.

Although we did not detect a correlation of pollen limitation with snowmelt timing, based on an exceptionally long time series of supplemental hand-pollinations, we found a declining trend in pollen limitation of seed production over a 21-year period. One caveat is that trend is driven particularly by the exceptionally high pollen limitation observed in the earliest year of study (1987). Although that result was consistent across two sites, there could have been something else unusual about 1987, so it would be valuable to have data from even more years. We know of only one other study of pollen limitation that lasted more than 10 years, involving the lily *Erythronium grandiflorum* in populations near the RMBL. Even though this species exhibited no trend in pollen limitation between 1993 and 2018 (Thomson, 2019), like *I. aggregata* it showed considerable variation in pollen limitation over years. In our study system, we saw no evidence for a systematic change over years in visitation by pollinators (correlation with year $r = 0.63$, $p = 0.12$, $N = 7$ years). Pollinator visitation actually appeared higher in years of early snowmelt (correlation of visitation rate with snowmelt, $r = -0.86$, $N = 7$, $p = 0.0123$). That may be because flower number in *I. aggregata* is not sensitive to snowmelt date in the current year (Campbell, 2019), while flower number of other important resources for hummingbirds in the area, including *Delphinium nuttallianum* and *Delphinium barbeyi*, does decline with early snowmelt (Miller-Rushing & Inouye, 2009). In years of early snowmelt hummingbirds may be attracted to *I. aggregata* as one of the few remaining resources, or alter visitation behaviour in response to lower nectar and pollen production in *I. aggregata* (Waser & Price, 2016).

A plausible explanation for the decline in pollen limitation over years is a trend towards greater water limitation on seed set as the intensity of drought increases. Seeds initiated per flower in hand-pollinated plants trended lower with earlier snowmelt date in our study, but not significantly so ($p = 0.32$). Although the intensity of pollen limitation has declined over years, we would have expected

it to also decline with date of snowmelt in the spring if drought effects were most important during early summer prior to the start of summer monsoon rains. Regardless of the mechanism, the general decline in pollen limitation with year suggests that natural selection through female function on floral traits will weaken in this species (see also Campbell & Powers, 2015).

Effects of seed predators (flies and the occasional caterpillar) on seed set were roughly comparable or greater than those of pollen limitation in this system. Unlike for pollen limitation, we detected no systematic temporal change in those effects. And neither the index of seed predation nor the rate of oviposition by flies ($r = -0.39$, $p = 0.46$, $N = 6$ years) depended on snowmelt date in the spring. The lack of effect contrasts with the responses of some other insect herbivores to snowmelt date or winter snowpack. For example, aphid abundance on the host plant *Ligusticum porteri* was higher when snow was added to delay melting in subalpine meadows (Mooney et al., 2020). And, abundance of beetles, some of which were herbivores, was higher in years with greater snowpack in northern hardwood forests (Harris et al., 2019). Overall, we saw no evidence that the impact of either biotic interaction (pollination or seed predation) with *I. aggregata* responded systematically to earlier snowmelt. This independence suggests that abiotic and biotic impacts of climate change on population growth could in some cases be studied separately.

Integral projection models revealed strong effects of snowmelt timing that were not due to the studied biotic interactions. Our calculations suggest that with full pollination, population growth would drop below replacement for snowmelt on day 128 of the year rather than on day 130, a gain of only 1.9 days. That 2-day difference is projected to represent only 14 years of further climate change in this area. There is, however, high uncertainty in that estimate, not only because of uncertainty around the estimates of pollen limitation (see Figure 1a), and responses of vital rates to snowmelt that influence λ (Campbell, 2019), but also because of high uncertainty in the change in snowmelt (1.36 ± 0.5 days per decade). As climate change causes earlier and earlier snowmelt, the impacts of both pollen limitation and seed predation are likely to become less and less important in comparison. Removing pollen limitation and seed predation together could not ameliorate the strong effects of early snowmelt on seed production, suggesting that abiotic factors (or unstudied biotic interactions) have a stronger influence on pollination and seed predation. For a year in which snow melts out on day 130, which is projected to yield stable population growth under unmanipulated conditions, providing full pollination and removing seed predators would only increase λ from 1.00 to 1.19.

