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Climate warming threatens the persistence of a community of disturbance-adapted native annual plants

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Abstract. With ongoing climate change, populations are expected to exhibit shifts in demographic performance that will alter where a species can persist. This presents unique challenges for managing plant populations and may require ongoing interventions, including in situ management or introduction into new locations. However, few studies have examined how climate change may affect plant demographic performance for a suite of species, or how effective management actions could be in mitigating climate change effects. Over the course of two experiments spanning 6 yr and four sites across a latitudinal gradient in the Pacific Northwest, United States, we manipulated temperature, precipitation, and disturbance intensity, and quantified effects on the demography of eight native annual prairie species. Each year we planted seeds and monitored germination, survival, and reproduction. We found that disturbance strongly influenced demographic performance and that seven of the eight species had increasingly poor performance with warmer conditions. Across species and sites, we observed 11% recruitment (the proportion of seeds planted that survived to reproduction) following high disturbance, but just 3.9% and 2.3% under intermediate and low disturbance, respectively. Moreover, mean seed production following high disturbance was often more than tenfold greater than under intermediate and low disturbance. Importantly, most species exhibited precipitous declines in their population growth rates (λ) under warmer-than-ambient experimental conditions and may require more frequent disturbance intervention to sustain populations. *Aristida oligantha*, a C4 grass, was the only species to have λ increase with warmer conditions. These results suggest that rising temperatures may cause many native annual plant species to decline, highlighting the urgency for adaptive management practices that facilitate their restoration or introduction to newly suitable locations. Frequent and intense disturbances are critical to reduce competitors and promote native annuals' persistence, but even such efforts may prove futile under future climate regimes.

Key words: adaptive management; climate manipulations; competition; cross-validation; demography; disturbance; latitude; Pacific Northwest prairies; population growth; range limits; recruitment; restoration.

Introduction

Managing vulnerable species in a rapidly changing environment is a major conservation challenge. Because many species are believed to be at risk of decline with climate change (Pereira et al. 2010, Moritz and Agudo 2013, Román-Palacios and Wiens 2020), an increasingly important task is to predict how demographic performance will be affected by future climatic conditions, as well as what other factors could be managed to mitigate climate effects. This leads to two important questions for conservation: Under what climatic conditions can species exhibit stable or increasing populations? And, how do nonclimatic effects such as disturbance alter population growth rates, potentially providing a way to mitigate climate change effects via local management?

Management of vulnerable plant populations, even before anthropogenic climate change became a complicating threat, has relied on understanding the factors most important in controlling local population growth rates. Disturbance is often a critical component to establishing and maintaining a population successfully (Connell and Slatyer 1977, Palmer et al. 1997, Macdougall and Turkington 2007). This is especially true for annual plants, which tend to be early-successional species and

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are therefore frequently limited by competition (Bazzaz 1979, Tilman 1990, Rees and Long 1992). Annuals are also subject to dramatic fluctuations in population size (Nunney 2002) and may be especially vulnerable to climate change (Morris et al. 2008). However, no studies to our knowledge have examined the controls of climate and disturbance together on the demographic success of a suite of co-occurring annual plants. It is critical to identify what factors have similar effects on co-occurring species to inform community-wide management in the face of climate change. Although many conservation and restoration plans attempt to optimize benefits for a suite of native species (Wang et al. 2020), doing so successfully requires an understanding of the extent to which demographic responses are generalizable.

Furthermore, although climate change may prove detrimental for species within portions of their current geographic ranges, it may also open the possibility for range shifts that support long-term persistence (Pfeifer-Meister et al. 2013, Rehm et al. 2015, Reed et al. 2021*b*). But because the ability to track favorable climatic conditions may be limited by dispersal (Loarie et al. 2009, Hargreaves et al. 2014, Bayly and Angert 2019, Cruzan and Hendrickson 2020, Pagel et al. 2020), vulnerable plants may require intentional translocations to newly suitable sites (Vitt et al. 2010). To justify such actions, it is important to understand how species will perform across climate gradients under projected climate change.

Experimentation provides a robust means to relate species' demographic performance to the effects of climate and disturbance. In particular, experimental manipulations that impose a range of current and future climatic conditions across multiple sites can disentangle the role of climate from local site factors (Dunne et al. 2004, Villellas et al. 2019), and identify the degree to which population growth rates might change under future (relative to current) conditions. In addition, field manipulations focused on multiple species can give insights into the generality of climate responses, as well as other factors limiting population growth rates. Although single-species studies have provided many insights into limiting factors, a key question is whether they can be generalized to multiple species.

Here, using 6 yr of data from two climate manipulation experiments spanning four sites across a latitudinal gradient, we examined the relationship between climate and demography for a suite of eight annual plant species native to prairie habitat in the western Pacific Northwest (PNW), United States. Although our experiments were principally designed to focus on climate manipulations, we were also able to address how management-driven disturbance conditions shaped demographic performance.

Of the eight annual species we studied (Table 1; see Appendix S1: Section S1 for species' descriptions), five have current northern range limits that occur south of at least one of our experimental sites (Fig. 1). These five species were therefore planted both within and beyond their current ranges. All eight species are important members of imperiled PNW prairie ecosystems (Noss et al. 1995), which have become the focus of many regional conservation and restoration efforts (Dunwiddie and Bakker 2011). Pacific Northwest prairies were historically widespread, in part due to frequent burning by Native Americans (Boyd 1999). Following Euro-American settlement, fire suppression, land conversion, and the establishment of nonnative species have contributed to the loss and modification of PNW prairie ecosystems (Dennehy et al. 2011). Native annual species, in particular, have suffered tremendous declines, and many have become locally extirpated from most remaining prairie fragments (Dunwiddie et al. 2014). Deliberate reintroductions are often necessary to restore this functional group to the landscape.

Table 1. The eight focal species in descending order of northern range limit (see Fig. 1).

Species	Family	Exp
Plectritis congesta (Lindl.) DC	Caprifoliaceae	Exp2
Collinsia grandiflora Lindl.	Plantaginaceae	Both
Clarkia purpurea (W. Curtis) A. Nelson & J.F. Macbr.	Onagraceae	Both
Plagiobothrys nothofulvus A. Gray	Boraginaceae	Exp2†
Aristida oligantha Michx.	Poaceae	Both
Achyrachaena mollis Schauer	Asteraceae	Both
Thysanocarpus radians Benth.	Brassicaceae	Both†
Navarretia pubescens (Benth.) Hook. & Arn.	Polemoniaceae	Both

Notes: All species have southern range limits in California. "Exp" column: *P. congesta* and *P. nothofulvus* were only planted in the second experiment (Exp2), while all other species were planted in both experiments.

