ECOLOGY

Climate warming drives local extinction: Evidence from observation and experimentation

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Despite increasing concern about elevated extinction risk as global temperatures rise, it is difficult to confirm causal links between climate change and extinction. By coupling 25 years of in situ climate manipulation with experimental seed introductions and both historical and current plant surveys, we identify causal, mechanistic links between climate change and the local extinction of a widespread mountain plant (*Androsace septentrionalis*). Climate warming causes precipitous declines in population size by reducing fecundity and survival across multiple life stages. Climate warming also purges belowground seed banks, limiting the potential for the future recovery of at-risk populations under ameliorated conditions. Bolstered by previous reports of plant community shifts in this experiment and in other habitats, our findings not only support the hypothesis that climate change can drive local extinction but also foreshadow potentially widespread species losses in subalpine meadows as climate warming continues.

INTRODUCTION

Earth is currently experiencing a global mass extinction that is threatening diversity across the taxonomic tree (*1*, *2*). Because biodiversity is critical to processes that sustain all life (*3*–*5*), we must identify factors driving these extinctions to predict, prepare for, and ultimately mitigate the loss of genetic-, species-, and ecosystem-level diversity.

Although numerous studies implicate climate change in population declines, local extinctions, and elevated global extinction risk (*6*–*10*), we have limited direct evidence of causal links between climatic changes and extinction. Observational studies that reveal correlations between changes in climate and documented extinctions may suggest, but cannot confirm, cause and effect (*11*, *12*). Experimentation remains the gold standard for identifying causation, yet time lags in ecological and evolutionary responses to local change limit the ability of short-term experiments to assess ultimate effects on population size (*13*, *14*). Finally, because climate change may have profoundly different effects on performance throughout an organism's life cycle, studies that use a subset of life history stages to predict long-term effects of local change on population viability may markedly under- or overestimate extinction risk (*15*).

Here, we report causal, mechanistic links between climate warming and local extinction. We identified these links by coupling 25 years of climate manipulation (the "Warming Meadow") with longitudinal abundance surveys and experimental seed introductions of a native, mountain wildflower (*Androsace septentrionalis*). This approach has allowed us to (i) demonstrate that local warming is driving local extinction and (ii) identify demographic mechanisms that underlie precipitous declines in population size and belowground seed reservoirs.

BACKGROUND

A. septentrionalis (Primulaceae; Fig. 1A) is an annual to short-lived perennial wildflower that grows along wide elevation and climate gradients across the Northern Hemisphere (*16*, *17*). Near the southern limit of its geographic range, *A. septentrionalis* naturally occurs in the Warming Meadow, the world's longest-running active-heating warming experiment (Fig. 1, B and C) (*18*–*20*). This climate manipulation experiment, conducted in the Rocky Mountains of Colorado, consists of five heated plots interspersed between five control plots. Since January 1991, infrared radiators suspended over heated plots have raised soil temperatures by 1.4° to 3.8°C, decreased growing season soil moisture by ~15 to 20%, and advanced spring snowmelt date by a magnitude that has increased from ~1 week to ~1 month over the course of the experiment (Fig. 2 and tables S1 and S2) (*18*, *19*). These warming-induced changes simulate the magnitude of predicted change over the next 25 to 50 years (*21*–*24*) and mimic the microclimatic conditions of *A. septentrionalis* populations growing at lower elevations (Fig. 2B).

RESULTS AND DISCUSSION

To answer the question, "can climate warming drive local extinction?" we conducted annual abundance surveys of *A. septentrionalis* in the Warming Meadow from 2013 to 2016, finding and permanently marking all individuals in heated and control plots. Although prewarming data reveal that *A. septentrionalis* was initially distributed evenly between treatments ($\chi^2 < 0.01$, $P = 0.964$) (fig. S1 and table S3), heated plots now have ~91% fewer individuals than control plots ($\chi^2 = 19.30$, $P < 0.001$) (tables S3 and S4). These annual surveys reveal that experimental warming induces precipitous declines in the abundance of seedlings ($\chi^2 = 19.19$, $P < 0.001$) and established plants ($\chi^2 = 20.95$, $P < 0.001$), driving population sizes to, or dangerously close to, zero (Fig. 3 and tables S3 and S4). *A. septentrionalis* is now locally extinct in one heated plot, and population sizes in the remaining heated plots are far below conservative quasi-extinction thresholds—the point below which populations are unable to rebound due to risks associated with genetic, demographic, and environmental stochasticity (*15*, *25*, *26*).

