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Climate change and plant demography in the sagebrush steppe

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CLIMATE CHANGE AND PLANT DEMOGRAPHY IN THE SAGEBRUSH STEPPE

by

Aldo Compagnoni

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2013

ABSTRACT

Climate Change and Plant Demography in the Sagebrush Steppe

by

Aldo Compagnoni, Doctor of Philosophy

Utah State University, 2013

Major Professor: Dr. Peter B. Adler
Department: Wildland Resources

Climate change poses tremendous challenges to natural resource management and makes ecological forecasts necessary for long-term planning. To aid research on ecological forecasts, we addressed the direct and indirect effects of climate change on the demography of sagebrush steppe plants. Indirect effects can occur when climate causes changes in the abundances of a focal species' neighbors which feedback to affect the focal species itself. We addressed three main questions: (1) Will warming increase cheatgrass (*Bromus tectorum*) abundance at high elevations in the sagebrush steppe? (2) Will snowmelt contribute to the positive effects of warming on cheatgrass? (3) Which are the species most affected by the indirect effects of climate change? The first two questions study the most problematic exotic plant invasion in North America. We addressed these questions with manipulative field experiments. The first experiment tested the response of three cheatgrass ecotypes to warming and vegetation removal along an elevation gradient. We hypothesized that cheatgrass' response to warming would

increase with elevation, but that neighbor competition and high elevation cheatgrass ecotypes would limit this positive response. We found warming increased cheatgrass population growth rate regardless of elevation, neighbor competition or cheatgrass ecotype. In the second experiment we imposed warming and snowmelt using infrared heaters. Our main hypothesis was that snowmelt contributes to the positive response of cheatgrass to warming. We found snowmelt contributed to this positive effect by increasing cheatgrass survival. To address the third question, we added four species to a pre-existing four-species population model based on a sagebrush steppe long-term data set. Our main hypothesis was that the indirect effects of climate should decrease with species rarity. This hypothesis depends on two assumptions. First, the size of indirect effects increases with the strength of stabilizing niche differences. These quantify the strength of heterospecific interactions experienced by a species. Second, stronger stabilizing niche differences decrease a species' relative abundance in a community. We used the parameterized eight-species model to estimate species' stabilizing niche differences and the size of indirect climate effects. Results supported both assumptions, suggesting neighbor competition has little effect on the response of rare species to climate.

PUBLIC ABSTRACT

Climate Change and Plant Demography in the Sagebrush Steppe

by

Aldo Compagnoni

We used demographic methods to address one of the main challenges facing ecological science: forecasting the effect of climate change on plant communities. Ecological forecasts will be crucial to inform long-term planning in wildland management and demographic methods are ideal to quantify changes in plant abundance. We carried out our research in the sagebrush steppe, one of the most extensive plant ecosystems of Western North America. Our research intended to inform ecological forecasts on an exotic invader, cheatgrass (*Bromus tectorum*). Moreover, we investigated the general question asking: to what degree competition among plants influences the outcome of ecological forecasts on the effect of climate change?

We carried out two field experiments to test the hypothesis that warming will increase cheatgrass abundance in the sagebrush steppe. This hypothesis was strongly supported by both experiments. Warming increased cheatgrass abundance regardless of elevation, neighboring vegetation or cheatgrass genotype. Moreover, we found cheatgrass was hindered by snow cover. Therefore, warming increases cheatgrass growth directly by increasing temperature, and indirectly by decreasing or removing snow cover.

In our last experiment, we tested whether forecasts of climate change effects on

rare species can ignore competition from neighbors. This should occur because rare species should have little niche overlap with other species. The lower the niche overlap, the less competition with other species. To test this hypothesis, we used a long-term data set from an Idaho sagebrush steppe. We built population models that reproduced the dynamics of the system by simulating climate and competition. Model simulations supported our hypothesis: rare species have little niche overlap and little competitive interactions with neighbor species.

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Aldo Compagnoni

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CHAPTER 1

INTRODUCTION

Climate change poses tremendous challenges to conservation and natural resource management. The rate of warming in the past century is unprecedented for the past 11,000 years (Marcott et al. 2013) and temperature is forecasted to increase for at least a century (IPCC 2007). Expected ecological impacts of climate change include changes in species ranges (Root et al. 2003), species extinctions (Thullier et al. 2005), shifts in community composition (Williams and Jackson 2007), and alterations of ecosystem function (Cramer et al. 2001). Considerable attention is devoted to forecasting the climate change response of vegetation because of its pivotal role in the functioning of terrestrial ecosystems.

