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Early snowmelt projected to cause population decline in a subalpine plant

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How climate change influences the dynamics of plant populations is not well understood, as few plant studies have measured responses of vital rates to climatic variables and modeled the impact on population growth. The present study used 25 y of demographic data to analyze how survival, growth, and fecundity respond to date of spring snowmelt for a subalpine plant. Fecundity was estimated by seed production (over 15 y) and also divided into flower number, fruit set, seeds per fruit, and escape from seed predation. Despite no apparent effects on flower number, plants produced more seeds in years with later snowmelt. Survival and probability of flowering were reduced by early snowmelt in the previous year. Based on demographic models, earlier snowmelt with warming is expected to lead to negative population growth, driven especially by changes in seedling establishment and seed production. These results provide a rare example of how climate change is expected to influence the dynamics of a plant population. They furthermore illustrate the potential for strong population impacts even in the absence of more commonly reported visual signs, such as earlier blooming or reduced floral display in early melting years.

climate change | fecundity | population dynamics | seed production | snowmelt

A critical challenge in predicting the biological impacts of climate change is to understand how the new environmental conditions will influence decline or growth of a population. Climate change has reduced the extent of snow cover in the Northern Hemisphere since the mid-20th century (e.g., by 11.7% per decade in June) and is projected to further reduce it as the average global temperature rises (1). In mountainous areas of the western United States, the snowpack water equivalent has declined (2), and, in at least some of those regions, the average date of snowmelt in the spring has advanced (3). That earlier snowmelt has been associated with shifts to earlier phenology in a large number of species, including blooming times in flowering plants (4–6). Whereas phenological shifts of plants in response to climate change are well documented (7), rarely is the impact of the phenological shift on reproduction known (8, 9). In general, few studies examine associations of climatic variables with the demography of individual plant populations. However, it is ultimately through changes in demographic vital rates that a population will persist or not in the face of environmental change.

An understanding of how climate influences plant demography can be separated into two problems: (*i*) how climate influences a vital rate and (*ii*) how that vital rate influences population growth. Studies of the climate sensitivity for any vital rate are relatively rare for plant populations (10), but that gap is most striking for the rate of reproduction through seed production, as reproduction is the vital rate that would be impacted by a shift in blooming time. Studies of how climate influences seed production have often focused on long-lived tree species, especially those exhibiting masting behavior (11–13). However, for tree species, there are only a handful of studies assessing seed limitation to population growth (reviewed in ref. 14). In contrast, for herbaceous species that lend themselves more easily to studies of seed limitation (14), studies of trends in fecundity that last longer than 10 y are extremely rare (15), especially in comparison with the large literature on masting trees (16). Only one study of which I am aware has combined these two types of information (17). Short-term experimental manipulations of climatic factors, including drought, CO_2, and temperature, have generally found larger effects on viability than fecundity components of fitness (18), but long-term consequences need not necessarily reflect responses seen in short-term experiments.

Here I report on a long-term study that integrated (*i*) the responses of vital rates to environmental conditions and (*ii*) the impact of those vital rates on population growth in the same plant species. It includes 15 y of data beginning in 2001 on how annual snowmelt date in the spring influences fecundity in the herbaceous subalpine plants *Ipomopsis aggregata* and *Ipomopsis tenuituba* (Polemoniaceae) and their hybrids. Plants were studied at two sites in the Colorado Rocky Mountains, a site at 2,900 m a.s.l. where *I. aggregata* grows and another at 3,050 m a.s.l. in a natural hybrid zone. Near these sites, the date of snowmelt has advanced by 1.34 d per decade over the years of 1935–2016 (3). For these plant species, there are also 25 y of demographic data on how survival and reproductive success influence the finite rate of increase for a population (19–21). Common garden data (22, 23) were analyzed with integral projection models (24) incorporating the dependence of vital rates on snowmelt and then projecting when early snowmelt is likely to drive the populations into decline. I asked four questions:

i) How does seed production by a plant depend upon the date of snowmelt in a given year?

Significance

Although negative impacts of climate change will ultimately occur by driving populations to extinction, we know remarkably little about such impacts on plant demography. Most long-term research focuses instead on shifts to early blooming. The present paper shows that climate change is expected to cause negative population growth in a plant population within a few decades. Early snowmelt is associated with reduced vital rates, with the effects on seedling establishment and seed production especially important to population dynamics. The negative impact is expected even without the changes in floral display so evident in other plant species in the same subalpine community. Thus, these mountain plant communities are at risk from declining snowpack.

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ii) To what extent is the pattern in seeds production driven by change in each of its multiplicative fitness components: number of flowers, fruits per flower, seeds per fruit, or likelihood that the seeds escape damage by predispersal seed predators?

iii) How will seed production change with expected future climate change and what is the predicted impact on population growth?

iv) How do responses of population growth to snowmelt timing depend on the changes in seedling establishment, survival, flowering probability, and seed production?

