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RESEARCH ARTICLE

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Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits

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Abstract

1. Predicting species' range shifts under future climate is a central goal of conservation ecology. Studying populations within and beyond multiple species' current ranges can help identify whether demographic responses to climate change exhibit directionality, indicative of range shifts, and whether responses are uniform across a suite of species.
2. We quantified the demographic responses of six native perennial prairie species planted within and, for two species, beyond their northern range limits to a 3-year experimental manipulation of temperature and precipitation at three sites spanning a latitudinal climate gradient in the Pacific Northwest, USA. We estimated population growth rates (λ) using integral projection models and tested for opposing responses to climate in different demographic vital rates (demographic compensation).
3. Where species successfully established reproductive populations, warming negatively affected λ at sites within species' current ranges. Contrarily, warming and drought positively affected λ for the two species planted beyond their northern range limits. Most species failed to establish a reproductive population at one or more sites within their current ranges, due to extremely low germination and seedling survival. We found little evidence of demographic compensation buffering populations to the climate treatments.
4. *Synthesis*. These results support predictions across a suite of species that ranges will need to shift with climate change as populations within current ranges become increasingly vulnerable to decline. Species capable of dispersing beyond their leading edges may be more likely to persist, as our evidence suggests that projected changes in climate may benefit such populations. If species are unable to disperse to new habitat on their own, assisted migration may need to be considered to prevent the widespread loss of vulnerable species.

KEYWORDS

climate change, demographic compensation, drought, integral projection models, Pacific Northwest prairies, species range distributions, vital rates, warming

1 | INTRODUCTION

With ongoing climate change, many species will need to shift their geographic ranges to persist. Indeed, multiple species have already shifted poleward and/or to higher elevations to track favourable climatic conditions (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Parmesan, 2006; Parmesan & Yohe, 2003; Thomas, 2010), although the magnitudes and patterns of range shifts vary substantially across taxa (MacLean & Beissinger, 2017). Range shifts have widespread consequences for ecosystem services (Pecl et al., 2017; Walther, 2010), and, if species are unable to shift their ranges rapidly enough, may further exacerbate biodiversity losses (Dawson, Jackson, House, Prentice, & Mace, 2011). Anticipating such effects must start with better predictions of how climate change will impact populations across species' geographic ranges.

Species range distributions are controlled by a complex set of factors including dispersal ability (Sexton, Mcintyre, Angert, & Rice, 2009), biotic interactions (Araújo & Rozenfeld, 2014; Louthan, Doak, & Angert, 2015) and tolerance of abiotic conditions, with climate often assumed to be the primary driver of broad distributional patterns across latitudinal and elevational gradients (MacArthur, 1972; Thomas, 2010). The overall effect of climate on population dynamics is driven by its composite effects on different vital rates (i.e. survival, growth, fecundity and recruitment). As temperatures increase, populations towards the warmer edges of a range may decline due to decreasing performance in one or more vital rates, leading to localized extinctions and potential range contractions at their trailing edges (Lesica & Crone, 2017; Panetta, Stanton, & Harte, 2018; Sheth & Angert, 2018). At the same time, climatic conditions near or beyond the cooler edge of a range may become increasingly favourable with warming (Rehm, Olivas, Stroud, & Feeley, 2015), leading to range expansions or shifts. Recent evidence, however, suggests that populations throughout a species range, not just at the warmer edges, may be at risk of decline if populations are locally adapted to climate (Peterson, Doak, & Morris, 2018). Demographic studies that can predict whether populations will decline or disappear towards the warmer range edges and/or expand at the cooler range edges are necessary to predict whether and how ranges will shift with future climate change.

Complicating the population-level effects of climate change are potentially opposing positive or negative effects on different vital rates, termed demographic compensation, which can buffer populations against perturbations (Doak & Morris, 2010; Villellas, Doak, García, & Morris, 2015). For example, Peterson et al. (2018) found that opposing survival and growth responses of the alpine plant *Silene acaulis* to warming contributed to the species' ability to persist across its range, while Oldfather and Ackerly (2019) found that inverse relationships in rates such as adult survival and germination contribute to stable population growth across a microclimate gradient in the alpine plant *Ivesia lycopodioides*. While demographic compensation may theoretically allow for a species to persist in its current range in the face of climate change, the presence of compensation does not guarantee long-term persistence, as extreme years may exceed a threshold at which the vital rates benefitting from climate change are outweighed by those being hindered (Doak & Morris, 2010; Sheth & Angert, 2018). Instead, species may be faced with a situation in which demographic compensation manages to slow the rate of decline but not rescue populations altogether.

To effectively address how climate change will impact populations across geographic ranges and whether species will need to shift their ranges to persist, manipulative experiments across environmental gradients are critical (Dunne, Saleska, Fischer, & Harte, 2004; Pfeifer-Meister et al., 2013). In particular, incorporating transplants of species to locales beyond their current limits allows for the direct testing of whether such species have the capacity to establish a population and persist beyond their current range limits (Baer & Maron, 2018; Gaston, 2009; Hargreaves, Samis, & Eckert, 2014). Since studies documenting changes in only one or a few demographic parameters can be misleading (Gaston, 2009), experiments that use population models to integrate the combined effects of climate across the entire life cycle are most compelling in this regard.

Previously (2010–2012), we used a fully factorial warming (+2.5°C) and precipitation (+20%) experiment at three sites spanning a latitudinal climate gradient of increasing temperature and summer drought severity from north to south in the Pacific Northwest (PNW), USA to study the vital rates of 12 native prairie species planted within and beyond their northern range limits (Pfeifer-Meister et al., 2013). Our key finding was that warming decreased recruitment within but not beyond a species' current range. However, this earlier study did not last long enough to allow perennial species to mature and thus could not be used to calculate overall population growth rates. Furthermore, the effect of warming was confounded by a strong reduction in soil moisture that is typical of warming treatments (Rustad et al., 2001). Here, we updated this experimental design with a drought treatment (−40% annual precipitation) replacing the minimally impactful +20% precipitation treatment, and a warming plus precipitation treatment that added enough moisture to offset the drying effect of warming. We measured vital rates and, using integral projection models (IPMs), calculated the population growth rates for six perennials, including two 'range-restricted' species whose northern range limits occur within our study area, from 2016 to 2018 at three experimental sites (the same southern and central sites as in Pfeifer-Meister et al. (2013) and a new northern site). IPMs have become widely adopted given their ability to accommodate both discrete and continuous states in projecting population dynamics, and there are many useful examples in the literature describing their implementation and methods (Ellner & Rees, 2006; Merow et al., 2014; Rees, Childs, & Ellner, 2014). To our knowledge, this is the first study incorporating both climate manipulations and a latitudinal climate gradient to conduct full-scale demographic modelling of multiple species planted both within and beyond their northern limits. In this study we ask:

1. Do prairie plant population growth rates change over a latitudinal gradient within their current range limits? Is warming and/or drought detrimental to populations within their ranges?

2. Are the range-restricted perennial species capable of establishing when planted north of their cooler edges? Is warming and/or drought benign for such pioneering populations?
3. Which vital rates contribute most substantially to climatic effects on population dynamics? Is there evidence of demographic compensation buffering population responses to climate change?