The primary effects of snowmelt date on population growth must be due either to direct abiotic effects or to indirect effects of biotic interactions that act at other stages of the life cycle besides seed production. IPMs showed that changes in λ with snowmelt date reflected the effect of snowmelt on seed germination most strongly, the effect on seed production second, and the effect on vegetative survival third (Campbell, 2019). In principle, seed germination could be influenced by interactions with soil microbes, upon which snowmelt timing has unknown

effects. Survival of vegetative rosettes to the next year is influenced by browsing of the apical meristem on vegetative rosettes, likely by pocket gophers or ground squirrels (Brody et al., 2007). Populations of these small mammals could in principle be changing with snowmelt date, but since *I. aggregata* survival responds only to snowmelt date the previous season, and not the current season (Campbell, 2019), they would have to impact population growth through effects on resource status which persist over winter. In populations at our study sites, 15% of vegetative rosettes are browsed, and they survive to flowering at a rate 70% as high as unbrowsed plants (Brody et al., 2007), such that survival averages 0.955 times ($=0.85 + [0.15 \times 0.70]$) as high in the presence of this biotic interaction. For a year in which snow melts on day 130, changing survival that much in our IPM only alters λ from 1.001 to 0.997, a negligible effect. Whereas we did not manipulate all biotic interactions in this study, these observations suggest that direct abiotic effects on survival are more likely to explain the influence of snowmelt timing on population growth. An experimental field study testing the impact of manipulating both snowmelt date and summer precipitation is in progress.

Most studies of pollen limitation and seed predation do not consider fitness during other parts of a plant's life cycle. For example, the most commonly used metric for assessing pollen limitation is fruit set (Knight et al., 2006), and it is rare to know to what extent those changes in fruit (or seed) set influence population growth rate (Price et al., 2008; Waser et al., 2010; see meta-analysis by Clark et al., 2007). Note that if we had only considered how changes in seed production influence λ , then the relative impacts of biotic interactions would have appeared much larger. This is likely for two reasons. First, in this system λ is generally higher if the impacts of early snowmelt during other parts of the life cycle are not accounted for (compare Figure 2a,b), and plant populations show more potential for strong impacts of herbivory at high population growth rates (Katz, 2016). Second, in *I. aggregata*, λ shows higher elasticity (proportional change with proportional change in a vital rate) to changes in survival and growth than to changes in reproduction (Campbell, 2019), as is common in perennial plants (Silvertown et al., 1993), lessening the importance of animals that interact at the reproductive stage in comparison with abiotic or other impacts on survival. Relatively few studies of population growth in plants consider both abiotic and biotic factors in the same system, but changes in soil potassium had stronger effects than seed predation for a perennial forest herb (Dahlgren & Ehrlén, 2009). Our results suggest that the relative impact of biotic interactions compared to abiotic factors can be overestimated if the entire life cycle is not accounted for as we did here. We urge other investigators of pollen limitation and seed predation to attempt to consider impacts in the context of a plant's entire life cycle.

5 | CONCLUSIONS

We found that pollen limitation and seed predation both contributed to seed production of *Ipomopsis aggregata* over a 21-year period.

Although the severity of pollen limitation declined over time, neither biotic interaction was related significantly to the date of snowmelt in the spring, an important climate variable in these subalpine ecosystems (CaraDonna et al., 2014). Overall, the strength of these biotic interactions as encapsulated in the impact of providing full pollination and eliminating seed predation could not compensate for the strong detrimental effects of early snowmelt on population growth rate in this subalpine plant, which may be driven directly through abiotic factors such as low soil moisture. We urge other investigators of population dynamics to explore how both abiotic factors and species interactions respond to climate change to provide more realistic predictions for changes in population growth rate than can be supplied with the more common focus on abiotic factors alone (Record et al., 2017).

ACKNOWLEDGEMENTS

We thank the many exceptional field research assistants who worked on these studies between 1995 and 2007. We also thank L. Bialic-Murphy and S. Kivlin for the inspiration for this study that grew from the opportunity to present the work at the American Society of Naturalists meeting in 2020. Comments by two anonymous reviewers strengthened the manuscript. Financial support was provided by NSF DEB-9805034 to M.V.P., N.M.W., D.R.C. and A.K.B., NSF DEB-0089643 to A.K.B. and R.E.I., NSF DEB-0455348 to R.E.I. and NSF DEB-1654655 to D.R.C. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

D.R.C. analysed the data and integrated the data into the integral projection model. M.V.P., N.M.W., A.K.B. and D.R.C. collected the field data in 1995 to 2002, and M.V.P. assembled the raw data. R.E.I. collected the field data in 2003 to 2007. D.R.C. wrote the first draft of the manuscript, and all authors contributed to the writing.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13875>.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Data Repository <https://doi.org/10.7280/D1D99J> (Campbell et al., 2022).