This study projects the impact of early snowmelt on the demography of a plant population based on integrating changes in component vital rates over the entire lifecycle. Whereas size of the floral display was relatively unaffected, early snowmelt was associated with low seed production as a result of changes in fruit production and seeds per fruit. Seedling establishment, probability of survival to the next year, and probability of flowering were also reduced by early snowmelt, but in some cases with a time lag of 1 y. The hybrid populations are likely already in decline and those of *I. aggregata* may follow within two to four decades, suggesting that even species not showing easily visible changes in floral display can experience high impacts of recent environmental change.

Results

Variation in Seed Production. At these two subalpine sites, an *Ipomopsis* sp. plant made 2.65 fewer mature seeds for every day earlier the snow melted in the spring [analysis of covariance (ANCOVA) on yearly means controlling for site, $F_{2,26} = 11.35$, $P = 0.0024$; $R^2 = 0.34$]. Mean seed production did not differ detectably between the two sites ($P = 0.21$). In a multiple regression, snowmelt date strongly predicted mean seed production ($F_{1,26} = 12.99$, $P = 0.0013$), whereas calendar year had no additional detectable linear effect ($F_{1,26} = 1.63$, $P = 0.2136$; Fig. 1). Mean seed production was not related to June and July rainfall in an ANCOVA controlling for site ($P = 0.17$). No evidence for lag effects of snowmelt or summer precipitation in the previous year were detected in ANCOVA on mean seed production ($P = 0.43$ for snowmelt in the previous year and $P = 0.61$ for summer precipitation in the previous year). The variance in relative seed production, a measure of the opportunity for natural selection (25), was not associated with site or snowmelt date in ANCOVA (both $P > 0.10$).

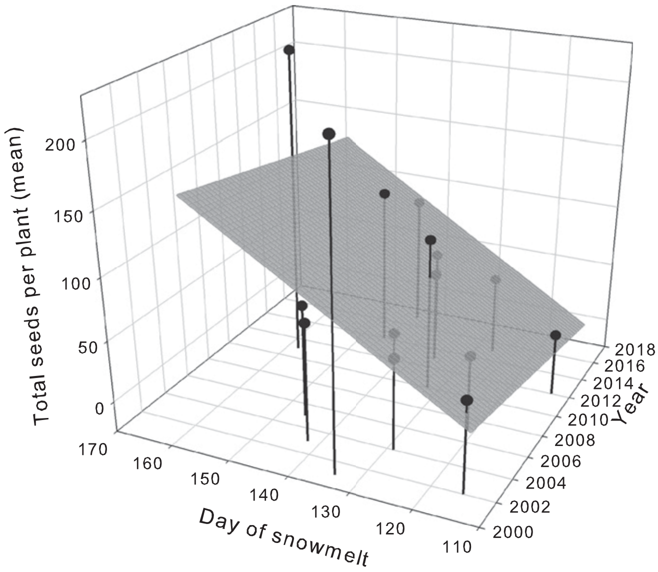

Fig. 1. The dependence of mean seeds per plant on ordinal day of snowmelt and year across 15 y of study. The plane represents the estimated partial regression coefficients from multiple regression.

Examining the multiplicative components of total seeds separately (Fig. 2 and *SI Appendix*, Table S1), these effects on total seeds were caused primarily by changes in two components: the proportion of flowers that set fruit and seeds per fruit. The first component (in order of timing), number of flowers produced by a plant, was not related to snowmelt date in the ANCOVA or a multiple regression that also included calendar year ($P = 0.39$ and $P = 0.34$, respectively). In contrast, proportion of flowers that set fruit declined with earlier snowmelt in an ANCOVA with site included ($F_{1,26} = 9.98$, $P = 0.0040$; Fig. 2*B*) and in a multiple regression that included calendar year ($F_{1,26} = 9.01$, $P = 0.0059$). Similar results were obtained for seeds per fruit, which declined by 0.025 for every day earlier the snow melted ($F_{1,26} = 5.28$, $P = 0.0299$; Fig. 2*C*) and remained significant in a multiple regression with calendar year ($F_{1,26} = 4.68$, $P = 0.0398$). For fruit set and seeds per fruit, only the effect of snowmelt date was detectable in multiple regression that also included calendar year. The proportion of fruits that escaped seed predation increased with earlier snowmelt, but the effect depended on site (snowmelt date × site interaction, $P = 0.05$). Nesting the effect of snowmelt date inside site showed a detectable effect of snowmelt only at the hybrid site (Fig. 2*D*), and the magnitude of the effect was small, with the proportion escaping seed predation increasing 0.005 for every day earlier the snow melted. Moreover, no independent effect of snowmelt date or calendar year on seed predation could be detected in a multiple regression (both $P = 0.07$). Of the four multiplicative fitness components of reproduction, only seeds per undamaged fruit showed a detectable difference between sites, with plants making 1.0 more seeds per fruit on average at the *I. aggregata* site ($F_{1,26} = 14.66$, $P = 0.0007$).