†*Plagiobothrys nothofulvus*and *T. radians* were also not planted in fall 2015 (see Methods).

Ongoing climate change may further threaten these ecosystems (Bachelet et al. 2011), as regional precipitation is expected to become more variable and mean annual temperature is expected to rise by ~3°C by the end of the 21st century (Mote and Salathé 2010). Indeed, previous studies from our climate manipulation experiments suggest that warming will be detrimental for native perennial species within their current geographic range limits (Pfeifer-Meister et al. 2013, Reed et al. 2021*b*), cause a greater risk of introduced annual grass invasions (Pfeifer-Meister et al. 2016), and shift native species' flowering and growth phenology (Reed et al. 2019). To understand how climate and disturbance will affect populations for this suite of native annual species, we asked:

1. How does demographic performance, and thus population growth rate, vary across a range of current and future climatic conditions?
2. Do species exhibit similar patterns in population growth rates across climatic space? Does being within

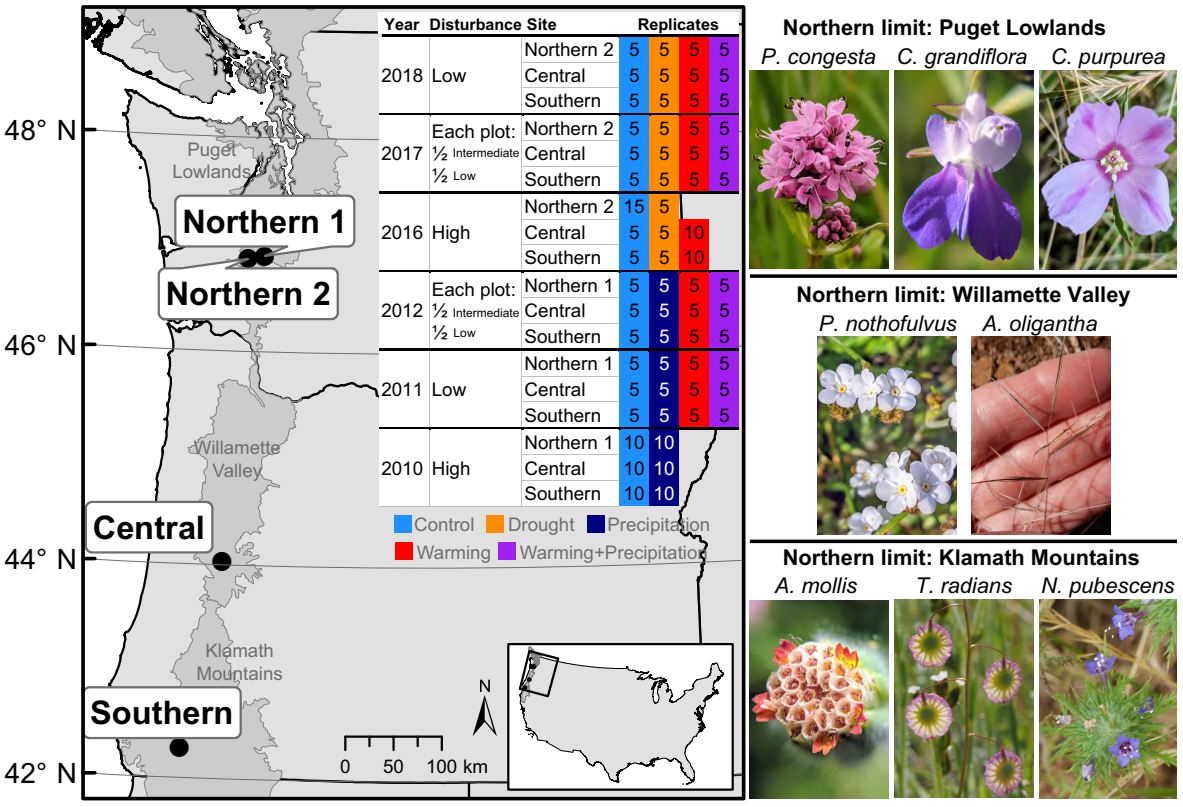

FIG. 1. On the left: map of the four experimental sites in the western Pacific Northwest, United States, with inset table describing the disturbance conditions, sites, and climate treatment plot replicates for each year of the experiments (Exp1: 2010–2012, Exp2: 2016–2018; see Methods). There were 62 unique year × site × climate treatment combinations and 360 replicates in total. On the right: the eight focal species grouped by their current northern-range-limit regions (*Plectritis congesta*, *Collinsia grandiflora*, *Clarkia purpurea*, *Plagiobothrys nothofulvus*, *Aristida oligantha*, *Achyrachaena mollis*, *Thysanocarpus radians*, and *Navarretia pubescens*). The Klamath Mountain species are within their current ranges only at the southern site; the Willamette Valley species are within their current ranges at the southern and central sites; the Puget Lowland species are within their current ranges at all four sites. Photo of *A. oligantha* by Ed Alverson; all other photos by Paul Reed and Bitty Roy.

vs. beyond current northern limits affect performance?

3. How important is the role of disturbance in determining performance and modulating climate effects on these annual species?

METHODS

Study sites and experimental design

This study combines 6 yr of data from two experiments (Exp1: 2010–2012; Exp2: 2016–2018) that occurred across four sites spanning a 520-km latitudinal Mediterranean-climate gradient in the western PNW (Fig. 1). The southern and central sites were used during both Exp1 and Exp2, whereas the northern 2 site replaced the northern 1 site between experiments because the northern 1 site was no longer available. Summer drought severity increases from north to south across this gradient. The 30-yr normal (1981–2010) mean annual temperatures are 10.6°C, 10.5°C, 11.4°C, and 12.3°C at the northern 2, northern 1, central, and southern sites, respectively, while mean annual precipitation is 1,240 mm, 1,196 mm, 1,134 mm, and 1,434 mm, respectively (PRISM Climate Group 2020). However, the southern site receives the greatest proportion of its precipitation in the early growing season (November–March), and is generally much drier than the other sites in the spring and summer (Reynolds et al. 2015). All sites are located within PNW prairie habitat and were dominated by introduced perennial grasses prior to plot establishment. Treatments were discontinued at the southern and central sites during the gap years between Exp1 and Exp2.