To identify mechanisms driving these warming-induced declines and local extinctions, we investigated the effects of experimental warming on the performance of *A. septentrionalis* throughout its life cycle (Fig. 4A). By combining results from a seed introduction experiment with those from a 4-year longitudinal study of naturally occurring Warming Meadow individuals, we found that experimental warming (i) stimulates seedling emergence ($\chi^2 = 12.10$, $P < 0.001$), (ii) reduces early seedling survival ($\chi^2 = 9.27$, $P = 0.002$), and (iii) decreases the probability

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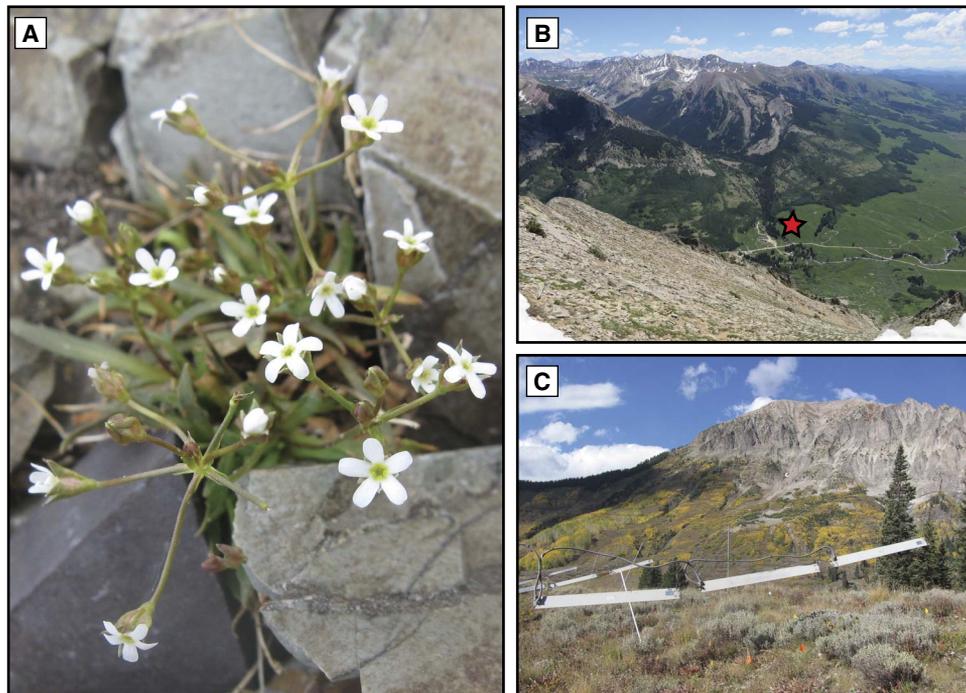
Fig. 1. A. septentrionalis and the Warming Meadow. (**A**) A. septentrionalis, also known as Northern rock jasmine and Northern fairy candelabra, grows along wide global and local climate gradients. Here, it is pictured growing on the rocky summit of Treasury Mountain in the Elk Range of the Colorado Rocky Mountains (elevation, 4103 m). (**B**) The Warming Meadow, indicated by the red star, is located at the Rocky Mountain Biological Laboratory (Gunnison County, CO; elevation, 2929 m). (**C**) In the Warming Meadow, suspended infrared radiators have actively warmed five heated plots night-, day-, and year-round since 1 January 1991. Photo credit: A. M. Panetta, University of Colorado, Boulder.
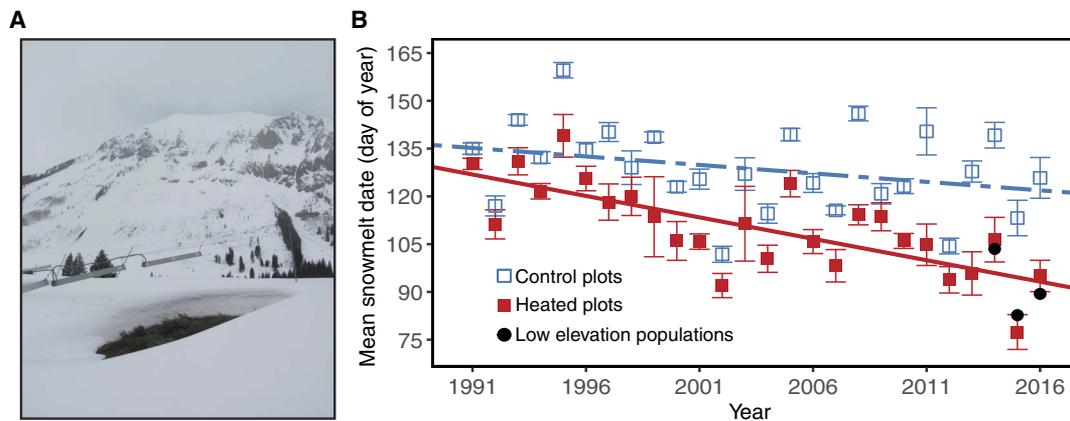