Impacts on Population Growth. Demographic impacts of snowmelt date were determined in two ways: (*i*) examining the impact of the changes in seed production by themselves, assuming no changes in other vital rates; and (*ii*) by using integral projection modeling (IPM) to incorporate impacts of changes in all vital rates. For the first approach, seed production required for positive population growth (i.e., finite rate of increase or $\lambda > 1$) was estimated from an age-structured model for an independent common garden experiment conducted between 1994 and 2006 at these same sites (21). For *I. aggregata* at the *I. aggregata* site, and assuming no changes in growth or survival, 77 undamaged seeds per reproductive plant were needed to maintain a stable population size. The analogous requirement was 74 undamaged seeds per plant at the hybrid site, using information for hybrids with *I. tenuituba* as the maternal parent, as natural hybrids almost always have that cytoplasmic genetic background (26). Mean seed production fell below that estimated replacement value for a stable population in 7 of 14 y at the *I. aggregata* site (Fig. 3*A*). At the hybrid site, mean seed production fell below replacement in 9 of 15 y, with SEs not overlapping the critical value in 8 of those years (Fig. 3*C*). Incorporating the percentage by which seed production differed in each year from values used in the original demographic model, and regressing the resultant value for λ on snowmelt date, the populations are predicted to be below replacement whenever snowmelt occurs before day 134 (14 May in nonleap years; SE = 20 d) or day 146 (25 May; SE = 20 d) at the two sites, respectively (Fig. 3 *B* and *D*). Over the past 84 y, snow has melted 0.138 d earlier each year (SE = 0.051, linear-regression $P < 0.01$; Fig. 4). Projecting a linear trend from the historical data on snowmelt date, the critical snowmelt day would be reached in 2035 at the *I. aggregata* site, with the hybrid site already past that point (Fig. 4), although there is high variance around the historical trend line.

The second approach used individual-level analyses in the two common garden experiments started in 1997 or later, and it revealed impacts of snowmelt timing on all vital rates. Like seed production, seedling establishment increased with snowmelt date in the year of measurement ($P = 0.0104$ at an independent but

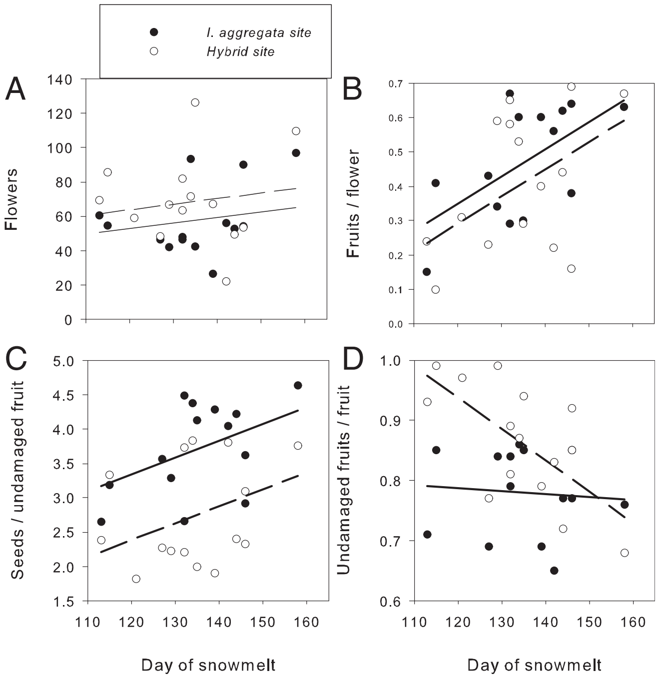

Fig. 2. The four multiplicative components of total seeds per plant as a function of ordinal day of snowmelt. Each point represents a mean value at the *I. aggregata* site (closed circle and solid line) or hybrid site (open circle and dashed line) in a particular year. Fits from ANCOVA are shown by parallel lines in cases in which the site-by-snowmelt day interaction was not significant ($P > 0.05$) and by separate lines for undamaged fruits/fruit (*D*). Bolded lines indicate models with significant effects of snowmelt day (*B* and *C*) or the interaction (*D*). Snowmelt day had no detectable effect on mean flower number (*A*).

nearby site; *SI Appendix*, Table S2). Vegetative growth did also at the *I. aggregata* site despite its measurement early in the season, but not at the hybrid site, yielding a site-by-snowmelt date interaction ($P < 0.001$). In contrast, late snowmelt increased survival to the next year and the probability of flowering in the next year only (*SI Appendix*, Table S2). A more conservative analysis on yearly mean values (ANCOVA as a function of mean size, lagged snowmelt date, and the factor of site) supported these effects of snowmelt date on mean survival ($P = 0.0106$ for date effect) and mean probability of flowering ($P = 0.0171$) with a 1-y time lag.