ORCID

Diane R. Campbell  <https://orcid.org/0000-0002-1147-846X>

Mary V. Price  <https://orcid.org/0000-0002-2223-7792>

Nickolas M. Waser  <https://orcid.org/0000-0001-8416-5037>

Rebecca E. Irwin  <https://orcid.org/0000-0002-1394-4946>

Alison K. Brody  <https://orcid.org/0000-0001-5759-2762>

REFERENCES

- Abdala-Roberts, L., Parra-Tabla, V., Campbell, D. R., & Mooney, K. A. (2014). Soil fertility and parasitoids shape herbivore selection on plants. *Journal of Ecology*, 102, 1120–1128.
- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525, 515–518.
- Baer, K. C., & Maron, J. L. (2018). Pre-dispersal seed predation and pollen limitation constrain population growth across the geographic distribution of *Astragalus utahensis*. *Journal of Ecology*, 106, 1646–1659.
- Bennett, J. M., Steets, J. A., Durka, W., Vamosi, J. C., Arceo-Gomez, G., Burd, M., Burklee, L. A., Ellis, A. G., Freitas, L., Li, J., Rodger, J. G., Wolowski, M., Xia, J., Ashman, T. L., & Knight, T. M. (2018). GloPL, a global data base on pollen limitation of plant reproduction. *Scientific Data*, 5, 180249.
- Bialic-Murphy, L., & Gaoue, O. G. (2018). Low interannual precipitation has a greater negative effect than seedling herbivory on the population dynamics of a short-lived shrub *Schiedea obovata*. *Ecology and Evolution*, 8, 176–184.
- Boggs, C., & Inouye, D. W. (2012). A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters*, 15, 502–508.
- Brody, A. K. (1992). Oviposition choices by a predispersal seed predator (*Hylemya* sp.). 1. Correspondence with hummingbird pollinators, and the role of plant size, density and floral morphology. *Oecologia*, 91, 56–62.
- Brody, A. K., & Irwin, R. E. (2012). When resources don't rescue: Flowering phenology and species interactions affect compensation to herbivory in *Ipomopsis aggregata*. *Oikos*, 121, 1424–1434.
- Brody, A. K., Irwin, R. E., McCutcheon, M. L., & Parsons, E. C. (2008). Interactions between nectar robbers and seed predators mediated by a shared host plant, *Ipomopsis aggregata*. *Oecologia*, 155, 75–84.
- Brody, A. K., & Morita, S. I. (2000). A positive association between oviposition and fruit set: Female choice or manipulation? *Oecologia*, 124, 418–425.
- Brody, A. K., Price, M. V., & Waser, N. M. (2007). Life-history consequences of vegetative damage in scarlet gilia, a monocarpic plant. *Oikos*, 116, 975–985.
- Campbell, D. R. (1991). Effects of floral traits on sequential components of fitness in *Ipomopsis aggregata*. *American Naturalist*, 137, 713–737.
- Campbell, D. R. (1997). Genetic and environmental variation in life-history traits of a monocarpic perennial: A decade-long field experiment. *Evolution*, 51, 373–382.
- Campbell, D. R. (2019). Early snowmelt projected to cause population decline in a subalpine plant. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 12901–12906.
- Campbell, D. R., Bischoff, M., Raguso, R. A., Briggs, H. M., & Sosenski, P. (2022). Selection of floral traits by pollinators and seed predators during sequential life history stages. *American Naturalist*, 199. <https://doi.org/10.1086/716740>
- Campbell, D. R., & Halama, K. (1993). Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology*, 74, 1043–1051.
- Campbell, D. R., & Powers, J. M. (2015). Natural selection on floral morphology can be influenced by climate. *Proceedings of the Royal Society B: Biological Sciences*, 282, 21050178.