We hypothesized that, due to climate warming in the recent past, population growth rates will increase from south to north, and that the range-restricted species will be capable of establishing when planted at sites north of their current leading edges. Within species' current ranges, we expected warming and/or drought to decrease population growth rates relative to controls, but to be neutral or beneficial for populations of the range-restricted species that establish at the sites north of their ranges. Lastly, where there are no effects of climate treatments on population growth rates, we expected some species to show evidence of demographic compensation.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiment took place from 2015 to 2018 at three sites across a 520 km latitudinal Mediterranean climate gradient in the PNW, USA (Figure 1). Each site contained 20 plots (each 7.1 m^2) randomly assigned to one of four climate treatments: control (ambient temperature and precipitation), drought (ambient temperature with annual precipitation reduced by 40%), warming (canopy temperature raised by 2.5°C with ambient precipitation) and warming + precipitation (canopy temperature raised by 2.5°C and irrigated to offset a warming-induced drying effect). Complete details about climate treatment implementation can be found in the Supplemental Methods.

The southern and central sites had an experimental legacy from 2010 to 2012 (Pfeifer-Meister et al., 2013, 2016), with some adult individuals of the focal species remaining from the previous experiment (which we included when collecting data in the current experiment), while the northern site was newly established in 2015.

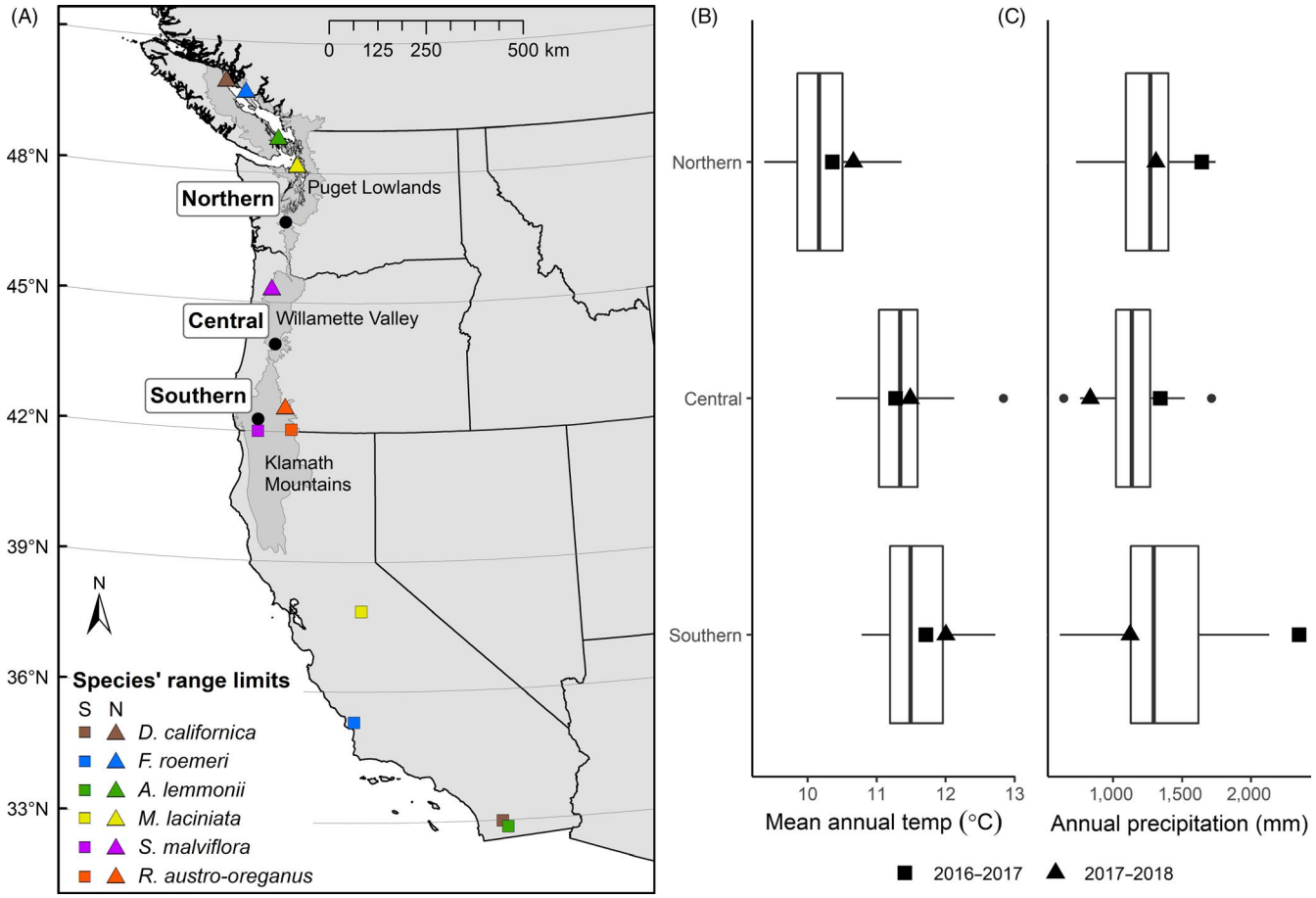

FIGURE 1 (A) Map of the southern, central and northern experimental sites (black dots) and the southernmost and northernmost known populations (squares and triangles, respectively) of the six perennial focal species west of the Cascade and Sierra mountain divides. See Supplemental Methods for details regarding species' range limits. From north to south, the Puget Lowland, Willamette Valley and Klamath Mountain ecoregions are highlighted in dark grey. (B) Mean annual temperatures and (C) annual precipitation over the period 1981–2010 (boxplots) and during the two annual transitions of this study (symbols) using the annual interval of 15-July to 14-July (data obtained from PRISM: http://www.prism.oregonstate.edu/). This annual interval was chosen as it encapsulates an entire growing season beginning before the onset of fall green-up and ending just after wilting point is reached

Between October 2014 and January 2015, plots at the southern and central sites were mowed and raked, while the northern plots were treated with herbicide (2% Glyphosate) three times to reduce the thick cover of introduced pasture grasses (a typical prairie restoration technique in the PNW). In January 2015 to establish similar baseline communities, we seeded all plots with a consistent mix of 29 native grass and forb species found in PNW prairies (including our focal species; Table S1).

Our demographic study centred on six focal perennial species (Table 1; see Supplemental Methods for more detailed descriptions). All species were selected for having medium to high fidelity to upland prairies with their northern range limits occurring within the PNW (42–50°N) and their southern limits occurring below the latitude of our southernmost site (Figure 1; see Supplemental Methods for determining species' range limits). In fall 2015, 2016 and 2017, for each focal species and plot, we sowed 25 seeds into each of eight 5.5-cm diameter plastic rings, using different rings each year (for a total of 200 seeds per species per plot per year, with two exceptions: 150 seeds within six rings per plot for *Ranunculus austro-oreganus* in 2015 due to seed quantity limitations, and 250 seeds within five rings per plot for *Achnatherum lemmonii* in 2017 due to space limitations). To allow for local adaptation, we used the nearest available seed sources for each site (Table S2). Due to low rates of germination with strong site differences in the field (see Section 3), we also conducted a greenhouse germination experiment in fall 2018 with field-collected soil to test whether these results were the consequence of soil differences across sites (see Supplemental Methods).

Lastly, to implement a treatment to examine the effect of aboveground competition on species' responses to the climate treatments, we initiated a biomass removal treatment in winter to early spring of 2017. In half of each plot, we reduced the presence of non-focal species with a combination of weeding and clipping. However, we found it impossible to regularly and consistently conduct this treatment throughout the growing season at all three sites, so we abandoned the treatment near the end of the 2017 growing season. To account for a potential treatment effect in 2017 or a legacy effect in 2018, we included a biomass removal treatment in our vital rate models.