Each site contained 20 plots of 7.1-m^2 that required heavy disturbance, prior to both experiments, to reduce existing vegetation and establish baseline starting communities. In late 2009 and 2015, plots were mowed, raked, and treated with herbicide (2% glyphosate and grass-specific Poast). These events created ample open space for the 2010 and 2016 growing seasons, which are hereafter referred to as "high-disturbance" conditions

(Fig. 1). Following the 2009 disturbance, we sowed the southern, central, and northern 1 plots with an establishment mix of 19 native prairie species (Pfeifer-Meister et al. 2013), and, following the 2015 disturbance, we sowed the southern, central, and northern 2 plots with an establishment mix of 29 native prairie species (Reed et al. 2021*b*). Beginning in Year 2 of each experiment (2011 and 2017), rapid regrowth of nonnative vegetation resulted from minimal plot maintenance (hereafter: "low-disturbance" conditions). This regrowth was moderately controlled in half of each plot in 2012 and 2017 by implementing an "intermediate-disturbance" treatment.

Each plot was assigned to a climate manipulation treatment. For Exp1, these were control (ambient temperature and precipitation), precip (+20% precipitation within the 2-week interval in which it occurred), warming (+2.5 to 3°C), and warming + precip (+2.5 to 3°C and +20% precipitation). Because we found the +20% precipitation treatment to have minimal effects and the warming treatment to be confounded by a reduction in soil moisture in other studies (Pfeifer-Meister et al. 2013, 2016), we modified treatments prior to Exp2. In Exp2, the climate treatments were control, drought (−40% precipitation), warming (+2.5°C), and warming + precip (automatically irrigated to offset the warming-induced drying effect fully). See Appendix S1: Section S2 for a complete description of all climate treatments. Although there were differences in the warming + precip treatments of Exp1 and Exp2, we group them together in our figures for simplicity. Thus, we define five broad climate treatments overall (control, drought, precip, warming, and warming + precip). Because of logistical constraints with heating and irrigation, some treatments had delayed starting dates, resulting in uneven treatment replicates during some years (Fig. 1; Appendix S1: Section S2). Within each plot, we continuously logged canopy temperature and soil volumetric water content over the course of each experiment. However, also because of logistical constraints, this did not begin until several months into each experiment.

To monitor germination and survival of focal species, we planted 200 seeds per species per plot (25 seeds into eight 5.5-cm-diameter subplot rings) in the fall prior to each experiment year, with a few exceptions. Neither *Plectritis congesta* nor *Plagiobothrys nothofulvus* were planted during Exp1, and neither *P. nothofulvus* nor *Thysanocarpus radians* were planted in fall 2015. Additionally, for *T. radians*, we only sowed 80 seeds in fall 2016 and 70 seeds in fall 2017 (10 seeds into eight and seven subplot rings, respectively) because of seed quantity limitations. To account for local adaptation, we used the nearest available seed sources for each site.

Because we observed very low recruitment 1 yr into both experiments, we implemented an intermediate-disturbance treatment in half of each plot in the winter–spring of 2012 and 2017. This intermediate disturbance consisted of weeding and clipping any nonfocal species to reduce their aboveground biomass. This resulted in only a moderate reduction in competitors compared to the high-disturbance conditions of 2010 and 2016, based on our visual assessment of the amount of open space created. However, there was a noticeable reduction in nonfocal species biomass compared to the plot halves not receiving the treatment, as well as the entire plots during the low-disturbance-only years of 2011 and 2018. Thus, both experiments (and all four sites) imposed high-, intermediate-, and low-disturbance conditions.

Demographic data

We quantified three vital rates each experiment year: germination, survival (from germination to flowering), and per-capita seed production. Between winter and spring, we conducted 2–4 censuses of each plot to count the number of germinants from the previous fall's planting. We thinned germinants in overcrowded subplots and corrected survival estimates for thinning. We aggregated germination and survival counts to the plot or the half-plot level (for 2012 and 2017). In 2018, we estimated germination from the seed bank by returning to subplot rings seeded in fall 2016 and fall 2015 to count second- and third-year germinants, respectively.

Per capita seed production (collected during the final spring censuses) was estimated differently for Exp1 and Exp2. In Exp2, we counted plant-level fruit and/or seed production on all or a subset of the individuals in a plot, harvesting a subset of fruits for the species that were too difficult to count seeds in the field directly. However, in Exp1, we harvested fruits from a known number of plants and combined these into a single sample (per plot), and then counted the total number of seeds (per plot) to estimate mean seeds per plant. Because we lacked plant-level seed production for Exp1, we calculated the mean number of seeds per plant for each year at the plot level for both experiments.

Analysis overview

Because we combined results from different sites, years, and experimental treatments into a single analysis, we needed to create common data currencies. We did so by categorizing plot preparation and management actions into three disturbance groups (noted above and in Fig. 1), and by replacing categorical climate treatments with continuous measures of temperature, precipitation, and composite variables (actual evapotranspiration and climatic water deficit). We then considered regression models that accounted for site, disturbance, and continuous climate covariates. In addition to allowing us to combine data from two experiments into a single, robust analysis, by regressing vital rates on actual climate variables (rather than taking an ANOVA approach with categorical treatments), we can (in future work) better project the effects of future changes in those climate variables.

However, this approach also meant that we could not account for interactions among sites and years, or

random effects within years that were not related to interannual differences in climate. We attempted to address this with a random year effect, but year was partially confounded with site and disturbance and there were unequal sample sizes among sites. This often resulted in poor model fit with unrealistic estimates for some site and year combinations.

Because we could not account for interactions among sites and years, the effects of disturbance and climate covariates may be overestimated because of excessively narrow standard errors on coefficient estimates. However, despite this caveat, we feel that our strategy made the best possible use of our unique data sets. It allowed us to combine multiple years of data from manipulative climate treatments across four sites into a climate response surface based on temperature and moisture, which are the climate forcing variables of interest to the larger scientific community. We also did this for suite of eight plant species rather than focusing on a single species.

Analyses

We conducted all analyses using R version 4.0.2 (R Development Core Team 2020). Because we noticed a strong decline in focal species' performance when disturbance was low, we first ran an ANOVA-based analysis looking at the effects of disturbance and site. Using mixed models, we ran logistic regressions on germination, survival, and recruitment into the reproductive class (total survival from planting to reproduction, or the product of germination and survival). Because we lacked plant-level seed data for Exp1 and thus could not use a Poisson-family generalized linear model, we ran linear models of the log-transformed mean number of seeds per plant (plus a small constant 0.1, because some means were zero) weighted by the number of plants per plot used to calculate the means. We treated site, disturbance, and their interaction as fixed effects and plot as a random effect (to account for repeated sampling across years) and tested for statistical differences among sites and disturbance levels using Tukey's post hoc comparisons.