Fig. 2. Experimental warming accelerates advancing spring snowmelt. (**A**) In early spring, bare ground appears in heated plots when adjacent control plots remain blanketed with snow. Photo credit: A. M. Panetta, University of Colorado, Boulder. (**B**) Experimental warming accelerates rates of advancing spring snowmelt caused by contemporary climate change (treatment × year: $F = 15.19$, $P < 0.001$). Over the past 2.5 decades, spring snowmelt in control plots has advanced by ~0.5 days per year ($F = 11.88$, $P < 0.001$), whereas spring snowmelt in heated plots has advanced by ~1.3 days per year ($F = 92.30$, $P < 0.001$). Experimental warming also simulates the timing of spring snowmelt in warmer, drier A. septentrionalis populations that occur naturally at lower elevations. Means indicate average yearly snowmelt date ($n_{control} = 5$, $n_{heated} = 5$, $n_{low-elevation\ populations} = 2$), and error bars indicate ±1 SE.

that established plants reach ages of peak reproductive output ($\chi^2 = 7.17$, $P = 0.007$) (Fig. 4B and tables S5 to S7). Moreover, experimental warming negatively affects multiple components of reproductive success, resulting in a ~92% drop in per capita seed production ($\chi^2 = 27.09$, $P < 0.001$) (tables S8 and S9).

Beyond explaining precipitous abundance declines, these heating-induced effects on performance throughout the life cycle reveal a relatively cryptic yet critically important response to local warming: the

decline of belowground seed banks. Seed banks, which consist of viable, dormant seeds, grow by yearly deposits made by reproductive individuals and decline by yearly withdrawals in the form of emerging seedlings (27). By simultaneously decreasing deposits ($\chi^2 = 27.31$, $P < 0.001$) (Fig. 5A and table S9) and increasing withdrawals (Fig. 5B and tables S5 and S6), local warming purges belowground seed banks. Consequently, in any given year (t), the abundance of seedlings occurring naturally in heated plots depends on the reproductive output of established plants
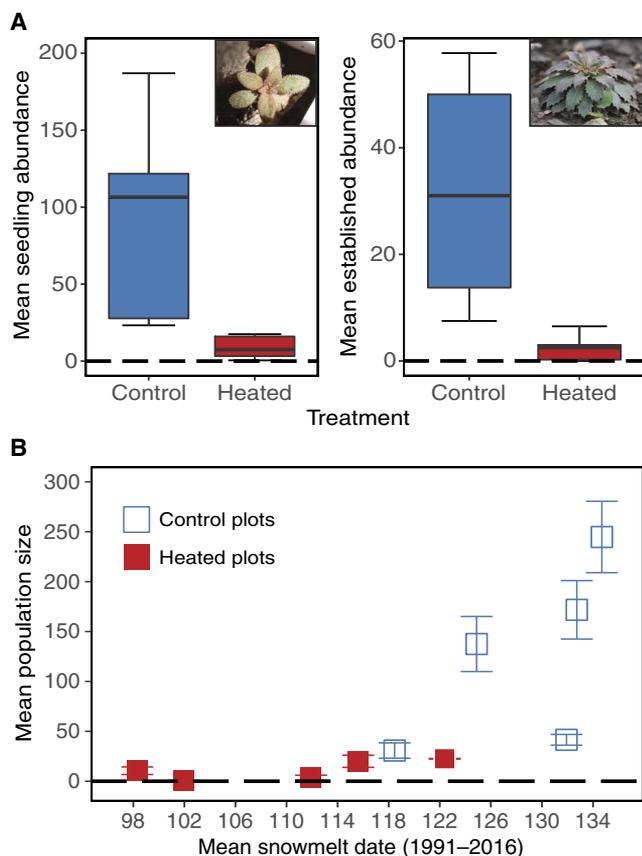
Fig. 3. Experimental warming reduces the abundance of seedlings and established plants, driving population sizes toward zero. (**A**) Relative to neighboring control plots, heated plots have ~90% fewer seedlings (C = 93.3 ± 30.8, H = 9.0 ± 3.4) and ~92% fewer established plants (C = 32.0 ± 9.8, H = 2.5 ± 1.2). Data indicate average yearly abundance per plot from 2013 to 2016 ($n_{control}$ = 5, n_{heated} = 5). Photo credit: J. B. Curtis, University of Colorado, Boulder. (**B**) After 25 years of experimental warming, heated-plot population sizes are either at or near absolute local extinction (indicated by dotted black line). Earlier snowmelt, across all meadow plots and both treatments, is strongly associated with lower population size (χ^2 = 21.76, P < 0.001). Means indicate average abundance in each of the ten warming meadow plots from 2013 to 2016 (n = 4 per plot). Error bars indicate ±1 SE.

in only $year_{t-1}$ (χ^2_{t-1} = 17.51, P_{t-1} < 0.001; χ^2_{t-2} = 0.75, P_{t-2} = 0.385), whereas the abundance of seedlings in control plots depends on the reproductive output of established plants in both $year_{t-1}$ and $year_{t-2}$ (χ^2_{t-1} = 9.16, P_{t-1} = 0.002; χ^2_{t-2} = 4.09, P_{t-2} = 0.043) (table S10).