2.2 | Demographic data and analyses

In 2016, 2017 and 2018, we marked and measured each individual in the plots and tracked them through subsequent years. To quantify germination and seedling survival, we conducted 2–4 censuses each winter-spring of the rings into which seeds had been added, counting the number of germinants and marking seedlings for subsequent tracking. During the final census of each spring, we recorded each existing plant's survival or death from the previous year and measured size and reproduction. To estimate the number of seeds each reproductive individual produced, we collected data on the number of flowers or spikelets per plant, the fraction of flowers becoming fruits, and the number of seeds per fruit. In some cases, for seed production, we only had data from a single site and/or a single year to provide estimates, as well as from a few natural populations in areas surrounding our study sites. Details on specific size and reproduction data collected for each species can be found in the Supplemental Methods. We then modelled all vital rates as functions of climate treatments and, where appropriate, plant size and then used IPMs to integrate vital rates into estimates of population growth rates for each annual transition for each level of the experimental treatments. Using these IPMs, we conducted life table response experiments (LTREs) to identify the contributions of grouped vital rates to differences in λ between treatments and controls (Caswell, 1989).

All the following analyses were conducted using R version 3.3.2 (R Core Team, 2016). We modelled the probabilities of binomial responses [survival, reproduction, fruit to flower ratio (for *Sidalcea malviflora*), and germination] using generalized linear mixed models

TABLE 1 Descriptions of the six focal species. S-limit and N-limit Lats give the latitudes of the southernmost and northernmost known populations, respectively, within the species' contiguous ranges west of the Cascade and Sierra mountain divides. We determined whether a species is within or beyond its current range at our three experimental sites based on these values (see 'Determining species' range limits' in Supplemental Methods for details)

Perennial species	Family	Growth habit	S-limit Lat	N-limit Lat	N-limit region
Ranunculus austro-oreganus L.D. Benson	Ranunculaceae	Forb	42.05°	42.60°	KM
Sidalcea malviflora (DC.) A. Gray ex Benth. ssp. *virgata* (Howell) C.L. Hitchc.	Malvaceae	Forb	42.00°	45.35°	WV
Microseris laciniata (Hook.) Sch. Bip.	Asteraceae	Forb	37.85°	48.21°	PL
Achnatherum lemmonii (Vasey) Barkworth var. *lemmonii*	Poaceae	Grass	32.84°	48.84°	WD
Festuca roemeri[a]	Poaceae	Grass	35.30°	49.90°	PL
Danthonia californica Bol.	Poaceae	Grass	32.99°	50.13°	WC

Abbreviations: KM, Klamath Mountains; PL, Puget Lowlands; WC, widespread and common; WD, widespread and disjunct; WV, Willamette Valley.

[a]Variety *roemeri* Yu. E. Alexeev at the central and northern sites; variety *Klamathensis* B.L. Wilson at the southern site.

with binomial error distribution and logit-link functions. We modelled mean growth and variance in growth (the squared-residuals of the growth model) using general linear mixed models, and various reproductive output parameters (flowers/spikelets per plant, seeds per flower/spikelet, etc.) with either general linear mixed models or generalized linear mixed models with Poisson error distribution (Gaussian if responses were based on averaged values, Poisson if total counts; see species descriptions in Supplemental Methods). We treated adult survival, reproduction, mean adult growth, growth variance and flowers/spikelets per plant as size-dependent vital rates, using both linear and quadratic effects of size. We used the LME4 package (version 1.1-17; Bates, Mächler, Bolker, & Walker, 2015) for mixed models, treating plot (or population for data from natural populations) as a random effect, except in one circumstance (*A. lemmonii* adult survival) in which we lacked enough data to include a random effect.

For each species and most vital rates (see Table S3 for exceptions), we built two global models: a climate global model (using the climate treatment variable with four levels: control, drought, warming and warming + precipitation) and a warming global model (collapsing the climate treatment into two temperature categories: ambient (control and drought) and warming (warming and warming + precipitation)). We used this collapsed warming treatment (in addition to the full climate treatment) because preliminary data exploration and evidence from previous experiments at these sites suggest changes in temperature have a stronger influence than changes in moisture on plant responses in this system (Pfeifer-Meister et al., 2013; Reed et al., 2019) and we gained degrees of freedom in doing so.

Both global models included all possible two-way interactions (and all possible main effects) involving site, climate or warming treatment, year and plant size (for size-dependent vital rates), plus a quadratic size term ($size^2$), and the main effect of the biomass removal treatment or a site × biomass removal treatment interaction for 2017/2018 germination (which could support such an interaction). We modelled 2016 germination separately from 2017/2018 since the sites did not have all climate treatments initiated yet. If a species had a constant failed response (e.g. no survival or reproduction) in a binomial vital rate at a given site, we dropped that site from that vital rate model to avoid a singular-fit issue (six sites dropped out of 73 possible cases; see Notes column in Table S3). Using the 'dredge' function from the MuMIn package (Barton, 2018), for both global models we compared all nested models with AICc and identified the best-fit model for each vital rate (Burnham & Anderson, 2004). On a few occasions, we removed quadratic size effects from models if they caused biologically unrealistic predictions towards the extremes of the size range. If the biomass removal treatment remained in the best-fit model for a vital rate, we used the non-weeded level when predicting that vital rate for the IPMs.

To synthesize the vital rate estimates into estimates of the population growth rate (λ), we built IPMs for each climate treatment at each site during both annual transitions. We did not fit an IPM at sites where we could not estimate the main effect of that site in one or more vital rate models for a species (e.g. if we were unable to estimate reproduction due to no individuals surviving to reproductive age). In our IPMs, we used plant size as our continuous state variable but included a discrete seedling stage. We set size limits to be just outside the maximum and minimum observed sizes across all sites, and discretized vital rate functions into 200 size bins using the midpoint rule (Easterling, Ellner, Dixon, & Mar, 2000; Ellner & Rees, 2006). We estimated growth probabilities of adults and seedlings as the differences of the cumulative distribution function (CDF) at size bin boundaries (Dibner, Peterson, Louthan, & Doak, 2019). For seedlings surviving to the next year, we used distributions of possible sizes based on empirical CDFs fit to the parameters found in the best-fit seedling growth models (Table S3). We determined the predicted number of recruits produced by a reproductive individual at a given size as the product of the individual's reproductive output (total seeds: determined by its flower (or spikelet/etc.) production, the fruit to flower ratio (if applicable) and seeds per flower) and the germination rate. We calculated λ as the dominant eigenvalue of each discretized IPM matrix and estimated bias-corrected 95% confidence intervals for λ by resampling the coefficients of each vital rate function 1,000 times using their means and covariance matrices and recalculating λ for each bootstrap replicate. We tested for statistical significance of a treatment effect on λ relative to the control by calculating the differences in λ between the treatment and control for each of the 1,000 resamples and then calculating 95% confidence limits in those differences. A treatment has a significant effect on λ if those confidence limits do not overlap zero. The λ values we computed for each annual transition, as well as the vital rate contributions from LTREs (see following paragraph), are the asymptotic values that would be reached if the vital rate values during that transition remained constant.

Following bootstrap iterations of IPMs, we used the 'LTRE' function in the POPBIO package (Stubben & Milligan, 2007) to determine the extent to which differences between climate treatments and controls in λ could be attributed to differences in the survival/growth (S/G) of seedlings, S/G of adults or fecundity. We obtained the LTRE contributions for each element of the discretized S/G matrix and fecundity matrix that constitute the IPM (e.g. approach two in Griffith, 2017). Sensitivities were evaluated midway between the treatment and control matrices (Caswell, 2001) and adult (non-seedling) contributions were summed over size bins. We utilized bootstrapped IPM matrices to estimate bias-corrected 95% confidence intervals in LTRE contributions. A contribution is significant when confidence intervals do not overlap zero. Evidence of demographic compensation under a climate treatment would exist if vital rates exhibited opposing contributions to differences in λ (Villellas et al., 2015).