To test for relationships between vital rates and climate, we focused on environmental variables related to temperature, precipitation, and drought stress because of their documented relevance for PNW prairie plant performance (Pfeifer-Meister et al. 2016, Reed et al. 2019, 2021*b*, DeMarche et al. 2021). To accommodate missing plot-level data on canopy temperature and soil moisture, and to estimate how large-scale climate conditions will alter plant performance, we ran a series of analyses that translated treatment-specific, plot-level climatic data into predicted measures of mean temperature, total precipitation, and drought stress that correspond to PRISM (PRISM Climate Group 2020) climate variables (Appendix S1: Section S3). Briefly, using directly measured data from control plots, we first established the relationship between monthly site-level PRISM estimates of temperature and precipitation with plot-level canopy temperature and soil volumetric water content. Using this relationship, we then estimated PRISM values of temperature and precipitation for each climate treatment plot using their unique temperatures and water contents. Finally, we used these estimates of temperature and precipitation to derive potential evapotranspiration (PET), actual evapotranspiration (AET—the amount of water removed by evaporation and transpiration) and climatic water deficit (CWD—PET minus AET), which were calculated using the Redmond 2019 R function using a modified Thornthwaite water balance model. For analyses of demographic rates, we aggregated monthly climate variables (mean temperature, total precipitation, AET, and CWD) into winter and spring seasonal values (November–February and March–June, respectively), because in the Mediterranean-type climate of the PNW these species generally germinate in the fall and winter, grow and reproduce in the spring, and senesce by the summer.

Using these seasonal values, we tested for climate effects on vital rates by fitting a series of mixed models that also accounted for site × disturbance effects and a random plot effect. We fit models that combined one temperature variable (winter or spring) with one moisture variable (winter or spring precipitation, AET, or CWD, excluding winter CWD, because it was always zero), resulting in seven total climate variables (two seasons × four variables, minus winter CWD). We excluded models containing combinations of winter temperature with winter AET and spring temperature with spring CWD because of high collinearity. We included quadratic effects of climate to allow unimodal (hump-shaped) relationships between vital rates and climate, as it is reasonable to expect vital rates to peak at intermediate conditions. We incorporated temperature × precipitation interactions but not temperature × AET or temperature × CWD, because temperature is directly incorporated into the calculations of AET and CWD.

We were unable to include climate × site or climate × disturbance interactions because of low within-site climate variation during the high-disturbance years (when not all climate treatments were operational yet), and limited data in later years when species' abundances were low. Including such interactions forced poor model fit with unrealistic predictions. Although this prohibited us from testing whether climate responses differed within vs. beyond current ranges, we could still establish relationships between vital rates and the climate across the entire latitudinal gradient.

We identified the model with the best predictive performance for each vital rate using a K-fold cross-validation procedure (James et al. 2013, Tredennick et al. 2021), where $K = 5$. Stratifying by site, disturbance, and year, we randomly split the data set into five groups (*folds*) and iteratively withheld one fold (20%) at a time to serve as an out-of-sample test set, and the remaining four folds (80%) served as a training set. Within each loop, we fit all possible subsets of the series of models we wanted to examine, including two no-climate null

models (one that accounted for site and disturbance effects and the other accounting for site only). For each model fitted to the training data set, we made predictions on the out-of-sample test data and compared these predictions to observed values to calculate a mean-squared error for each model within each fold. We then calculated the average mean-squared error for each model across the five folds and considered the model with the lowest average mean-squared error to have the best predictive performance. We then fit this "best" model formula to the entire data set.

To estimate population growth rates (λ), we sampled 1,000 random sets of our seven climate variables from a multivariate normal distribution based on their means and covariances across all sites and years of the study. We then predicted germination, survival, and seed production for each site and disturbance level on that set of climate values using our models with the best predictive performance, and calculated λ as the product of the three predicted vital rates. To estimate uncertainty in each vital rate, we used the 'predictInterval' function from the merTools package (Knowles and Frederick 2020), using 2,000 simulations to obtain 95% prediction intervals. We multiplied the three upper limits of the vital rates to get the upper prediction limit for λ, and the three lower limits of the vital rates to get the lower prediction limit for λ. We did not include a seed bank when calculating λ as our limited seed-bank germination data suggested these rates were minimal (see Results).

To visualize λ as a function of climate, we performed a principal-components analysis (PCA) on our measured climate data. Using a PCA was necessary because different vital rates could be explained by different combinations of the seven climate variables (e.g., a germination model may include winter temperature and winter precipitation, but the survival model includes spring temperature and spring CWD). Using the simulated set of multivariate climate values, we plotted smoothed contours of λ against PC1 and PC2 scores using a loess fit. We acknowledge that this loess-fit procedure adds a second dimension of uncertainty to our analyses. However, our goal with these analyses was simply to visualize the best-estimated relationships between λ and climate, and not to estimate full uncertainty in these effects. Thus, we felt this was the simplest procedure to use and interpret.

Lastly, we also explored how climate and disturbance event frequency jointly determined each species' long-run (geometric mean) annual population growth rate. For an annual plant with no seed bank living in an environment with stochastic disturbances, the long-run growth rate is given by

$$\lambda_g = \lambda_h^{p_h(d)} \lambda_i^{p_i(d)} \lambda_l^{p_l(d)},$$

where λ_h, λ_i, and λ_l are the population growth rates in years of high-, intermediate-, and low-disturbance conditions, respectively, and $p_h(d)$, $p_i(d)$, and $p_l(d)$ are the proportions of years with high-, intermediate-, and low-disturbance conditions, which depend on the frequency of disturbance events d. We assumed that high-disturbance conditions prevail in a year with a disturbance event, intermediate conditions prevail in the first year after the disturbance event, and low-disturbance conditions two or more years after the disturbance. We used a Markov model in which we calculated λ_g across disturbance event probabilities (d) ranging from 0 to 1 in increments of 0.02. The proportions of years with high-, intermediate-, and low-disturbance conditions are then given by the dominant right eigenvector (normalized to one) of the Markov matrix that governs transitions between disturbance states (where columns represent the high-, intermediate-, and low-disturbance conditions this year and rows represent the conditions next year, in the same order):

$$\begin{bmatrix} d & d & d \\ 1-d & 0 & 0 \\ 0 & 1-d & 1-d \end{bmatrix}.$$

For *P. nothofulvus, which* was not planted under high-disturbance conditions, we assumed intermediate conditions in a disturbance event year and low-disturbance conditions one or more years after the disturbance event.