By using size-dependent integral projection models, elasticity of λ, or response to proportional changes, was higher for changes in growth and survival (0.389 and 0.680 at the *I. aggregata* and the hybrid site) than for changes in fecundity (0.306 and 0.160; in a 1-y time-delay model as implemented here, the elasticity for fecundity has to be multiplied by 2 for elasticities to sum to 1). Nevertheless, because seed production changed strongly with snowmelt date, λ responded more strongly to the changes in seed production than to any other vital rate except for seedling establishment (Fig. 5). The same change in seedling establishment had less impact on λ at the hybrid site because of differences in other vital rates that made λ less sensitive to that particular vital rate. Growth and survival depended less strongly on snowmelt date at the hybrid site than at the *I. aggregata* site (interaction of site and date; *SI Appendix*, Table S2), and allowing them to change with snowmelt had little influence on λ at the hybrid site (Fig. 5*B*). Incorporating the environmental sensitivity of all vital rates, λ is predicted to fall below a replacement value of 1 if the snow melts before day 130 (10 May) at the *I. aggregata* site or day 139 (19 May) at the hybrid site. Those values intersect the historical trendline for snowmelt (solid line in Fig. 4) in year 2064 for the *I. aggregata* site and 1999 for the hybrid site. Snowmelt dates before 1975 were estimated from runoff in the nearby East River, rather than direct observation. Excluding those data, snow is now melting 0.297 d earlier each year (SE = 0.155, $P = 0.0626$), making the projections direr for *I. aggregata* (intersections of the critical snowmelt date with the dotted line in Fig. 5 occur in 2018–2030).

Discussion

Widespread reductions in snowpack cover are one of the consequences of recent climate change (1, 2). One way they can influence terrestrial ecosystems is through an associated earlier date of snowmelt in the spring. For the subalpine plants studied here, earlier snowmelts in recent years are associated with reduced vital rates. In the region where these *Ipomopsis* plants were studied, the date of snowmelt is strongly correlated with snowpack water equivalent (www.gothicwx.org; $r = 0.87$, $P < 0.0001$ for the 15 y in this study). These factors result in a longer period of reduced soil moisture before onset of the summer monsoon rains in July. That lower water availability can in turn influence plant growth, survival, or reproduction.

One recent study also uncovered responses of vital rates to snowmelt timing in a subalpine plant (*Helianthella quinquenervis*) (9). Although that study suggested that survival would drive most of the response in population growth, it did not explicitly include the environmental sensitivity of the seed-to-seedling transition or of seed production. For *Ipomopsis*, those are the two vital rates that contributed the most to changes in λ with snowmelt in the integral projection model. Seedling establishment increased with later snowmelt despite the inability of a previous study on *Ipomopsis* with fewer data to detect the relationship (20), although that study did report a positive correlation coefficient and note that seedling establishment increases with precipitation during May and June.

Although λ showed greater elasticity to growth and survival, the strong increase in seed production in years of later snowmelt meant that it drove much of the environmental sensitivity in population growth. The two components of seed production that responded most were proportion fruit set and seeds per fruit

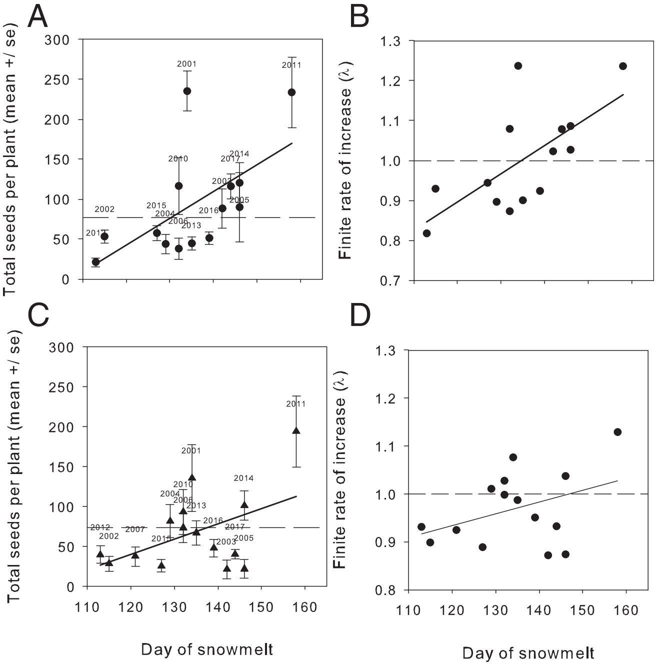

Fig. 3. Total seeds per plant against ordinal day of snowmelt separately for the two sites, including common garden and in situ plants. The predicted impact on the finite rate of increase (λ) based on demographic information from an independent experiment is also shown. (*A* and *B*) *I. aggregata* site. (*C* and *D*) Hybrid site. Error bars are SEs around the plotted means. The dashed lines indicate the seed production required for a stable population with $\lambda = 1$ assuming no changes in other vital rates with snowmelt.