3 | RESULTS

Population growth rates (λ) varied substantially across species, annual transitions and sites (Figure 2). We were unable to fit an IPM at one or more sites for four of the six species due to their inability to establish a reproductive population (hereafter: 'establish') over

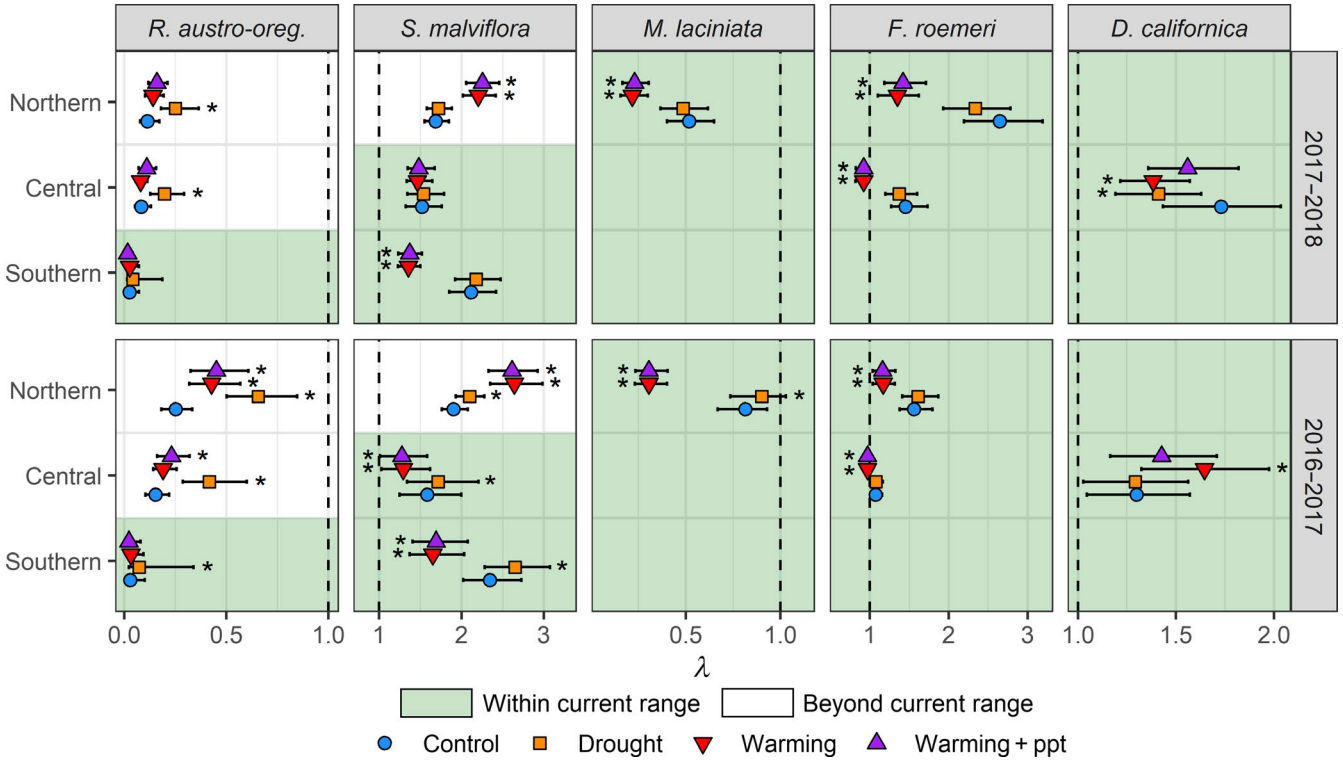

FIGURE 2 Population growth rates (λ) under climate treatments (control, drought, warming and warming + ppt) for five perennial species at the southern, central and northern experimental sites for 2017–2018 and 2016–2017. Species are arranged from left to right in ascending order of northern range limit. Lack of λ values at a given site for a species indicates that we did not fit an integral projection model (IPM) because the species did not establish a reproductive population. *Achnatherum lemmonii* is excluded entirely from the figure since we could not fit an IPM at any site. λ values are depicted with bias-corrected 95% confidence intervals obtained by resampling the coefficients of each vital rate function 1,000 times using their covariance matrices. We tested for statistical significance of a treatment effect on λ relative to controls, as indicated by *, by calculating the differences in λ between the treatment and control for each of the 1,000 resamples and then calculating 95% confidence limits in those differences (see Table S4). λ overlapping 1.0 (dashed line) = estimated stable population, $\lambda < 1.0$ = estimated declining population and $\lambda > 1.0$ = estimated growing population. Note the differing scales across species

the course of the experiment. This outcome was most common at the southern site, where only *R. austro-oreganus* and *S. malviflora* reached reproductive status. At the central and northern sites, two of the six species failed to establish (*Microseris laciniata* and *A. lemmonii* at the central site and *Danthonia californica* and *A. lemmonii* at the northern site). For the three species that established at more than one site, *R. austro-oreganus* and *Festuca roemeri* exhibited increasing λ from south to north while *S. malviflora* performed lowest at the central site, where it naturally occurs (Figure 2).

In all but one case within current ranges, the warming treatments had neutral to significantly negative effects on λ relative to the controls (Figure 2: green backgrounds; Table S4). The lone exception was a positive effect under warming for *D. calfornica* in 2016–2017, but this switched to a negative effect in 2017–2018. In contrast, the warming treatments had neutral to significantly positive effects on λ at sites beyond the northern limits of the two range-restricted species, *R. austro-oreganus* and *S. malviflora* (Figure 2: white backgrounds; Table S4). In general, the warming and warming + precipitation treatments had similar effects on λ relative to the controls. The drought treatment had neutral to significantly positive effects whether within or beyond ranges for *R. austro-oreganus* and *S. malviflora*, and a single significantly positive and negative effect within ranges for *M. laciniata* and *D. californica* respectively (Figure 2; Table S4). Overall, negative effects of the warming treatments within current ranges were of greater magnitude and more frequent than those of the drought treatment.

Life table response experiments revealed the extent to which differences between climate treatments and controls in the survival/growth (S/G) of seedlings, S/G of adults and/or fecundity contributed to differences in λ. We found no consistent evidence for demographic compensation: in most cases, a given climate treatment affected all three sets of vital rates in the same direction relative to control (i.e. all positive or all negative contributions; Figure 3). While the LTREs provide contributions of grouped vital rates, in many cases only one of the vital rates within a group (e.g. only seedling survival OR growth, not both) was involved in the contribution. Specific vital rate results can be found in the Supporting Information (best-fit model results: Figures S1–S16; best-fit model structures: Table S3; best-fit model coefficients: Table S5; all candidate models with 95% of the cumulative Akaike weights: Table S6).