Results

Recruitment was greatest under high disturbance for most species and sites (Fig. 2A; site × disturbance: $P < 0.05$ for all species). *Plectritis congesta* was the major exception, having highest recruitment under intermediate disturbance regardless of site. Predicted recruitment was 11.0 ± 2.1% (mean ± 1 SE) across all species and sites under high disturbance but fell to just 3.9 ± 1.3% and 2.3 ± 0.8% under intermediate and low disturbance, respectively. Germination and survival, the two components of recruitment, exhibited similar responses to disturbance but significant differences were more common for germination (Appendix S2: Fig. S1). Most species also had greatest per capita seed production under high disturbance regardless of site, with seed counts often more than tenfold greater compared to intermediate and low disturbance (Fig. 2B). Again, *P. congesta* (at the northern 2 site) was the major exception to this finding. Germination from the seed bank was mostly negligible, with high-end estimates of just 0.6% and 0.3% of the seeds germinating after 2 and 3 yr in the seed bank, respectively, in 2018 across all species and sites (Appendix S3: Table S1).

We established strong relationships between monthly PRISM estimates of temperature ($R^2 = 0.985$) and precipitation ($R^2 = 0.828$) from control plot canopy temperatures and soil volumetric water contents. When performing a PCA on our set of seven climate variables,

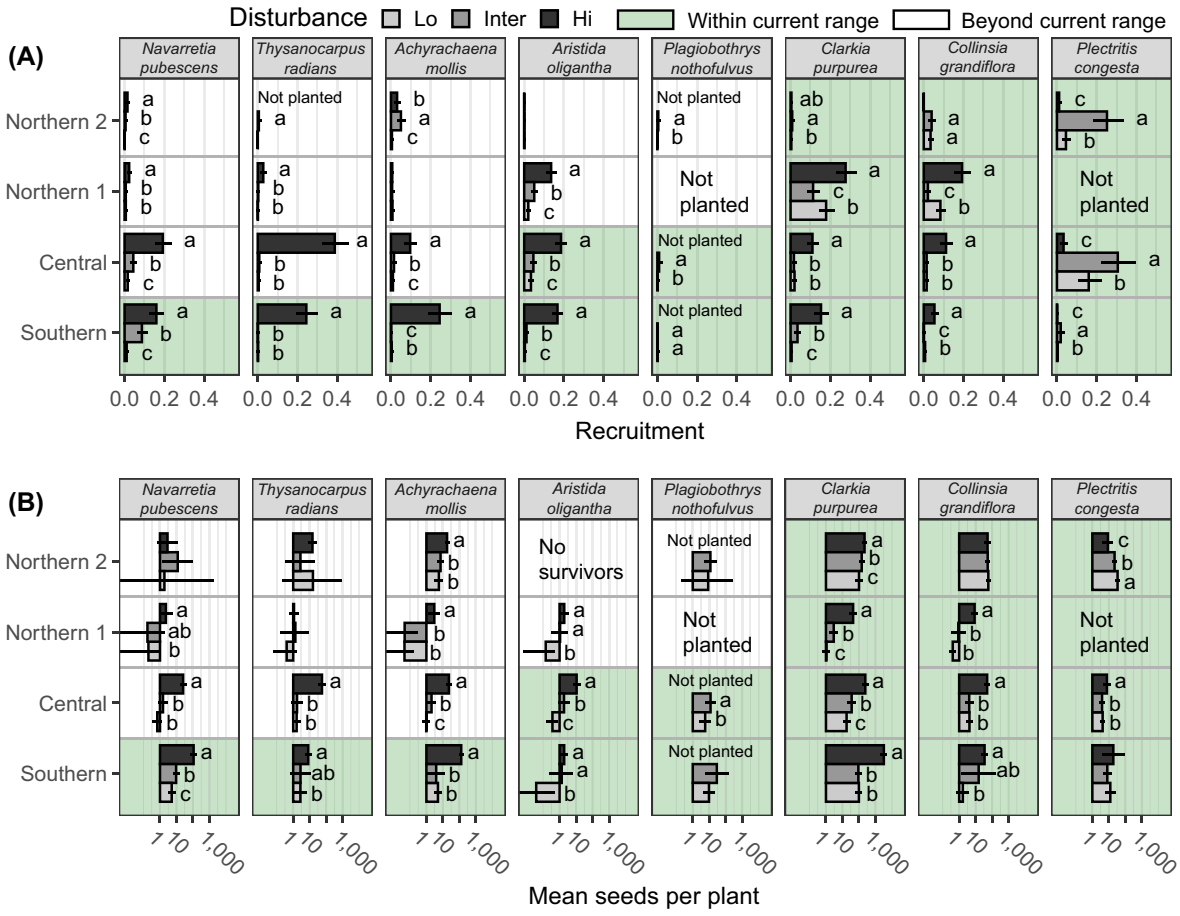

FIG. 2. The role of disturbance (high, intermediate, low) on species' (A) recruitment (surviving plants per seed planted) and (B) seeds per surviving plant (note the log-scale axis). Bars show estimated marginal means ± 95% confidence limits. "High" disturbance includes all data from 2010 and 2016; "intermediate" disturbance includes all data from the plot halves receiving the intermediate-disturbance treatments of 2012 and 2017; "low" disturbance includes all data from 2011 and 2018, as well as all data from the plot halves that did not receive the intermediate-disturbance treatments in 2012 and 2017 (see Methods). Letters indicate significant differences ($P < 0.05$) between disturbance levels for a given site and species. Species are arranged from left to right in ascending order of northern range limit.

the first two principal components accounted for 50.02% and 23.77% of the variance in the climate data, respectively (Fig. 3). PC1 was mostly driven by variation in temperature (cooler to warmer from left to right), whereas PC2 generally reflected additional variation explained by moisture (drier to moister from bottom to top). Most of the climate-space variation was between the warmed and not-warmed treatments regardless of site, rather than among sites (Appendix S2: Fig. S2).

With the exception of *P. nothofulvus* seed production, the vital rate models with the best predictive performance included at least one climate term (Appendix S3: Table S2). In general, most of these models substantially reduced average mean-squared error relative to the two no-climate null models (Appendix S3: Table S3). Most vital rates predicted by temperature and/or climatic water deficit (CWD) had negative or unimodal relationships with these variables, whereas relationships to precipitation and actual evapotranspiration (AET) were more variable (Appendix S2: Figs. S3–S10). Although disturbance and site influenced the intercepts of vital rate–climate relationships, there was no consistent tendency for certain sites to support higher performance.