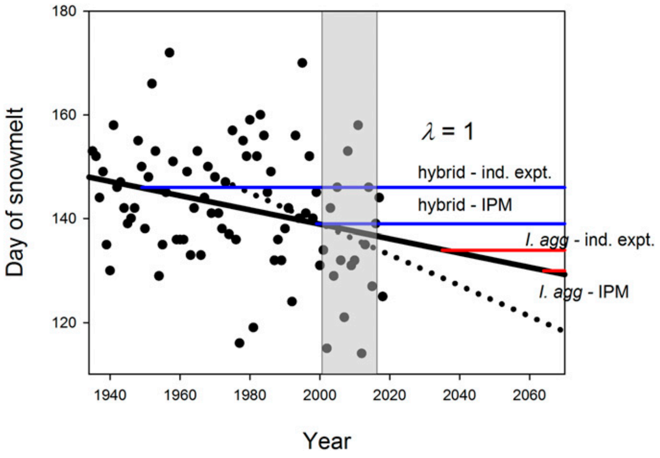

Fig. 4. Historical trend in ordinal day of snowmelt used to predict the year that a population will drop below replacement. Data on day of snowmelt are from ref. 3 and www.gothicwx.org. The solid black line shows the least-squares regression. The day of snowmelt for which the population is expected to have a finite rate of increase <1 is shown in red for the *I. aggregata* site (day 130 or 134 depending on model) and blue for the hybrid site (day 139 or 146 depending on model), using the data for seed production in the 15 y covered by the gray box. These snowmelt dates intersect the historical trend line in 2035 and 2064 at the *I. aggregata* site, depending on the demographic model. The hybrid site is already below replacement. The two models are based on an independent experiment starting in 1994 (ind. expt.) and the two common gardens analyzed with IPM. For comparison, the dotted line is the least-squares regression using just the directly observed snowmelt data from 1975 on, which, at the *I. aggregata* site, would intersect the critical day of snowmelt earlier.

rather than flower number. Those results suggest that the effects might be mediated indirectly through an influence on pollination as well as directly on resources for provisioning seeds, as supplemental pollination increased both of those components, and adding water and nitrogen increased seeds per fruit (as well as flower number) in previous studies of *I. aggregata* (27). A possible mechanism is that nectar or pollen production increase with higher soil moisture, as seen in an experimental study of *I. aggregata* (28). Hummingbird pollinators of that species visit high nectar-producing plants at increased rates (29). In contrast, flower size in a given year appears not to be associated with snowmelt date (23). It is also theoretically possible that snowmelt influences the extent of phenological match between blooming and presence of hummingbird or hawkmoth pollinators (30).

Survival of vegetative rosettes and probability that an *Ipomopsis* plant flowered were also reduced to some extent by early snowmelt, but with less impact on population dynamics. Survival and flowering probability depended on snowmelt timing in the previous year, such that current floral display in a year of poor snowpack (in terms of flowering probability and flower number) would show no apparent visual response.

The finding here of a long-term effect of climate on plant birth rate is extremely rare, as very few investigators have examined seed production over such long periods (reviewed in ref. 15). Impacts of climate change on demography have been far more commonly studied in animal populations (reviewed in ref. 10), but it is essential to understand these impacts in primary producers as well. Only one previous plant study of which I am aware has put long-term data on environmental sensitivity into a demographic model to predict likelihood of extinction (17). In that system, a perennial shrub on a lowland European island, negative impacts of increasing temperature on some vital rates were compensated by positive impacts on others, as was also observed in one spatial comparison of populations (31), and tempered by density-dependent population growth. In contrast, these mountain populations of *Ipomopsis* do not show compensation among vital rates. Furthermore, in *I. aggregata*, the finite rate of increase showed density dependence to seed input in only one of three populations that had some exceptionally low values for seed input (20). Therefore, density dependence would not often compensate for the negative impacts of early snowmelt on seed production.