In addition to identifying proximate, demographic links between climate warming and local extinction, this study reveals that responses to experimental warming accurately predict ongoing population declines that are likely caused by anthropogenic climate change. In the early 1990s, *A. septentrionalis* was evenly distributed across control plots, exhibiting no relationship with snowmelt date (χ^2 = 0.01, P = 0.904) (fig. S2 and table S3). After decades of accelerated climate warming (23, 24) and associated advances in spring snowmelt (Fig. 2B) (21), abundance in control plots exhibits a positive relationship with snowmelt date (χ^2 = 3.15, P = 0.076) (Fig. 3B and table S3), and the population size of *A. septentrionalis* in the warmest, earliest-melting control plot now matches that in the coolest, latest-melting heated plots (Fig. 3B).

CONCLUSIONS

Mounting evidence suggests that climate warming is a driver of population declines and local extinctions, causing shifts in community composition and reductions in diversity across a variety of species and systems (6, 7, 28–34). The study reported here shows that climate warming can cause local extinction and provides unique insight into demographic mechanisms that likely underlie these more widespread patterns of decline. Our findings also demonstrate that the proximate drivers of local extinction due to climate warming affect multiple life stages and, thus, serve to guide future investigations into the ultimate ecological and physiological mechanisms of warming-induced population declines. Finally, our findings paint a bleak picture for the persistence of native, shallow-rooted subalpine wildflowers in the face of climate change. Because the Warming Meadow is in a site with locally high *A. septentrionalis* densities, short-distance seed immigration undoubtedly occurred into the experimental plots. Nevertheless, heated populations are either gone or at the brink of local extinction, and control populations in the warmest microenvironments are in decline. Thus, local dispersal is unlikely to prevent local extinction as spring advances and temperatures rise. Furthermore, warming depletes seed banks, which reduce extinction risk in variable environments (35–38). Because climate change is projected to increase environmental variation and the frequency of extreme events (39), negative effects of warming on extinction-buffering seed banks will likely compound population declines. Although this study focuses on *A. septentrionalis*, decades of climate warming in the Warming Meadow have caused community-level shifts from non-woody to woody vegetation (18, 19). These shifts, driven by reductions in some of the largest, most abundant wildflower species (for example, *Erigeron speciosus*, *Delphinium nuttallianum*, *Mertensia fusiformis*, and *Lathyrus leucanthus*) and an accompanying increase in the dominant woody shrub *Artemisia tridentata* (18, 19, 40–42), suggest that *A. septentrionalis* is likely a "canary in a coal mine"—its precipitous decline in warmed microsites is a warning of potentially widespread local extinctions across subalpine meadow communities as climate warming continues.