The inability of most species to establish populations at one or more sites was mostly driven by extremely low rates of germination and seedling survival. Despite sowing thousands of seeds per species per site during each fall of 2015, 2016 and 2017, few germinated

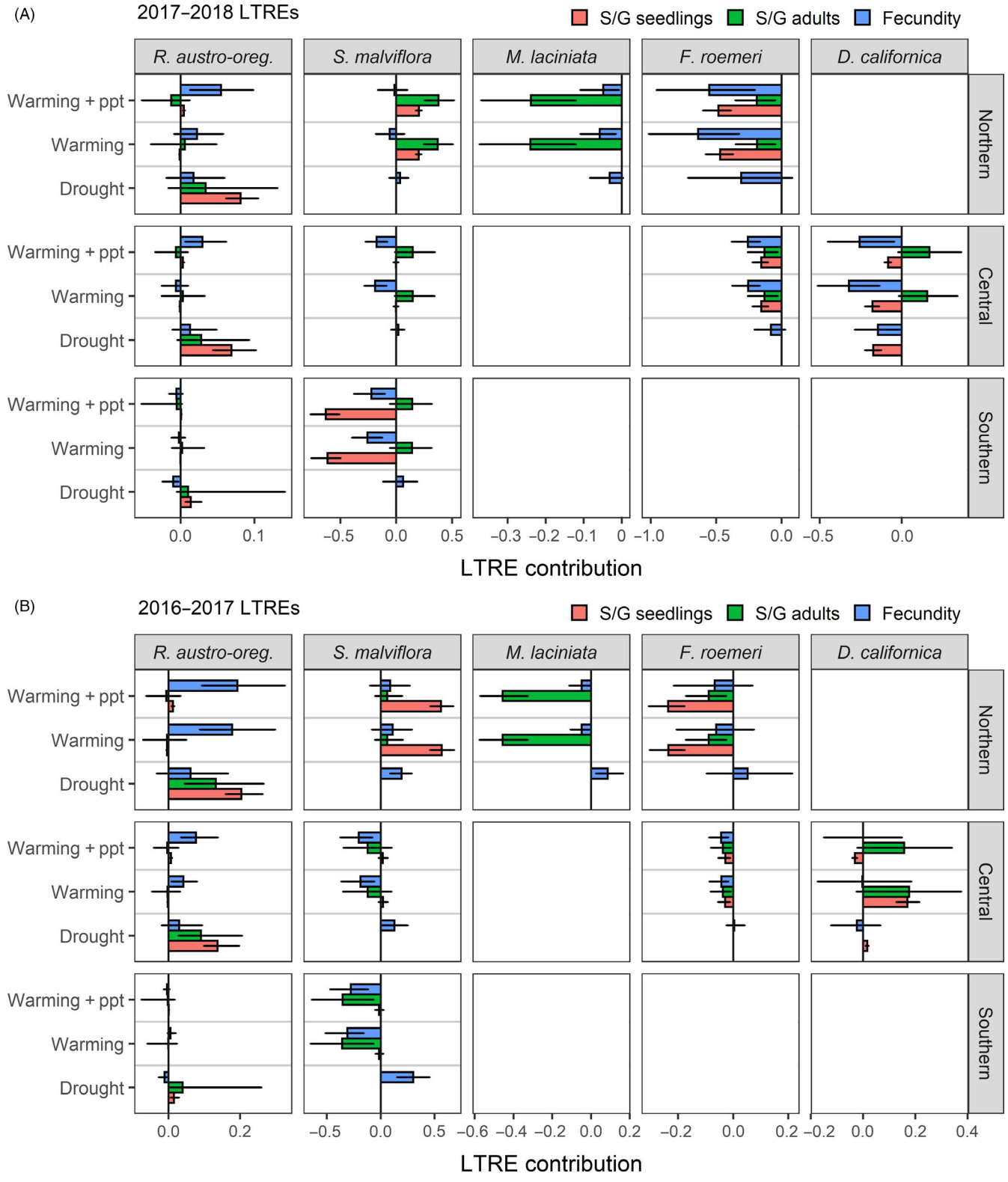

FIGURE 3 Life table response experiment (LTRE) results for (A) 2017–2018 and (B) 2016–2017 to determine the extent to which differences in population growth rates (λ) between each climate treatment (drought, warming or warming + ppt) and the controls can be attributed to differences in the survival/growth (S/G) of seedlings, S/G of adults or fecundity. Where a species lacks data at a given site due to failed establishment, we could not conduct an LTRE. *Achnatherum lemmonii* is excluded entirely from the figure since it failed to establish at any site. Contributions of each vital rate group are depicted with bias-corrected 95% confidence intervals by utilizing bootstrapped IPM matrices generated by resampling the coefficients of each vital rate function 1,000 times using their covariance matrices. A vital rate group has a significant contribution towards a treatment's effect on λ relative to the control if its confidence interval does not overlap zero. Note the differing scales across species and annual transitions

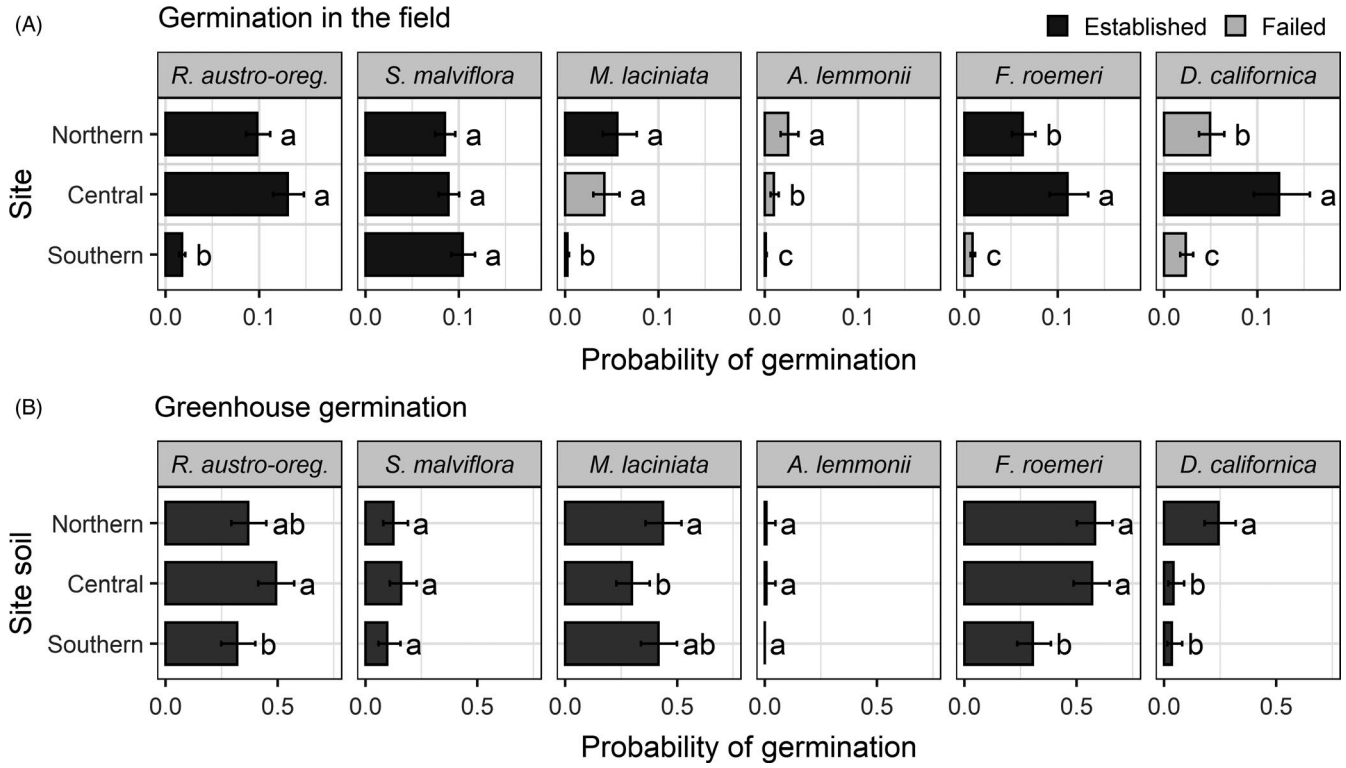

FIGURE 4 (A) Species' site-wide germination rates across years and treatments, where lowercase letters indicate significant differences among sites ($p < 0.05$) unique to each species. (B) Greenhouse germination rates in fall 2018 for each species by experimental site soil. Lowercase letters indicate significant differences between site soils for a species. Bars show estimated marginal means ±95% confidence intervals. Note the different scales on the *x*-axis