When integrating vital rate models into predicted population growth rates (λ), we observed a wide range in the magnitude of λ by species and disturbance (Fig. 4: note each species' response is averaged across sites). However, with few exceptions, λ was $\ll 1$ under low disturbance but $\gg 1$ under high disturbance. These patterns hold true at the 95% prediction limits (Appendix S2: Figs. S11, S12). The only exceptions were *P. congesta*, for which λ peaked at intermediate disturbance, and *Collinsia grandiflora*, which showed relatively weak effects of disturbance. λ also differed strongly by site, but this effect did not appear to be a simple function of latitude (Appendix S2: Figs. S13–S15).

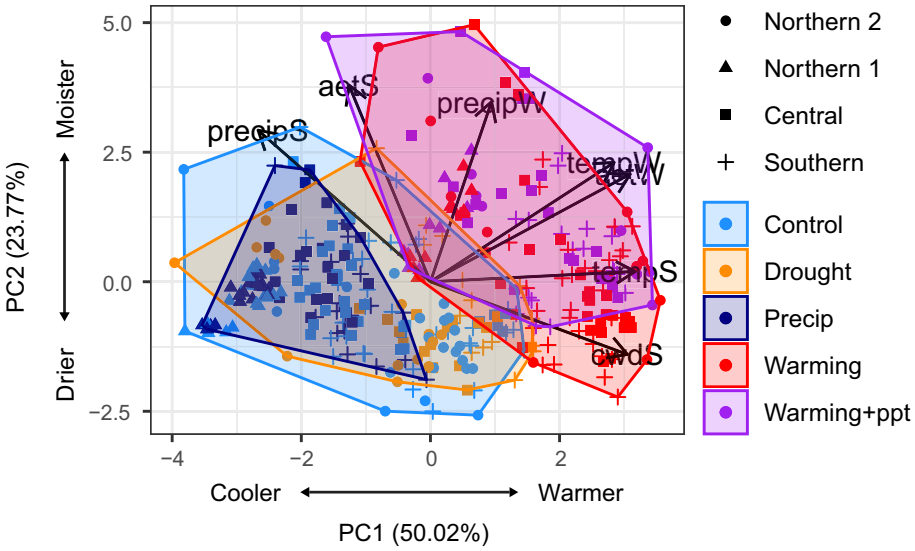

FIG. 3. Principal-components analysis of the seven climate variables used in the study, using all 360 unique replicates from Exp1 and Exp2. Polygons encapsulate the five broad climate treatments. 'temp' = mean temperature, 'precip' = total precipitation, 'aet' = total actual evapotranspiration, 'cwd' = total climatic water deficit; 'W' = winter, 'S' = spring. PC1 is primarily driven by temperature (cooler to warmer from left to right), and PC2 reflects additional variation explained by moisture (drier to moister from bottom to top). There is considerable separation in climatic space as a result of the warming treatments, regardless of site.

For most species, λ increased toward cooler climatic conditions (Fig. 4: negative scores for PC1; note the colored polygons depicting the range of climatic conditions that occurred in each treatment). *Navarretia pubescens*, *T. radians*, and *P. nothofulvus* peaked at cooler, drier conditions, and *Achyrachaena mollis*, *Clarkia purpurea*, *Clarkia grandiflora*, and *P. congesta* peaked at cooler, moister conditions. *Aristida oligantha* was the major exception, as it increased toward warmer, drier conditions (Fig. 4). Again, responses remain consistent at the 95% prediction limits (Appendix S2: Figs. S11, S12). These patterns become especially apparent when plotting log(λ) against PC1 (Fig. 5; note each species is plotted under its optimal disturbance condition). Five of the

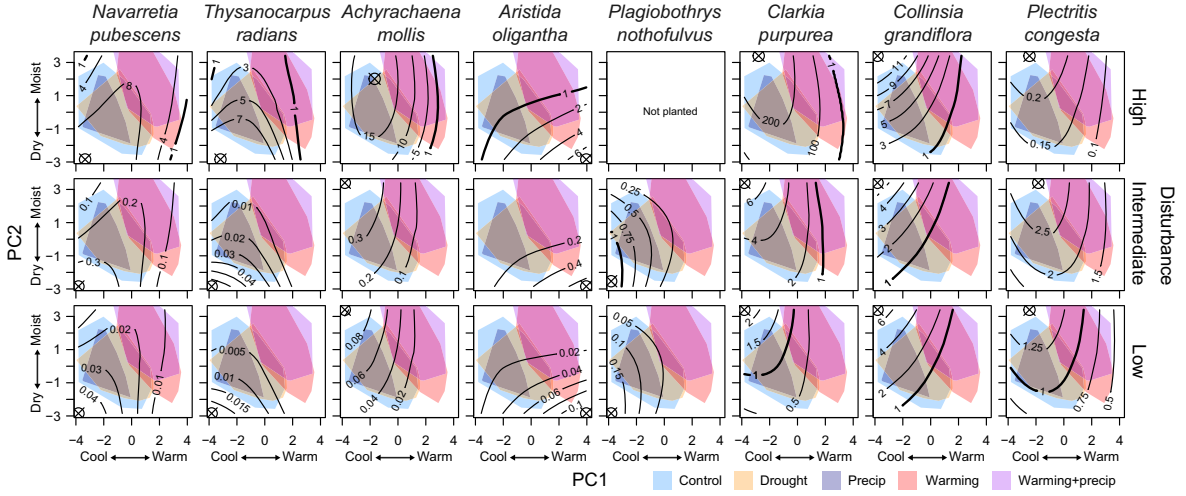

FIG. 4. Contour plots of estimated population growth rates (λ) as a function of climate (PC1 and PC2) and disturbance (high, intermediate, and low) averaged across sites for each of the eight focal species. Climate is depicted as the first two principal components of all seven climate variables used in the study, with PC1 reflecting temperature (cooler to warmer left to right) and PC2 reflecting moisture (drier to moister bottom to top). Colored polygons depict the range of climatic conditions that occurred in each climate treatment over the course of the experiments. ⊠ indicates the location of highest λ.