## MATERIALS AND METHODS
Study sites
The Warming Meadow
The Warming Meadow is located at the Rocky Mountain Biological Laboratory [Gunnison County, CO; (latitude, 38°57′29″; longitude, −106°59′20″; elevation, 2920 m)], near the southern range limit of *A. septentrionalis* (17). This climate warming experiment consists of five heated plots interspersed between five control plots, each of which is 3 m wide by 10 m long. Arrayed linearly across the arc of a glacial moraine, the ten plots span a natural gradient in snowmelt, soil temperature, and soil moisture caused by a variation in solar aspect (43). Each plot has an upper, middle, and lower zone (18, 43). We conducted all work for this study in the upper zone of each plot because the upper zone is most representative of subalpine meadow habitats of the western United States and has a continuous record of annual snowmelt date over the past quarter century (19, 44).
Low-elevation populations of A. septentrionalis
We selected two lower-elevation *A. septentrionalis* populations as microclimatic points of comparison to Warming Meadow heated plots. Selection criteria included *A. septentrionalis* presence and ease of access by county road. Geodesic distances from the Warming Meadow to these lower-elevation populations are 18 km (site 1: latitude, 38°49′17″;
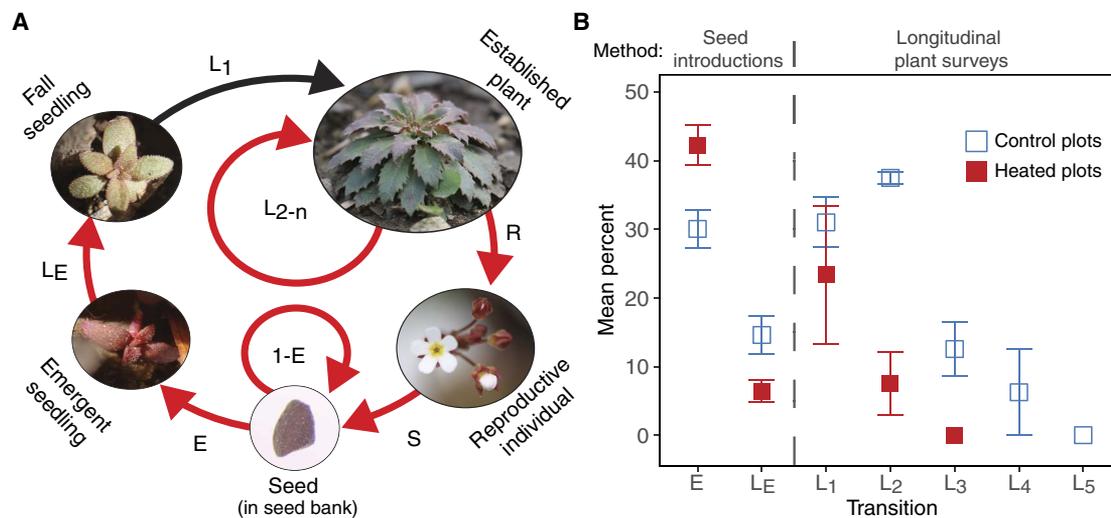
Fig. 4. Experimental warming affects performance across multiple life stages. (**A**) The life cycle of *A. septentrionalis*. Emergence (E) from seed occurs from late summer to early fall in late-season monsoonal moisture. Emergent individuals are highly susceptible to drought stress, thus their survival (L_E) to become fall seedlings depends on the timing and amount of rainfall. Fall seedlings that survive under winter's snowpack and through their first growing season (L_1) become established plants at age 1. Established plants may survive a second (L_2), third (L_3), and in rare cases fourth (L_4) year. Individuals typically become reproductive (R) in their second year of life, producing white flowers, each of which develops into a small fruit containing seeds (S). Red arrows indicate life stages significantly affected by experimental warming (tables S5 to S9). Photo credit: J. B. Curtis, University of Colorado, Boulder. (**B**) The effects of experimental warming on emergence and survival throughout the life cycle of *A. septentrionalis*. Experimental seed introductions demonstrate that warming increases seedling emergence (E) but decreases fall survival of those that emerge (L_E). Longitudinal plant surveys reveal that although warming has no significant effect on the survival of fall seedlings to age one, it substantially reduces the survival of established plants to age two (L_2) and beyond. Data indicate average percent emergence (L_E) and average percent survival $L_{(1-5)}$. Treatment sample sizes vary by transition (see table S6), and error bars indicate ±1 SE.
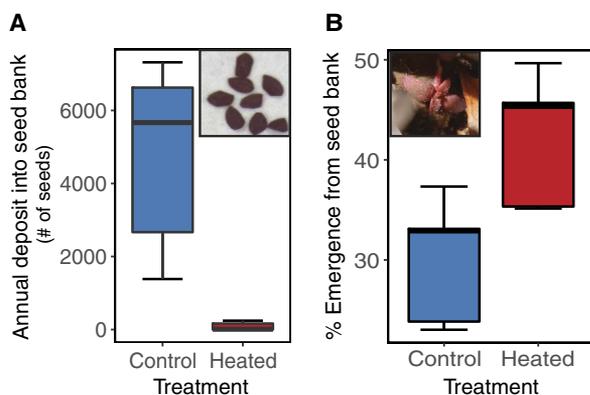
Fig. 5. Experimental warming depletes *A. septentrionalis* seed banks by reducing deposits and increasing withdrawals. (**A**) Warming reduces annual seed deposits into belowground seed reservoirs by ~98% (C = 4732.0 ± 1153.9, H = 83.4 ± 50.9). Data represent the average number of seeds produced per plot from 2013 to 2016 ($n_{control}$ = 5, n_{heated} = 5). (**B**) Warming decreases seed dormancy, stimulating emergence by ~41% (C = 30.0 ± 2.8, H = 42.2 ± 3.0). Data indicate average percent emergence from experimental seed banks introduced into each Warming Meadow plot ($n_{control}$ = 5, n_{heated} = 5). Photo credit: (A) A. M. Panetta and (B) J. B. Curtis, University of Colorado, Boulder.

longitude, 106°52′9″; elevation, 2682 m) and 30 km (site 2: latitude, 38°43′18″; longitude, 106°49′9″; elevation, 2683 m).