and survived to adulthood. Across all species, these critical early-life vital rates were significantly lower where species failed to establish compared to where species successfully established (logistic regressions, $p < 0.001$ for both germination and survival). All species except *S. malviflora* had significantly lower germination at the southern site relative to the remaining two sites (Figure 4A). In the greenhouse germination study, we also found significant differences in germination across the soils from the three sites. However, only for *F. roemeri* did the southern soil have the lowest greenhouse germination rate (Figure 4B), so there was no consistent evidence that this site's soil was inhibitory for germination. In general, germination rates were considerably higher or comparable in the greenhouse relative to the field (Figure 4A,B; note the different scales), except for *D. californica* in the central soil (considerably lower than its germination rate in the field).

4 | DISCUSSION

In this study, we examined the population dynamics of six native perennials under experimental climate change within their northern range limits, as well as beyond the northern limits for two of the species. We found evidence suggesting that these species may become increasingly vulnerable to decline within their current ranges due to warming. Contrarily, for the two range-restricted species also planted beyond their northern limits, projected changes in climate may benefit such pioneering populations. These findings support the expectation that species' ranges will shift with climate change.

Population growth rates for two species, *R. austro-oreganus* and *F. roemeri*, exhibited a latitudinal pattern, increasing from south to north. Annual temperatures in the PNW have already risen by ~0.8°C during the 20th century and the rate of increase has been accelerating (Abatzoglou, Rupp, & Mote, 2014; Mote, 2003), indicating that warmer temperatures may have caused these leading edge-trailing edge patterns in this system. The results of our climate treatments support this: a consistent result (with one exception) was that the warming treatments only decreased λ at sites within species' current ranges and increased λ at the sites beyond the northern limits of the two range-restricted species. This was also consistent with the prior experiment, in which warming reduced recruitment within but not beyond current ranges (Pfeifer-Meister et al., 2013). Increasing temperatures at sites within ranges generally caused these sites to become *less* hospitable, whereas increasing temperatures (and reduced precipitation) at sites beyond ranges caused those sites to become *more* hospitable. These circumstances may be attributed to direct physiological/thermal tolerance thresholds being surpassed (within ranges) or met (beyond ranges; Angert, Sheth, & Paul, 2011; Peterson, Doak, & Morris, 2019), or by changes to biotic interactions causing greater competition (within ranges) or facilitation (beyond ranges; Ettinger & HilleRisLambers, 2017).

Interestingly, since the negative effects of the warming treatments on λ within current ranges were of greater magnitude and more

frequent than that of the drought treatment (which had only a single negative effect), warming itself, rather than reduced soil moisture, appears to be driving the demographic decline in this system. We have previously found that warming also had a greater influence than moisture on these and other species' phenological responses to climate change (Reed et al., 2019), and we observed a similar response for soil respiration (Reynolds, Johnson, Pfeifer-Meister, & Bridgham, 2015). It seems that these phenomena are a function of the region's Mediterranean climate system, in which very wet soils occur throughout the winter and very dry soils throughout the summer until the onset of fall rains. Thus, there is only a narrow window in the spring growing season during which plants are negatively affected by changes in precipitation up to a 40% drought. Given the predicted rise in temperatures for the PNW (Mote & Salathé, 2010), these species will face increasingly difficult demographic pressures within their current ranges.

We also discovered that most species failed to establish reproductive populations at one or more sites regardless of climate treatment. Extremely low rates of germination and seedling survival drove this lack of establishment, which was especially pronounced in the southern site, where four of the six species could not establish and five of the six had their lowest rates of germination. Importantly, with the exception of *D. californica*, which was not included in the original experiment, these species also had an additional 3 years (2010–2012) for establishment to take place at the southern and central sites from the previous experimental legacy (Pfeifer-Meister et al., 2013), yet still failed to establish in most cases in the south.

Our greenhouse germination data suggest that soil conditions may be partially implicated in the failed establishment for *F. roemeri* in the south, but not for the other species, which germinated just as well in the southern soil as they did in the soil(s) from where they could establish in the field. Instead, an inability to cope with the biotic community present may have contributed to the poor recruitment at this site. Shortly after reestablishing this experiment, our southern site became dominated by exotic annual grasses (P. B. Reed, L. E. Pfeifer-Meister, B. A. Roy, B. R. Johnson, G. T. Bailes, A. A. Nelson, & S. D. Bridgham, unpubl. data). Changes in species interactions, such as an increase in competition, can contribute to localized extinctions or demographic decline (Cahill et al., 2012; Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016). This appears to be the case at our southern site, where the rapid shift towards a dense cover of annual grasses coincided with low recruitment and, consequently, an inability to establish for most of our focal species. The invasive annual grasses which came to dominate (e.g. *Bromus tectorum*, *Bromus hordeaceus* and *Vulpia myuros*) are winter-annual species, reaching full maturity early in the growing season (January to April), during the period of germination for most of our focal perennials. Thus, the perennial germinants likely experienced a strong competitive disadvantage relative to the winter-annual grasses, which were able to use up resources before the perennial germinants had an opportunity. This shift towards annual grass dominance also occurred between 2010 and 2012 and may become increasingly common in PNW prairies with hotter, drier conditions (Pfeifer-Meister et al., 2016), suggesting that recruitment challenges for these native perennials may become more commonplace.

Given our results, expectations under future climate change for the two range-restricted species, *R. austro-oreganus* and *S. malviflora*, differ considerably. Despite establishing populations at all three sites and the climate treatments being generally beneficial for populations outside its range, *R. austro-oreganus* exhibited consistently poor demographic performance ($\lambda \ll 1$). This suggests that even if *R. austro-oreganus* could disperse beyond its range, it may face many challenges in maintaining viable populations. This species is endemic to a single county in southwestern Oregon and may be especially vulnerable in the future. *S. malviflora*, in contrast, exhibited high demographic performance ($\lambda \gg 1$) across all three sites, with higher population growth rates in the south and north relative to the central site. Natural populations of this species are much less common in southern Oregon relative to the Willamette Valley, so its population growth rates being lowest at our central site suggests a possible role of enemy escape for this species at the southern and northern sites (Mlynarek et al., 2017). Indeed, *S. malviflora* is known to be affected by seed weevil larvae (*Macrorhoptus* ssp., among others) in the Willamette Valley (Young-Mathews, 2012), and we observed evidence of weevil damage at our central site but not at the southern and northern sites (B. Roy, pers. obs.). Although the IPMs consistently predicted $\lambda > 1$ for *S. malviflora*, the warming treatments did significantly reduce λ at the southern and central sites, suggesting it may only take a few extreme years to drive populations towards decline. At the northern site, beyond its range, populations exhibited high performance, especially under the warming treatments. Thus, if *S. malviflora* can disperse north of the Willamette Valley, our experimental results suggest that it may be capable of persisting.