- Campbell, D. R., Price, M. V., Waser, N. M., Irwin, R. E., & Brody, A. K. (2022). Data from: Comparative impacts of long-term trends in snowmelt and species interactions on plant population dynamics. *Dryad Digital Repository*. <https://doi.org/10.7280/D1D99J>
- Campbell, D. R., & Wendlandt, C. (2013). Altered precipitation affects plant hybrids differently than their parental species. *American Journal of Botany*, 100, 1322–1331.
- 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, 4916–4921.
- Cariveau, D., Irwin, R. E., Brody, A. K., Garcia-Mayeya, L. S., & von der Ohe, A. (2004). Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. *Oikos*, 104, 15–26.
- Chu, C., Kleinhesselink, A. R., Havstad, K. M., Peters, D. P., Vermeire, L. T., Wei, H., & Adler, P. B. (2015). Direct effects dominate responses to climate perturbations in grassland plant communities. *Nature Communications*, 7, 11766.
- Clark, C. J., Poulsen, J. R., Levey, D. J., & Osenberg, C. W. (2007). Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist*, 170, 128–142.
- Clow, D. W. (2010). Changes in the timing of snowmelt and streamflow in Colorado: A response to recent warming. *Journal of Climate*, 23, 2293–2306.
- Dahlgren, J. P., & Ehrlén, J. (2009). Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology*, 97, 666–674.
- de Jong, T., Waser, N. M., Price, M. V., & Ring, R. M. (1992). Plant size, geitonogamy, and seed set in *Ipomopsis aggregata*. *Oecologia*, 89, 310–315.
- Doak, D., & Morris, W. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–962.
- Ehrlén, J., Munzbergova, Z., Diekmann, M., & Eriksson, O. (2006). Long-term assessment of seed limitation in plants: Results from an 11-year experiment. *Journal of Ecology*, 94, 1224–1232.
- Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations: A practical guide to the integral projection model*. Springer International Publishing.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, 25, 325–331.
- Gomez, J. M. (2008). Sequential conflicting selection due to multispecific interactions triggers evolutionary trade-offs in a monocarpic herb. *Evolution*, 62, 668–679.
- Grant, V., & Wilken, D. (1986). Taxonomy of the *Ipomopsis aggregata* group (Polemoniaceae). *Botanical Gazette*, 147, 359–371.
- Harris, J. E., Rodenhouse, N. L., & Holmes, R. T. (2019). Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biological Conservation*, 240, 108219.
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89, 353–363.
- IPCC (2014). Climate change 2014: Synthesis report. In R. K. Pachauri & L. A. Meyer (Eds.), *Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change* (pp. 1–151). IPCC.
- Irwin, R. E., & Brody, A. K. (2011). Additive effects of herbivory, nectar robbing and seed predation on male and female fitness estimates of the host plant *Ipomopsis aggregata*. *Oecologia*, 166, 681–692.
- Juenger, T. E., & Bergelson, J. (1998). Pairwise versus diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. *Evolution*, 52, 1583–1592.
- Katz, D. S. W. (2016). The effect of invertebrate herbivores on plant population growth: A meta-regression analysis. *Oecologia*, 182, 43–53.
- Kearns, C. A., & Inouye, D. W. (1993). *Techniques for pollination biologists*. University Press of Colorado.
- Knight, T. M., Steets, J. A., & Ashman, T. L. (2006). A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany*, 93, 271–277.
- Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mitchell, R. J., & Ashman, T. L.