Much more frequently studied as a vital rate in plant populations, perhaps because the data are easier to obtain, is the number of flowers. In the subalpine communities studied here, not only has phenology of many plant species shifted, but earlier snowmelt has also led to a longer midsummer period of low flower density (32). Unlike *Ipomopsis*, which showed no concurrent change in size of the floral display, several other herbaceous species in these subalpine communities (*Delphinium barbeyi*, *Erigeron speciosus*, and *H. quinquenervis*) show strongly reduced numbers of flowers in years of early snowmelt, primarily as a result of damage in early-season frost (4, 33). Seed production was also reduced in *E. speciosus* (34). The decline in seed production in *Ipomopsis* indicates that changes in climate can impact populations even in species that do not show easily visible changes in floral display.

An important finding of this study is that the reductions in seed production with early snowmelt and reduction in snowpack water equivalent were sufficient to expect populations to decline with climate change. The population at the center of the hybrid zone appears already to be below replacement, as are nearby populations of *I. tenuituba*, as a result of scarcity of hawkmoth pollinators, even without taking into account trends in snowmelt timing or how the pollinators themselves might respond to climate change (35). The population of *I. aggregata* is predicted to fall below replacement within two to four decades unless the ecological loss in fecundity is outpaced by evolutionary adaptation, which would have to be very rapid (36). Uncertainty in these estimates is relatively high, and seedling establishment had to be estimated from a different site. The prognosis is for even more rapid decline if projections use only the more rapid observed snowmelt from the past four decades, although the impact of the high variance around the trendline was not explored, and variability in climate can have large demographic impacts depending on longevity (37). That uncertainty underscores the need for more long-term data of this sort to refine our ability to

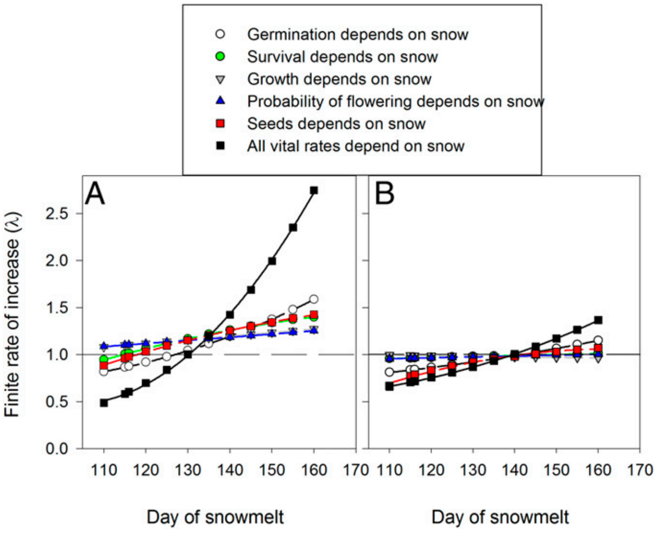

Fig. 5. Results of integral projection models showing the responses of the finite rate of increase (λ) to changes in each vital rate with snowmelt (bottom half of *SI Appendix*, Table S2). (*A*) *I. aggregata* site. (*B*) Hybrid site. Each vital rate followed its basic size-dependent model (top half of *SI Appendix*, Table S2) when it was not varied. Dashed lines show best second-order polynomial fits for environmental sensitivity of individual vital rates. Solid lines show fits when all vital rates are allowed to vary with snowmelt.

predict the impacts of climate change. However, sufficient demographic data even to make a prediction about average date of population decline, as done here, are very rare. Temporal studies of plant responses to climate have tended instead to focus on phenological changes in blooming, changes in distribution (7), or, more rarely, change in sex ratio (38). Phenology of flowering, in particular, is one of the most visible signs of climate change worldwide and has received much attention (6). There are abundant data on blooming date over four decades for 60 other plant species in this region of the Colorado Rocky Mountains (4, 5), providing one of the longest data sets in the world on plant phenology, but it is rarely known whether the observed changes in blooming impact vital rates sufficiently to cause a population to decline (9). To understand the expected impacts of climate change, it will be important in future studies to address directly the impacts on population dynamics.

Methods

Study Sites and Species. *I. aggregata* is an herb that is widely distributed through the mountains of the western United States and British Columbia. In some areas, it comes into contact with its close congener *I. tenuituba* (39). The two sites used in this study were located at Poverty Gulch, Gunnison National Forest, Colorado. The lower elevation site (site L in ref. 30) was at 2,900 m elevation, where populations of *I. aggregata* subsp. *aggregata* grow. The higher elevation site (site I in ref. 30) was at 3,050 m elevation in the center of a natural hybrid zone between that species and *I. tenuituba* subsp. *tenuituba*. The herbaceous plants are monocarpic, spending 5 y on average at these sites as a vegetative rosette, then blooming only once before setting seed and dying (21). Population growth, at least in *I. aggregata*, is known to be seed-limited, and there is no seed bank (19).