Across their current ranges in this experiment, *M. laciniata* and *A. lemmonii* both seem vulnerable to decline. Nearest its northern limit, *M. laciniata* populations experienced considerable reductions in λ under warming, and at the southern and central sites, failed to establish altogether due to extremely poor recruitment. Data collected from four natural populations across part of its range from 2015 to 2018 support these suggestions of vulnerability, as early-season senescence and high rates of herbivory caused poor demographic performance in all populations (P. Reed, unpubl. data). *Achnatherum lemmonii* failed to establish at all in our experiment, with extremely low germination observed both in the field as well as in our greenhouse germination study. Low germination success can be indicative of inbreeding depression, which is often greater in species with isolated populations (Richards, 2000). While we consider *A. lemmonii* 'widespread' across the PNW, its populations are small (a few hundred plants) and markedly disjunct, suggesting inbreeding depression may be a factor leading to its decline.

While *Festuca roemeri* exhibited leading edge-trailing edge patterns in this experiment, data from natural populations of *A. lemmonii*, *F. roemeri* and *D. californica* collected between 2015 and 2018 show an opposing pattern of λ decreasing from south to north (Peterson et al., in press). However, that study also showed that local performance of those natural populations decreases with warmer, drier conditions, suggesting that factors other than climate (e.g. habitat quality, biotic interactions) may control the

natural latitudinal patterns in λ, but that climate change will still negatively impact populations across their ranges. Thus, these species may be vulnerable to population decline and range contractions with climate change, and their future viability may well depend on an increase in performance for their northern peripheral (leading edge) populations, as well as their potential to disperse to newly suitable habitats.

Demographic compensation has been hypothesized as a mechanism which can 'buffer' populations from a perturbation (e.g. climate change), potentially rescuing them from decline (Doak & Morris, 2010). Using a life table response experiment analysis, we found little evidence for demographic compensation in our focal species. However, we caution that our results are not entirely conclusive: survival and growth are two commonly opposing vital rates (Peterson et al., 2018), but our methods only considered their combined contribution, and also did not examine potentially opposing responses across size classes. Thus, we may be underestimating the cases of compensation. Whether compensation will rescue species in the coming decades as warming continues is unanswered, although other studies suggest it is unlikely (Doak & Morris, 2010; Sheth & Angert, 2018).

While our study provides strong evidence that climate change will alter demographic performance within and, for two species, beyond northern range limits, there are a few notable caveats. First, the 3-year study period is relatively short compared to the lifespan of these perennial plants, so it is possible that reproductive populations could establish given more time. Notably here, however, most species (all but *D. californica*), actually had 6 years of potential establishment at the southern and central sites (given the previous experiment). Second, the patterns we observed were often driven by germination and seedling survival, but these early-life vital rates may have low impact on λ relative to adult performance. Given relatively low adult sample sizes for some vital rates and species (Table S3), we lacked complete estimates of adult performance in some cases. Regarding the low germination in this experiment, it is also possible that the seeds are only dormant and thus still viable (Trask & Pyke, 1998). However, if true, our evidence suggests germination might be restricted to rare 'optimal' years. If the frequency of optimal years is too low to compensate for seed loss due to biotic and abiotic factors, the net result would still be decreasing demographic performance. Lastly, other site factors not related to climate, including the biotic communities (see above Section 4), disturbance history and soil characteristics, may be potentially relevant in the responses we observed.

5 | CONCLUSIONS

To our knowledge, this study was the first to construct complete demographic models of multiple perennial species planted within and beyond their northern range limits under a climate manipulation experiment embedded within a latitudinal gradient. Overall, our findings imply that some native perennial prairie species in the PNW are at risk of decline with climate change, and that these species may need to shift their ranges to persist in the future. Population decline within ranges appears to be driven by warming in this Mediterranean climate system. Increased temperature tended to reduce population growth rates within but not beyond northern range limits, and poor demographic performance within ranges was often attributable to low germination and seedling survival.

Our findings have important management implications. The low establishment rates of these perennial species suggest that transplanting larger plants may be a more effective strategy than seed sowing for restoration practitioners hoping to reestablish or manage populations under climate change (Wallin, Svensson, & Lönn, 2009), particularly for areas that experience a shift towards winter-annual grass dominance with climate change. Beyond their current range limits, species may be capable of establishing populations if they can disperse to suitable habitats. Indeed, our two range-restricted perennials are capable of establishing north of their ranges (and even outperforming when compared to their current ranges), and evidence from other transplant studies suggest that this is a relatively common phenomenon (Baer & Maron, 2018; Hargreaves et al., 2014; Norton, Firbank, Scott, & Watkinson, 2005; Prince & Carter, 1985; Samis & Eckert, 2009). Thus, dispersal limitation may be a critical factor in the persistence of many species in the future, especially considering the potential for further landscape fragmentation. In managing for native biodiversity, these implications beg the questions: should restoration practitioners consider 'restoring' based on future range suitability? Is assisted migration a viable option for protecting vulnerable species? The best answers to these questions depend upon a species' capacity to adapt to climate change (Dawson et al., 2011), its potential for expansion outside its current range, and the value society chooses to place on protecting biodiversity. This ethical dilemma may become increasingly important to debate as climate change continues to threaten species' persistence.

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AUTHORS' CONTRIBUTIONS

P.B.R. analysed the data and wrote the first draft of the manuscript; L.E.P.-M., B.A.R., B.R.J. and S.D.B. conceived the experiment while

all authors contributed to the design; P.B.R., L.E.P.-M., B.A.R., B.R.J., G.T.B., A.A.N. and S.D.B. contributed to data acquisition. All authors provided important intellectual content during revisions and gave final approval for publication.

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REFERENCES

Abatzoglou, J. T., Rupp, D. E., & Mote, P. W. (2014). Seasonal climate variability and change in the Pacific Northwest of the United States. *Journal of Climate*, *27*(5), 2125–2142. https://doi.org/10.1175/JCLI-D-13-00218.1

Angert, A. L., Sheth, S. N., & Paul, J. R. (2011). Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integrative and Comparative Biology*, *51*(5), 733–750. https://doi.org/10.1093/icb/icr048

Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, *37*(5), 406–415. https://doi.org/10.1111/j.1600-0587.2013.00643.x

Baer, K. C., & Maron, J. L. (2018). Declining demographic performance and dispersal limitation influence the geographic distribution of the perennial forb *Astragalus utahensis* (Fabaceae). *Journal of Ecology*, (October 2018), 1250–1262. https://doi.org/10.1111/1365-2745.13086

Barton, K. (2018). *MuMIn: Multi-model inference*. R package version 1.40.4. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., … Wiens, J. J. (2012). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750). https://doi.org/10.1098/rspb.2012.1890

Caswell, H. (1989). Analysis of life table response experiments I: Decomposition of effects on population growth rate. *Ecological Modelling*, *46*, 221–237. https://doi.org/10.1016/0304-3800(89)90019-7

Caswell, H. (2001). *Matrix population models* (2nd ed.). Sunderland, MA: S. A. Inc.