- (2005). Pollen limitation of plant reproduction: Pattern and process. *Annual Review of Ecology, Evolution and Systematics*, 36, 467–497.
- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vázquez, P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A. M., Regetz, J., & Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, 10, 299–314.
- Kuss, P., Rees, M., Aegisdóttir, H. H., Ellner, S. P., & Stöcklin, J. (2008). Evolutionary demography of long-lived monocarpic perennials: A time-lagged integral projection model. *Journal of Ecology*, 96, 821–832.
- Maron, J. L., Baer, K. C., & Angert, A. L. (2014). Disentangling the drivers of context-dependent plant-animal interactions. *Journal of Ecology*, 102, 1485–1496.
- Miller-Rushing, A. J., & Inouye, D. W. (2009). Variation in the impact of climate change on flowering phenology and abundance: An examination of two pairs of closely related wildflower species. *American Journal of Botany*, 96, 1821–1829.
- Mooney, E., Mullins, M., Uyl, D., Trail, S., Nguyen, P., Owens, J., Godtfredsen, E., & Heschel, S. (2020). Early snowmelt reduces aphid abundance (*Aphis asclepiadis*) by creating water-stressed host plants (*Ligusticum porteri*) and altering interactions with ants. *Arthropod-Plant Interactions*, 15, 33–46.
- Morris, W. F., Ehrlén, J., Dahlgren, J. P., Loomis, A. K., & Louthan, A. M. (2020). Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 1107–1112.
- Nicholson, A. J., & Bailey, V. A. (1935). The balance of animal populations. Part I. *Journal of Zoology*, 105, 551–598.
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326.
- Pederson, G. T., Gray, S. T., Woodhouse, C. A., Betancourt, J. L., Fagre, D. B., Littell, J. S., Watson, E., Luckman, B. H., & Graumlich, L. J. (2011). The unusual nature of recent snowpack declines in the north American Cordillera. *Science*, 333, 332–335.
- Powers, J. M., Briggs, H. M., Dickson, R. G., Li, X., & Campbell, D. R. (2022). Earlier snowmelt and reduced summer precipitation alter floral traits important to pollination. *Global Change Biology*, 28, 323–339.
- Price, M. V., Campbell, D. R., Waser, N. M., & Brody, A. K. (2008). Bridging the generation gap in plants: Pollination, parental fecundity, and offspring demography. *Ecology*, 89, 1596–1604.
- Price, M. V., & Waser, N. M. (1982). Experimental studies of pollen carryover: Hummingbirds and *Ipomopsis aggregata*. *Oecologia*, 54, 353–358.
- Price, M. V., & Waser, N. M. (1998). Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology*, 79, 1261–1271.
- Price, M. V., Waser, N. M., Irwin, R. E., Campbell, D. R., & Brody, A. K. (2005). Temporal and spatial variation in pollination of a montane herb: A seven-year study. *Ecology*, 86, 2106–2116.
- Price, M. V., Waser, N. M., Lopez, D. A., Ramirez, V. D., & Rosas, C. E. (2021). Predispersal seed predation obscures the detrimental effect of dust on wildflower reproduction. *International Journal of Plant Sciences*, 182, 277–285.
- Record, S., Strecker, A., Tuanmu, M., Beaudrot, L., Zarnetske, P., Belmaker, J., & Gerstner, B. (2017). Does scale matter? A systematic review of incorporating biological realism when predicting changes in species distributions. *PLoS One*, 13, e0194650.
- Sage, T. L., Price, M. V., & Waser, N. M. (2006). Self-sterility in *Ipomopsis aggregata* (Polemoniaceae) is due to pre-zygotic ovule degeneration. *American Journal of Botany*, 93, 254–262.
- Silvertown, J., Franco, M., Pisanty, I., & Mendoza, A. (1993). Comparative plant demography—Relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology*, 81, 465–476.
- Sloat, L. L., Henderson, A. N., Lamanna, C., & Enquist, B. J. (2015). The effect of the foresummer drought on carbon exchange in subalpine meadows. *Ecosystems*, 18, 533–545.
- Thomson, J. D. (2019). Progressive deterioration of pollination service detected in a 17-year study vanishes in a 26-year study. *New Phytologist*, 224, 1151–1159.
- Wadgyman, S. M., Ogilvie, J. E., Inouye, D. W., Weis, A. E., & Anderson, J. T. (2018). Phenological responses to multiple environmental drivers under climate change: Insights from a long-term observational study and a manipulative field experiment. *New Phytologist*, 218, 517–529.
- Waser, N., & Price, M. (1991). Reproductive costs of self-pollination in *Ipomopsis aggregata* (Polemoniaceae): Are ovules usurped? *American Journal of Botany*, 78, 1036–1043.
- Waser, N. M., Campbell, D. R., Price, M. V., & Brody, A. K. (2010). Density-dependent demographic responses of a semelparous plant to natural variation in seed rain. *Oikos*, 119, 1929–1935.
- Waser, N. M., & Price, M. V. (2016). Drought, pollen and nectar availability, and pollination success. *Ecology*, 97, 1400–1409.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Campbell, D. R., Price, M. V., Waser, N. M., Irwin, R. E. & Brody, A. K. (2022). Comparative impacts of long-term trends in snowmelt and species interactions on plant population dynamics. *Journal of Ecology*, 110, 1102–1112. <https://doi.org/10.1111/1365-2745.13875>