Snowpack and temperature data
Snowpack
From 1991 to 2016, we used digital photographs (taken two to three times per week) to capture yearly spring snowmelt date in each of the ten Warming Meadow plots. We defined snowmelt date as the first date on which

there was a continuous absence of snow cover. From the fall of 2013 to the spring of 2016, we used temperature data downloaded from iButtons (details below) to confirm snowmelt and snow cover dates in heated and control plots and at our two low-elevation populations of *A. septentrionalis*. We defined spring snowmelt date as the first date on which daily maximum soil temperatures reached and remained at or above 1.5°C, and we defined fall snow cover date as the first date on which daily maximum soil temperatures fell and remained below 1.5°C. Finally, we defined snow-free duration as the number of days between snowmelt and snow cover. For each snowpack variable (table S1), reported means and SEs for each treatment (n_{heated} = 5, $n_{control}$ = 5) are based on plot-level means across the study period.

Temperature
From fall 2013 to spring 2016, we used Maxim Integrated Thermochron iButtons (part no. DS1921G-F5#, Mouser Electronics) to log soil temperature every 4 hours at two locations within each Warming Meadow plot. Each iButton was placed at a depth of 5 cm to capture soil temperature in the root zone of shallow-rooted *A. septentrionalis*. We downloaded temperature data from iButtons once per year using Maxim Integrated's OneWireViewer and Java Web Start software. To calculate annual and seasonal minimum, maximum, and mean temperatures for each treatment (table S1), we first calculated minimum, maximum, and average daily temperatures for each day, in each year, for each plot. For each plot, we then averaged these daily values to calculate annual and seasonal minimum, maximum, and mean temperatures for each year. Finally, we averaged these plot-level values to calculate annual and seasonal means and SEs for each treatment (n_{heated} = 5, $n_{control}$ = 5).

Presence/absence surveys conducted prior to long-term experimental warming
The Warming Meadow plots were established in 1990, and experimental warming began on 1 January 1991. Annually, between 1990 and

1992, N. M. Waser and M. V. Price conducted plant presence/absence surveys using 25-cm × 25-cm quadrats flanking the length of our present-day study plots. Waser and Price included *A. septentrionalis* in their presence/absence surveys, providing a retrospective glance at the distribution of *A. septentrionalis* across Warming Meadow plots in the years before, and immediately after, warming began. To assess this initial distribution, we calculated the frequency of *A. septentrionalis* in each of the ten Warming Meadow plots from 1990 to 1992 by summing the number of quadrats with *A. septentrionalis* present and dividing by the total number of quadrats sampled. We then averaged these plot-level frequencies to calculate mean frequencies and SEs for heated and control treatments in each of the three initial years ($n_{heated} = 5$, $n_{control} = 5$) (fig. S1).

Longitudinal surveys of naturally occurring plants after decades of experimental warming

Each fall from 2013 to 2016, we conducted annual surveys of naturally occurring *A. septentrionalis* in the Warming Meadow to assess the effect of experimental warming on (i) abundance, (ii) survival and reproduction from the fall seedling stage to senescence, and (iii) yearly deposits into seed banks. During each survey, we divided each of the five heated and five control plots into 25-cm quadrats. We then carefully searched each quadrat for *A. septentrionalis* individuals. This fine-scale search allowed us to find, map, and permanently mark all individuals in heated and control plots.

Age/stage classifications

We classified naturally occurring individuals as seedlings (<1 year old) or established plants (≥1 year old). Established plants were further classified on the basis of their age (for example, 1, 2, or 3 years old). For example, *A. septentrionalis* seedlings emerge in late summer to early fall, concurrent with the arrival of monsoonal moisture. A seedling that emerges in the fall and survives through winter, spring, and summer to the following fall becomes a 1-year-old established plant. An established 1-year-old plant that survives to the following fall after a second growing season becomes a two-year-old established plant. We knew the age of all plants in our study plots for the duration of this study (2013 to 2016) because we began marking and monitoring individuals in 2009; *A. septentrionalis* in this study area are predominantly annual to biennial, and we never observed an individual reach the age of 5.

Abundance

Following each annual survey, we assigned a count of "1" to every living *A. septentrionalis*. We summed yearly counts to determine annual population size for each heated and control plot. We averaged the four annual abundance counts to calculate mean population size from 2013 to 2016 for each plot (Fig. 3B and table S4). To calculate the mean population size for each treatment from 2013 to 2016, we averaged plot-level means ($n_{heated} = 5$, $n_{control} = 5$). We used this same process to calculate the mean abundance of established plants and seedlings for each plot (table S4) and each treatment (Fig. 3A).