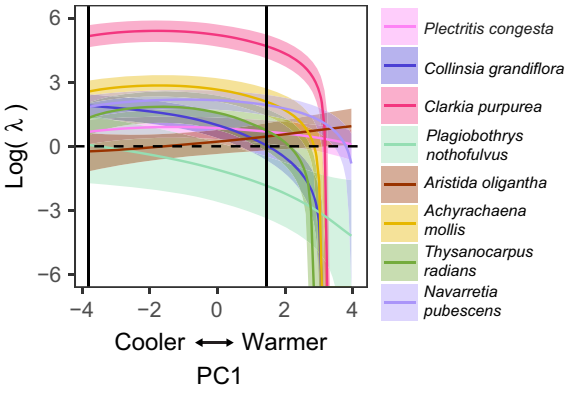

FIG. 5. Log-transformed population growth rates (λ) of each species against PC1 (at PC2 = 0). Shaded bands indicate 95% prediction intervals. Dashed horizontal line at Log(λ) = 0 indicates a "stable" population. Black vertical lines identify the range of PC1 values in the control treatment plots across all sites and years.

eight species exhibit a steep decline in log(λ) once outside of ambient PC1 conditions, and *P. nothofulvus* and *P. congesta* exhibit more subtle, but consistent, decline. *Aristida oligantha* is the lone species to have log(λ) increase with PC1.

Lastly, the long-run annual population growth rate, calculated as a function of climate and disturbance frequency, revealed that more frequent disturbances would increase population growth rates for every species except *P. congesta* (Fig. 6). With greater warming (increasing PC1), *N. pubescens*, *T. radians*, *A. mollis*, *P. nothofulvus*, *C. purpurea*, and *C. grandiflora* would all require more frequent disturbance to sustain population growth rates. In contrast, although *A. oligantha* would also benefit from more frequent disturbance, this would not be necessary for it to sustain its populations under future conditions.

DISCUSSION

We have shown how both disturbance and warming strongly drive the demographic performance of a suite of native annual species reintroduced to PNW prairies. We found evidence suggesting that most species' population growth rates decline precipitously following the initial boom of a major disturbance event, and that seven of the eight species have increasingly poor performance under future climatic conditions. Although stressing the importance of implementing common prairie restoration disturbances such as fire, grazing, and mowing (Davison and Kindscher 1999) when managing annual plant populations, these results also warn that future warming may lead to local extirpations despite best management practices. This is consistent with studies of very different systems (Bickford et al. 2010, Linares and Doak 2010, Montero-Serra et al. 2019), suggesting that although managing local demographic drivers may partially mitigate climate change effects, the impacts of climate change may overwhelm such efforts for many species.

Extremely few studies of the demographic drivers of plants have compared multiple species to ask whether responses can be generalized (but see DeMarche et al. 2021, Reed et al. 2021*b*). The observation that climate warming caused declining population growth rates was remarkably consistent across these eight species, with *A. oligantha*, a C4 grass (Adams and Wallace 1985) and our only C4 focal species, being the lone exception that exhibited the opposite response. This is perhaps unsurprising, given that C4 species generally reach highest dominance in warmer environments (Edwards and Still 2008). Given the projected increase in regional temperatures of ~3°C by the 2080s (Mote and Salathé 2010, Dalton and Fleishman 2021), *A. oligantha* may be poised to persist and even thrive in the future. Contrarily, the consistently negative responses to warming among the remaining species does not bode well for the future of native plant biodiversity in PNW prairies. It is estimated that the richness of native annuals in western Washington prairies has already declined from ~50% of the native flora in the early 1800s to ~18% today (Dunwiddie et al. 2014). As the climate shifts toward warmer conditions, these species may further drop out of communities and cause native diversity to decline (Pfeifer-Meister et al. 2016). Indeed, data at the community level show that native cover and diversity decline with increasing temperature and drought severity, while introduced annual cover increases (Reed et al., *unpublished manuscript*).

The observation that warming caused declining demographic performance agrees with previous work on other PNW prairie species in these experiments (Pfeifer-Meister et al. 2013, Reed et al. 2021*b*), as well as on a widespread mountain plant in Colorado (Panetta et al. 2018) and two North American tundra plants (Doak and Morris 2010). However, although some studies only report declining population growth rates at species' trailing edges (Lesica and Crone 2017, Sheth and Angert 2018), we found declining rates across a large latitudinal gradient, including near our species' leading (northern) edges. This echoes the warning of DeMarche et al. (2018) that species may be at risk of decline throughout their geographic ranges. If declines in vital rates such as survival and fecundity are left unchecked, populations could be eliminated (Panetta et al. 2018). Although multiyear seed banks may allow for some buffering, this decline may be more rapid for annual species, which, unlike perennials, are not also buffered by persistent adult stages (Morris et al. 2008).

Furthermore, several of these focal species have relatively restricted ranges along the west coast of the United States, only occurring from parts of California to southern Oregon (*N. pubescens*, *T. radians*, and *A. mollis*) or the Columbia River Gorge (*P. nothofulvus*). Range-restricted species may be more susceptible to warming (Parmesan 2006, Sheth and Angert 2014), and if a species becomes increasingly restricted, it may