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. https://doi.org/10.1126/science.1206432

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: Biodiversity conservation in a changing climate. *Science*, *332*, 53–58. https://doi.org/10.1126/science.1200303

Dibner, R. R., Peterson, M. L., Louthan, A. M., & Doak, D. F. (2019). Multiple mechanisms confer stability to isolated populations of a rare endemic plant. *Ecological Monographs*, *89*(2), 1–16. https://doi.org/10.1002/ecm.1360

Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, *467*, 959–962. https://doi.org/10.1038/nature09439

Dunne, J. A., Saleska, S. R., Fischer, M. L., & Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, *85*(4), 904–916. https://doi.org/10.1890/03-8003

Easterling, M. R., Ellner, S. P., Dixon, P. M., & Mar, N. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, *81*(3), 694–708. https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *The American Naturalist*, *167*(3), 410–428. https://doi.org/10.1086/499438

Ettinger, A., & HilleRisLambers, J. (2017). Competition and facilitation may lead to asymmetric range shift dynamics with climate change. *Global Change Biology*, *23*(9), 3921–3933. https://doi.org/10.1111/gcb.13649

Gaston, K. J. (2009). Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1395–1406. https://doi.org/10.1098/rspb.2008.1480

Griffith, A. B. (2017). Perturbation approaches for integral projection models. *Oikos*, *126*, 1675–1686. https://doi.org/10.1111/oik.04458

Hargreaves, A. L., Samis, K. E., & Eckert, C. G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist*, *183*(2), 157–173. https://doi.org/10.1086/674525

Lesica, P., & Crone, E. E. (2017). Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. *Ecology Letters*, *20*(2), 166–174. https://doi.org/10.1111/ele.12718

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, *30*(12), 780–792. https://doi.org/10.1016/j.tree.2015.09.011

MacArthur, R. H. (1972). *Geographic ecology*. New York, NY: Princeton University Press.

MacLean, S. A., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, *23*(10), 4094–4105. https://doi.org/10.1111/gcb.13736

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., … McMahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. *Methods in Ecology and Evolution*, *5*, 99–110. https://doi.org/10.1111/2041-210X.12146

Mlynarek, J. J., Moffat, C. E., Edwards, S., Einfeldt, A. L., Heustis, A., Johns, R., … Heard, S. B. (2017). Enemy escape: A general phenomenon in a fragmented literature? *Facets*, *2*(2), 1015–1044. https://doi.org/10.1139/facets-2017-0041

Mote, P. (2003). Trends in temperature and precipitation in the Pacific Northwest during the 20th century. *Northwest Science*, *77*(4), 271–282.

Mote, P. W., & Salathé, E. P. (2010). Future climate in the Pacific Northwest. *Climatic Change*, *102*(1), 29–50. https://doi.org/10.1007/s10584-010-9848-z

Norton, L. R., Firbank, L. G., Scott, A., & Watkinson, A. R. (2005). Characterising spatial and temporal variation in the finite rate of population increase across the northern range boundary of the annual grass *Vulpia fasciculata*. *Oecologia*, *144*(3), 407–415. https://doi.org/10.1007/s00442-005-0102-8

Oldfather, M. F., & Ackerly, D. D. (2019). Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant. *New Phytologist*, *222*(1), 193–205. https://doi.org/10.1111/nph.15565

Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V., & Klanderud, K. (2016). From facilitation to competition: Temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology*, *22*(5), 1915–1926. https://doi.org/10.1111/gcb.13241

Panetta, A. M., Stanton, M. L., & Harte, J. (2018). Climate warming drives local extinction: Evidence from observation and experimentation. *Science Advances*, *4*(2), 1–9. https://doi.org/10.1126/sciadv.aaq1819

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.2307/annurev.ecolsys.37.091305.30000024

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42. https://doi.org/10.1038/nature01286

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/science.aai9214

Peterson, M. L., Bailes, G. T., Hendricks, L. B., Pfeifer-Meister, L. E., Reed, P. B., Bridgham, S. D., … Morris, W. F. (in press). Latitudinal gradients in population growth do not reflect demographic responses to climate. *Ecological Applications*.

Peterson, M. L., Doak, D. F., & Morris, W. F. (2018). Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Global Change Biology*, *24*(4), 1614–1625. https://doi.org/10.1111/gcb.13990

Peterson, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. *Global Change Biology*, *25*(3), 775–793. https://doi.org/10.1111/gcb.14562

Pfeifer-Meister, L., Bridgham, S. D., Little, C. J., Reynolds, L. L., Goklany, M. E., & Johnson, B. R. (2013). Pushing the limit: Experimental evidence of climate effects on plant range distributions. *Ecology*, *94*(10), 2131–2137. https://doi.org/10.1890/13-0284.1

Pfeifer-Meister, L., Bridgham, S. D., Reynolds, L. L., Goklany, M. E., Wilson, H. E., Little, C. J., … Johnson, B. R. (2016). Climate change alters plant biogeography in Mediterranean prairies along the West Coast, USA. *Global Change Biology*, *22*, 845–855. https://doi.org/10.1111/gcb.13052

Prince, S. D., & Carter, R. N. (1985). The geographical distribution of prickly lettuce (*Lactuca serriola*): III. Its performance in transplant sites beyond its distribution limit in Britain. *The Journal of Ecology*, *73*(1), 49–64. https://doi.org/10.2307/2259767

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reed, P. B., Peterson, M. L., Pfeifer-Meister, L. E., Morris, W. F., Doak, D. F., Roy, B. A., … Bridgham, S. D. (2020). Data from: Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.rxwdbrv5d

Reed, P. B., Pfeifer-Meister, L. E., Roy, B. A., Johnson, B. R., Bailes, G. T., Nelson, A. A., … Bridgham, S. D. (2019). Prairie plant phenology driven more by temperature than moisture in climate manipulations across a latitudinal gradient in the Pacific Northwest, USA. *Ecology and Evolution*, *9*(6), 3637–3650. https://doi.org/10.1002/ece3.4995

Rees, M., Childs, D. Z., & Ellner, S. P. (2014). Building integral projection models: A user's guide. *Journal of Animal Ecology*, *83*, 528–545. https://doi.org/10.1111/1365-2656.12178

Rehm, E. M., Olivas, P., Stroud, J., & Feeley, K. J. (2015). Losing your edge: Climate change and the conservation value of range-edge populations. *Ecology and Evolution*, *5*(19), 4315–4326. https://doi.org/10.1002/ece3.1645

Reynolds, L. L., Johnson, B. R., Pfeifer-Meister, L., & Bridgham, S. D. (2015). Soil respiration response to climate change in Pacific Northwest prairies is mediated by a regional Mediterranean climate gradient. *Global Change Biology*, *21*, 487–500. https://doi.org/10.1111/gcb.12732

Richards, C. M. (2000). Inbreeding depression and genetic rescue in a plant metapopulation. *The American Naturalist*, *155*(3), 383–394. https://doi.org/10.2307/3078873

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., … Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, *126*(4), 543–562. https://doi.org/10.1007/s004420000544

Samis, K. E., & Eckert, C. G. (2009). Ecological correlates of fitness across the northern geographic range limit of a Pacific coast dune plant. *Ecology*, *90*(11), 3051–3061. https://doi.org/10.1890/08-1914.1

Sexton, J. P., Mcintyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(10), 201715899. https://doi.org/10.1073/pnas.1715899115

Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, *22*(11), 1–23.

Thomas, C. D. (2010). Climate, climate change and range boundaries. *Diversity and Distributions*, *16*(3), 488–495. https://doi.org/10.1111/j.1472-4642.2010.00642.x

Trask, M. M., & Pyke, D. A. (1998). Variability in seed dormancy of three Pacific Northwestern grasses. *Seed Science and Technology*, *26*, 179–191.

Villellas, J., Doak, D. F., García, M. B., & Morris, W. F. (2015). Demographic compensation among populations: What is it, how does it arise and what are its implications? *Ecology Letters*, *18*(11), 1139–1152. https://doi.org/10.1111/ele.12505

Wallin, L., Svensson, B. M., & Lönn, M. (2009). Artificial dispersal as a restoration tool in meadows: Sowing or planting? *Restoration Ecology*, *17*(2), 270–279. https://doi.org/10.1111/j.1526-100X.2007.00350.x

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021

Young-Mathews, A. (2012). *Plant guide for rose checkermallow (Sidalcea virgata)*. Corvallis, OR: USDA-Natural Resources Conservation Service, Plant Materials Center.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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