Survival

During each annual survey, we assessed the status (that is, alive or dead) of all *A. septentrionalis* that had been alive in the previous census. An individual was considered dead if its rosette easily detached from its roots or if it was gone and not found in subsequent surveys.

Reproduction

We scored each individual as reproductive or nonreproductive based on the presence of reproductive stalks that emerge from basal rosettes. For each reproductive individual, we counted its number of flowering stalks. We then used yearly stalk counts to estimate the number of seeds (*S*)

produced by each plant (*i*) per year (*y*) using the following relationship between stalks (*T*), fruits produced per stalk (*f*), and seeds produced per fruit (*s*)

$$S_{i,\,y} = T_{i,\,y} {*} f {*} s_t$$

where *t* indicates warming treatment (heated or control). We calculated *f* and *s* from a subset of plants included in our longitudinal study.

Yearly deposits into seed banks

We used our estimates of seed production (*S*) to calculate total annual input (*I*) into each plot's seed bank as follows

$$I_{p,y} = \sum_{i=1}^{i=n} S_{i,y}$$

where subscripts *p*, *y*, and *i* refer to plot, year, and plant, respectively.

Experimental introduction of seeds into the Warming Meadow

We experimentally introduced *A. septentrionalis* seeds into the Warming Meadow to estimate the effects of local warming on (i) rates of emergence from seed banks and (ii) early life–stage survival. This transplant experiment was necessary for two reasons. First, to calculate rates of emergence from belowground seed banks, one must know how many individuals could potentially emerge. Although it is virtually impossible to know the size of seed banks occurring naturally in the soil, it is straightforward to control (and thus know the size of) experimental seed banks. Second, to estimate early life–stage survival, one must mark and subsequently monitor seedlings very soon after they emerge. Emerging *A. septentrionalis* seedlings are <2 mm in diameter, making them extremely difficult to find, mark, and track amid neighboring plants and plant litter. By transplanting seeds into marked grid cells that we monitored continuously throughout the fall germination period, we were able to accurately monitor emergence and post-emergence survival rates of seedlings in heated and control plots.

Seed sources

In 2011, we collected *A. septentrionalis* seeds from 19 randomly selected, naturally occurring maternal plants from two populations located near the Warming Meadow. From 2011 to 2013, we took each of these 19 lineages through two generations in a greenhouse common garden to reduce potential differences in offspring performance due to maternal environmental effects (*45–47*). For each greenhouse generation, we allowed reproductive individuals to automatically self-fertilize, producing seeds for subsequent common-garden plantings and ultimately introduction into Warming Meadow heated and control plots. Before planting, seeds were stored in the dark at 1°C for 7 months to simulate conditions experienced by seeds overwintering in belowground seed banks.

Experimental design

In June 2014, we randomly selected four planting locations from available *A. septentrionalis* habitat within each Warming Meadow plot. At each planting location, we clipped aboveground vegetation and removed large roots and rocks. We then sank one 13-cm × 13-cm plastic grid (each cell was 1 cm²) into the soil at each planting location, securing it with nails hammered into the ground. In preparation for planting, we adhered two seeds from each lineage to wooden toothpicks using a tiny amount of water-soluble glue. This toothpick method facilitates field planting, reduces the potential for seed loss, and enables the accurate

identification of planted individuals that emerge adjacent to their tooth-picks (48–50).

In mid-July 2014, immediately before the arrival of monsoonal moisture that triggers the emergence of *A. septentrionalis* seedlings, we distributed seeds from the 19 *A. septentrionalis* lineages across all Warming Meadow planting sites, placing one toothpick per lineage into randomized locations within each experimental grid. In total, we planted 1520 seeds (19 lineages × 10 plots × 4 blocks per plot × 2 seeds per block). During planting, toothpicks with attached seeds were placed into the center of their randomly selected grid cell, with seeds facing the cardinal southwest direction. This allowed us to distinguish between seedlings emerging from introduced seeds (which emerged next to the southwest side of their toothpick) and seedlings emerging from nat-urally occurring seed banks in each plot. Before the onset of winter, we removed toothpicks from experimental grids, leaving seedlings and un-germinated seeds in the ground. Toothpicks cannot overwinter in ex-perimental grids because frost heave pushes them out of the ground, resulting in disturbance to the delicate root systems of young seedlings.