Most measurements of vital rates came from plants growing from seed produced through hand-pollinations and planted into these two sites as parts of common garden studies. Seed production was also obtained from naturally occurring plants, and seedling establishment relied on separate studies (19, 20). The first set of plantings was made in 1997 and 1998, as described in ref. 22. It included seeds of *I. aggregata*, *I. tenuituba*, both reciprocal F_1 hybrids (i.e., with *I. aggregata* as the maternal plant and *I. tenuituba* as the maternal plant), both reciprocal F_2 hybrids, reciprocal backcrosses of the F_1 to both parent species, and seeds from crosses between natural hybrids. These plants mostly bloomed during 2001–2007, generating 7 y of data on fecundity.

A second set of seeds was planted in 2007 and 2008, as described in ref. 23. It included seeds of *I. aggregata*, *I. tenuituba*, both reciprocal F_1 hybrids, and F_2 hybrids generated by crossing pairs of F_1 plants in both reciprocal directions. These plants bloomed during 2010–2017, generating an additional 8 y of data on fecundity. Because relatively few plants bloomed after 2012, fecundity from in situ naturally occurring plants at the two sites in 2013–2017 were also tracked. The 141 in situ plants were *I. aggregata* and natural hybrids, which include advanced-generation hybrids, just as in the experimental plantings (26, 40). In total, 7,963 seeds from 308 families were planted in these two common garden experiments, 1,736 seedlings established, and 393 survived to flowering (after 2–11 y).

Measurement of Vital Rates. As seeds were planted into the common gardens in a grid every 10 cm, it was possible to track individuals throughout their lifetimes. The inclusion of four planting years and the addition of in situ plants decoupled calendar year (and hence snowmelt date) from the size of the plants so that it was possible to examine dependence of survival of vegetative individuals, growth, probability of flowering, and seed production on both variables. To determine survival of vegetative individuals and probability that a surviving plant flowered, seedlings were followed in subsequent years until they died or until they flowered and then died. Starting with individuals of age 2 y, size was measured in millimeters as length of the longest leaf during late June or early July. Size was measured only on vegetative rosettes, so seed production was modeled as a function of size in the previous year. For each plant that bloomed, total seeds produced by the plant were measured as described in ref. 41, giving the few plants that bloomed but failed to set any seed a value of zero. Four multiplicative components of total seeds were also determined: number of flowers produced, proportion of flowers that set a fruit (whether intact or with seeds consumed), proportion of fruits that were undamaged, and seeds per undamaged fruit. Damage was caused by a fly that consumes all seeds in the fruit before dispersal (42), *Delia* sp. (Anthomyiidae), or a caterpillar that consumes the entire fruit (Noctuidae) (43).

In these common garden experiments, the seeds were deliberately planted just under the soil surface to enhance germination. Thus, seedling establishment was instead estimated from 10 y of independent data on natural seed input, or seeds sown to mimic natural input, and seedling density the following years from other sites. Specifically, the 10 y (1996–2005) of published observational data on natural seed input and emergence of 9,938 seedlings from sites at the Rocky Mountain Biological Lab (RMBL), Gothic, CO (20), were combined with additional data from two experiments that overlapped and provided a second estimate in 1998 and two additional estimates in 1999 from 3,932 seeds (19). In each of the 10 y, results were averaged across studies to estimate the proportion of seedlings that emerged.

Basic Analyses of Seed Production. To address question 1, ANCOVA was used to model the mean total seed production in a given year as a function of date of snowmelt and the fixed factor of site. Values were averaged across plants from a given year (or site–year combination) before analysis. A preliminary analysis had shown that *I. aggregata*, *I. tenuituba*, and hybrid plants showed similar responses of total seed production to snowmelt date ($P = 0.139$ for interaction between type of plant and day of snowmelt). Later snowmelt is associated with greater soil moisture in mountainous regions, with effects lasting for as long as 4 mo after snowmelt (44). Date of snowmelt was taken from records at nearby Gothic, CO, 8 km from the common gardens and at a similar elevation near 2,900 m (http://gothicwx.org/). A similar ANCOVA was run by using summer precipitation between June 1 and July 15, the period when inflorescences of these *Ipomopsis* plants are forming buds and flowers. Lag effects were tested by rerunning these analyses of covariance but using snowmelt date (or summer precipitation) in the preceding year. To test whether snowmelt date or other environmental variables that change with year better predict seed production, a multiple regression of seed production on date of snowmelt and calendar year was also performed. Because no evidence for a site-by-snowmelt date interaction was found ($P = 0.39$), this multiple regression used the mean seed production averaged over both sites. Question 2 was addressed by running these same statistical models for each of the four fitness components that multiply to total seeds. ANCOVAs and multiple regressions were performed with procedure GLM and type III SS in SAS version 9.3. Including the common garden and in situ individuals, fecundity was measured for 534 plants across the 15 y.