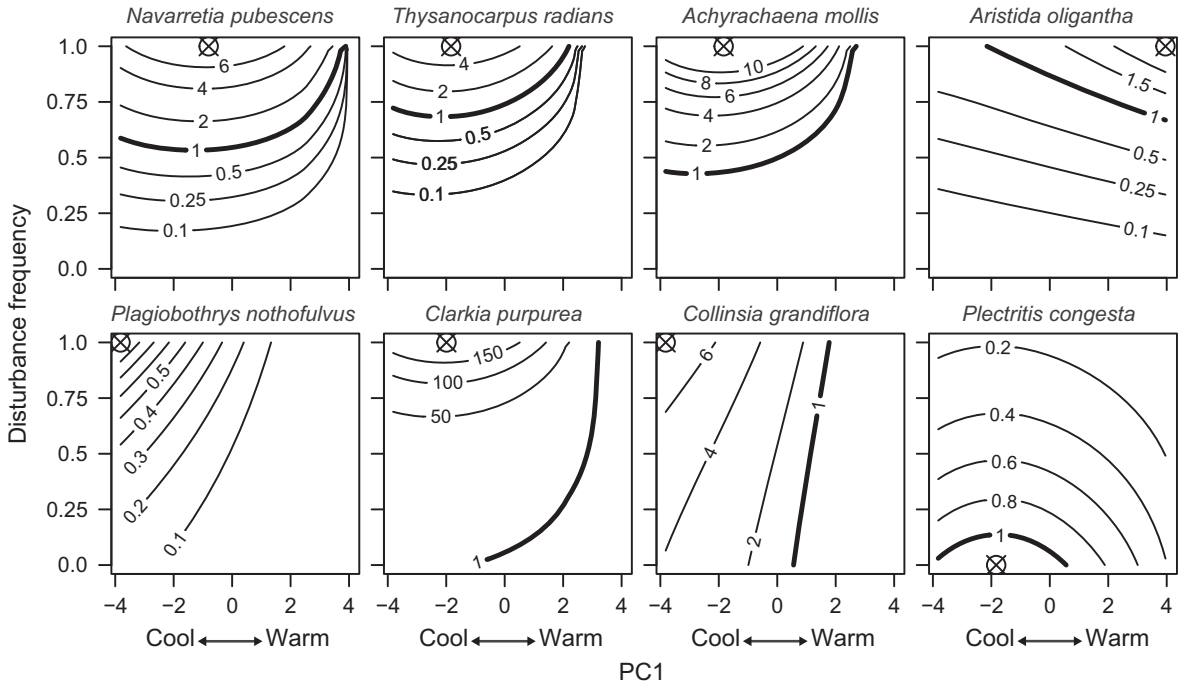

FIG. 6. Contour plots of the long-run (geometric mean) annual population growth rate (λ) for each species as a function of climate (PC1) and disturbance frequency. Long-run population growth rates were calculated using Markov models (see Methods), assuming that high-disturbance conditions prevail in a disturbance event year, intermediate conditions in the first year after the disturbance event, and low-disturbance conditions two or more years after the disturbance event. For *P. nothofulvus*, which was not planted during a high-disturbance year, we used intermediate conditions in a disturbance event year, and low-disturbance conditions one or more years after the disturbance event. ⊠ indicates the location of highest λ.

eventually become found only within microclimate refugia. In PNW prairies, key refugia habitats are known to be critical in supporting vulnerable species' persistence (Bachelet et al. 2011). However, such locations will likely not remain refugia in future climates (Ulrey et al. 2016).

Whether a species was planted within or beyond its current northern range limit did not appear to influence the magnitude of the site effect on demographic performance. Instead, the idiosyncratic site effects we document may be attributed to other local factors such as nutrients, soil characteristics, and the surrounding biotic communities. Unfortunately, we were unable to test whether the demographic responses to climate differed by site, as we did in Pfeifer-Meister et al. (2013) and Reed et al. (2021*b*), because we lacked enough within-site climate variation during the important establishment years when competition was low. With such data, we may have observed opposing demographic responses such as warming being detrimental within but not beyond northern range limits (Reed et al. 2021*b*). Although this could have hinted at the potential benefits of geographic range shifts, our results at least provide broad conclusions that these species are vulnerable.

Given the increasing urgency to intervene when species become vulnerable to climate change, the responses to disturbance observed here have important management implications. Without the presence of a substantial long-lived seed bank, most of these species appear to require the low-competition environments that followed major disturbance events. Intermediate levels of disturbance (i.e., weeding and clipping of nonfocal species) often provided a boost relative to low-disturbance conditions (i.e., minimal maintenance), but these were generally small effects. Although disturbance can facilitate the spread of invasive species (Bradford and Lauenroth 2006, Lembrechts et al. 2016), it can also play an important role in managing vulnerable species by helping them to establish in new locations (Coates et al. 2006, Holl and Hayes 2006) or to maintain viable populations where currently found.

In these experiments, we introduced or reintroduced our focal species to degraded prairie sites where they are not otherwise currently found. Although the strong disturbance events that preceded both experiments caused most of these species to initially exhibit a "boom" year, these were often followed up with "bust" years that were exacerbated by warming. The major exception was *P. congesta*, which did not appear to depend on intense disturbance events. For the other species, our evidence suggests that maintaining high disturbance frequencies (short return intervals) will be critical for successfully establishing and maintaining populations in the face of

climate warming (Fig. 6). Indeed, ecological and ethnographic evidence indicates that PNW prairies historically burned with a typical fire return interval of 1–2 yr, driven by both natural ignitions and those set by Native Americans to manage prairie resources (Boyd 1999, Storm and Shebitz 2006). Frequent fire would thus have been a key to their more widespread distribution and greater abundance prior to Euro-American settlement (Dunwiddie et al. 2014). A return to such short disturbance intervals may be even more critical under projected climate warming. Although the nature of disturbances (e.g., burrowing mammals, floods, fire, etc.) may differ in other systems, we suspect that an interplay between climate change and altered disturbance in their effects on disturbance-adapted plants is likely to be common.

Despite compelling evidence for climate and disturbance as important demographic controls, there are a few remaining caveats. First, it is important to note that our contour plots of λ are meant to represent directional trends and the actual values should not be taken literally. Fig. 4 is averaged across sites, which had very different and idiosyncratic effects on the magnitude of λ. True population growth rates of these species would inevitably be site- and context-dependent, although we expect that the negative effects of warming would hold true in many cases. Second, our λ calculations do not account for intraspecific competition. Given that we only planted 200 seeds per species per plot in each year (and never had close to 100% germination), we believe that this force was negligible, especially relative to interspecific competition (given far greater cover from nonfocal species). Lastly, it is possible that species were "hedging their bets" by delaying germination through the unfavorable years post establishment (Gremer and Venable 2014). If this is the case, the species may have built adequate seed banks (through our continued seed addition) to have more "booms" in subsequent years. Although second- and third-year germination in 2018 suggest minimal seed-bank activity (Appendix S3: Table S1), these data were limited to a single low-disturbance year, and we cannot discount the possibility of continued seed dormancy. *Clarkia purpurea* seed can remain viable after 3 yr of dry lab storage, but its germination rate may be reduced by 50–60% at that point (Thomson et al. 2016). *Plectritis congesta* is thought to lack dormancy (Young-Mathews 2012). Little else is known about dormancy potential in these native annual forbs or their longevity in the seed bank, other than the belief that their seed banks are already depleted in most remaining prairie sites (Dunwiddie et al. 2014). In general, our finding that declining disturbance frequency could be a threat is unlikely to be changed by the inclusion of a seed bank.

In conclusion, we identified the important roles of warming and disturbance on the demographic performance of a suite of annual species native to Pacific Northwest prairies, seeded at multiple sites over multiple years. This type of comprehensive study using climate manipulations is exceedingly rare and provides a robust analysis of how species may fare in future climatic conditions. Although active management and intervention, including frequent disturbance, will be essential to lessen the risk of climate change for vulnerable annual plant populations, their long-term persistence may still be in jeopardy.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3464/suppinfo

Open Research

Data (Reed et al. 2021*a*) are archived in the Dryad digital data repository: https://doi.org/10.5061/dryad.q573n5tj0