Data collection
During the 2014 fall emergence period (August to September), we conducted weekly surveys to follow the performance of introduced seeds. We scored each seed for emergence, and once a seedling emerged, we scored that seedling for survival. In addition, we recorded the distance of each seedling to the planted toothpick. If two individ-uals emerged, then both were followed until either one died or they both reached the four-leaf stage, at which point one of the seedlings was randomly selected and removed. Removed individuals were in-cluded in estimates of the fraction of introduced seeds that emerged but were not included in estimates of the fraction of emergent seed-lings that survived through the late fall. In mid-October 2014, we con-ducted a final census to score each seedling for survival to the late-fall seedling stage. Finally, in the fall of 2015, we resumed weekly censuses to capture emergence from remaining, ungerminated seeds. In the first fall of our experiment (2014), seedlings emerged from 36% of the seeds we planted. In the second fall of our experiment (2015), seedlings emerged from only 3.5% of the remaining seeds. Because the 2015 emergence rate approaches our estimated assignment error (see below), this paper focuses on the emergence and post-emergence survival of 2014 seedlings.

Estimating and minimizing assignment error
We planted this experiment into native soil within Warming Meadow heated and control plots. Hence, contamination from existing, natural seed banks, especially in control plots, inevitably accounts for a fraction of the emergence we observed in experimental grids. To estimate, and ultimately minimize, assignment error associated with this contamina-tion, we did not plant seeds into 56% of all experimental grid cells. Across the entire transplant experiment, *A. septentrionalis* emerged in 3.5% of these blank cells. When individuals that emerged 3 mm or more away from the planted toothpick were excluded, emergence rates in blank cells dropped to 1.4%. Accepting the lower assignment error, we have excluded individuals that emerged ≥3 mm from their toothpick from all analyses.

Statistical analyses
Linear mixed-effects models (LMMs) and generalized LMMs (GLMMs) were used to investigate the effects of experimental warming on (i) temperature and snowpack (tables S1 and S2), (ii) the abundance and distribution of *A. septentrionalis* (table S3), (iii) the survival and fecundity of *A. septentrionalis* throughout its life cycle (tables S5 and

S9), and (iv) seed bank dynamics (tables S5, S9, and S10). All models were implemented in R version 3.4.2 (51), package lme4 (52).

In general, for LMMs and GLMMs used to assess the effects of ex-perimental warming on temperature, snowpack, and the abundance and performance of *A. septentrionalis*, treatment (control versus heated) and position (a continuous covariate describing plot location along the glacial moraine) were included as fixed effects. Year (accounting for chance fluctuation in microclimate due to interannual variation) and plot (accounting for repeated measurement of the same plots over the duration of the study) were treated as crossed, random ef-fects. GLMMs used to assess the initial distribution of *A. septentrionalis* across heated and control plots also included quadrat (nested within plot) as a random effect. GLMMs used to investigate the effects of ex-perimental warming on the likelihood that an established plant be-came reproductive, as well as those used to investigate warming's effect on the number of stalks produced per plant, also included plant (nested within plot) as a random effect. For GLMMs used to assess the performance of seeds experimentally introduced into heated and con-trol plots, experimental block (nested within plot) and lineage (nested within source population) were included as crossed, random effects. Finally, for GLMMs used to assess the effect of past reproductive suc-cess on present-day seedling abundance, quadrat (nested within plot) and year were included as crossed, random effects. When model resid-uals indicated overdispersion, an observation-level factor was included as a random effect (53). Reported F and χ^2 statistics, along with their associated P values, are the result of Wald F and χ^2 tests (54–56), ob-tained using R package car (57).

SUPPLEMENTARY MATERIALS
Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/2/eaaq1819/DC1

fig. S1. The initial distribution of *A. septentrionalis* across Warming Meadow heated and control plots.
fig. S2. The initial distribution of *A. septentrionalis* across Warming Meadow control plots with respect to snowmelt date.
table S1. The effects of experimental warming on snowpack and soil temperature.
table S2. The effects of experimental warming and contemporary climate change on snowmelt date in the Warming Meadow.
table S3. The effects of experimental and contemporary warming on the abundance and distribution of *A. septentrionalis* in Warming Meadow.
table S4. Mean abundance (±1 SE) of *A. septentrionalis* in control and heated plots from 2013 to 2016.
table S5. The effects of experimental warming on emergence and post-emergence survival of *A. septentrionalis*.
table S6. The emergence and post-emergence survival of *A. septentrionalis* in control and heated plots.
table S7. Mean number of seeds produced per plant (±1 SE) by age in control and heated control plots.
table S8. Components of *A. septentrionalis* mean reproductive success (±1 SE) in control and heated plots.
table S9. The effects of experimental warming on the reproductive success of *A. septentrionalis* in the Warming Meadow.
table S10. The ghosts of reproduction past: Relationships between seedling abundance in year$_t$ and the number of flowering stalks in year$_{t−1}$ and year$_{t−2}$.

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Climate warming drives local extinction: Evidence from observation and experimentation

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