Demographic Models. To address question 3, I took two approaches. The first approach had the advantage of using an independent set of data on demography, did not require any estimates of size, and specifically focused on the types of plants that would occur naturally at those sites. The second approach had the advantage of allowing IPM based on size, which facilitated incorporation of the dependence of vital rates on snowmelt but had to be estimated for seedlings. For the first approach, I made use of a third common garden experiment started from 3,129 seeds from 44 full-sib families in 1994 at these same sites (21), for which all plants have now died, with or without leaving descendants, providing complete demographic information over 12 y. As seeds were all planted in the same year, age was associated with snowmelt date, so I did not include this experiment in the IPM incorporating snowmelt date explicitly. As in the other common garden experiments, the seeds were deliberately planted just under the soil surface to enhance survival of seedlings, so I adjusted survival rates by using my independent measure of seedling establishment from naturally sowed seeds (mean of 0.056 = 41% as high as for individually planted seeds). I used an age-dependent model, as in previous studies with *Ipomopsis*, including that particular experiment (21), to model its demography. For this purpose, I restricted the estimates to (*i*) crosses between two *I. aggregata* plants planted at the *I. aggregata* site and (*ii*) F1 hybrids planted at the hybrid site, including only those with *I. tenuituba* as the maternal parent, as nearly all natural hybrids have that cytoplasmic background (26). For those two scenarios, I determined the actual mean fecundity and the new mean fecundity needed to generate zero population growth (λ or finite rate of reproduction = 1). The finite rate of reproduction was the dominant right eigenvalue for the Leslie projection matrix with entries averaged over the full-sib families of seeds. Then, to find the corresponding estimated day of snowmelt, I used the regression equation for seed production at the given site. SEs and CIs on those days of snowmelt were calculated with the function inverse.predict in the package "chemical" in R 3.4.1. Finally, to estimate the year in which snowmelt is projected to occur at that time, I used the 82-y data set for Gothic, CO, analyzed in ref. 3 plus the additional years of 2017–2018 now available from http://gothicwx.org/ to describe the regression relationship between snowmelt date and calendar year.

My second approach to examining the influence of seed production on population growth was also used to answer question 4 and address more generally the dependence of population growth on environmentally sensitive vital rates. I used integral projection models, returning to the two later common garden experiments (planting years 1997, 1998, 2007, and 2008) for these models. Seedling establishment (seedlings in year $t + 1$/seeds in year t) ranged from 0.0004 to 0.1008 across the 10 y of data from other sites (19, 20). Those

10 yearly averages were modeled as a function of snowmelt date in year $t + 1$ (*SI Appendix*, Table S1), employing a logit link to bound the function above zero, although residuals for these proportions were normally distributed. For seedling establishment only, the same vital rate function was thus used for both the *I. aggregata* and hybrid sites. Other vital rates were modeled as functions of size (ln-transformed length of longest leaf), snowmelt date, and site (fixed factor). Interactions with site were included only if they were significant in initial models according to likelihood ratio statistics for type III analyses. I first ran models without snowmelt date to obtain overall parameter estimates and then added in snowmelt date and potential interactions of size and site with snowmelt date to those basic models. Models were tried with snowmelt date in the current year and with snowmelt date in the previous year to allow for lag effects of soil moisture, with the function explaining the most variance chosen for the IPM, as the intent was to model the impact of sustained changes. For each vital rate, I then added the type of plant (*I. aggregata*, *I. tenuituba*, or hybrid) to the model. Type of plant had a detectable effect ($P < 0.05$) only on the probability of flowering, so, for that vital rate, I estimated parameter values after excluding *I. tenuituba*. Distributions and link functions used for the generalized linear models, implemented in Proc Genmod in SAS version 9.3, are provided in *SI Appendix*, Table S2.

In building the IPM, I used a time-delay model for a monocarpic plant, in which fecundity in year $t + 1$ depended on size in year t, as size was not measured on the flowering individuals (45). In a time-delay model, the overall kernel describes transitions from one size to another for individuals of current size and for individuals of size 1 y previously (24, 45). Size was also unavailable for seedlings, and mean size and SD for those individuals of age 1 y were estimated by back-calculation of one time step from the measured size at age 2 y, using the growth model for vegetative rosettes (*SI Appendix*, Table S2). I determined λ for 12 snowmelt dates ranging from days 110 to 160 through iterating the model until convergence, following the time-delay model previously described (45). I determined the overall elasticity to survival/growth and to fecundity numerically through perturbation of the survival/growth and fecundity kernels, as deterministic solutions are unavailable for a time-delay model. I performed all IPM modeling in R 3.4.1 by using code modified from ref. 45 to allow all vital rate parameters to vary with snowmelt date instead of just seedling establishment as in the original code (details in *SI Appendix*, *SI Methods*).

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