Demographic methods are an important tool in forecasting plant response to climatic factors. Vegetation response to climate change is usually quantified using abundance measures such as biomass (e.g. Suttle et al. 2007, Harte et al. 1995). However, focusing on plant abundance alone is potentially misleading. For example, experimental warming might increase a plant's biomass (i.e. its growth) but decrease its survival in early life stages. In this case, biomass data suggests warming increases the population's abundance even though this effect is transient. Demographic data allows constructing population models that decrease this uncertainty. By quantifying the contribution of each life stage to population growth rate, these models provide a more mechanistic explanation of dynamics. Using information on how climate affects life stages, demographic models can be used to project how population growth rates respond to, for example, increased temperature. This is an elegant way to produce realistic climate change scenarios.

Among the world's biomes, drylands might be especially sensitive to future climate change. In these systems relatively small changes in abiotic factors can trigger large ecological responses (Scheffer et al. 2001, Kefi et al. 2007). The sagebrush steppe of North America is an example of such vulnerability to climate change (Bradley 2010). Warming threatens this system by restricting the ranges of dominant native species (Schlaepfer et al. 2012) and by promoting the spread of plant invaders (Chambers et al. 2007, Bradley 2009). The most troublesome among these invaders is cheatgrass (*Bromus tectorum*), an exotic annual grass. This species promotes an uncharacteristically short fire return interval that impedes the re-colonization by native species (Whisenant 1990). Recent studies suggest future warming will spread the impacts of this species into higher elevations (Chambers et al. 2007, Bradley 2009) which escaped the brunt of its invasion. Moreover, warming could indirectly favor cheatgrass by decreasing snow cover. Previous research has shown snow cover decreases cheatgrass population growth (Griffith and Loik 2010, Concilio et al. 2013). Because a few degrees of warming can cause large decreases in snow cover (IPCC 2007), this could further favor cheatgrass.

The direct effects of climate change on a species such as cheatgrass can be modified or reversed by the indirect effects resulting from altered species interactions. If climate change shifts the relative abundances of a community, the effect of interspecific interactions on any species will change as well. Indirect effects resulting from non-trophic interactions such as competition are common (Tylianakis et al. 2008, Gilman et al. 2010). Therefore, there could be a bias when modeling climate change effects without considering species interactions. However, data on species interactions is expensive and

time-demanding to collect. Hence, there is a need to identify the species most susceptible to indirect climate change effects. One recent study hypothesized and tested that the species least susceptible to indirect effects are the ones with the largest stabilizing niche differences (Adler et al. 2012). These are the demographic proxy for niche overlap. However, stabilizing niche differences can only be estimated through extensive modeling of long-term demographic data. Ecological forecasters need easier ways to identify species susceptible to the indirect effects of climate change.

The results of recent studies indirectly suggest that the rarer a species, the less susceptible it will be to indirect climate change effects. This is because stabilizing niche differences increase with species rarity. These studies show that conspecific density dependence increases with species rarity, but heterospecific density dependence is uniformly low across species (Comita et al. 2010, Johnson et al. 2012). The strength of stabilizing niche differences co-varies with the ratio of conspecific to heterospecific density dependence. Therefore, the less abundant a species, the smaller the indirect effects of climate change should be.

We used a demographic approach to address three questions regarding the effect of climate change on sagebrush steppe vegetation: (1) Will warming increase cheatgrass population growth rate at high elevations? (2) Does decreased snow cover contribute to the increase of cheatgrass population growth rate? (3) Are rare species less affected by the indirect effects of climatic change? We addressed the first two questions using manipulative field experiments. We designed these experiments to quantify cheatgrass population growth rate and its vital rates. In the first experiment, we examined the effects

of warming on cheatgrass along an elevation gradient. We also verified whether warming effects changed according to neighbor competition and cheatgrass ecotype. In the second experiment, we quantified the effect of snowmelt and warming on cheatgrass population growth rate. Our objective was to understand whether snowmelt contributes to the effects of warming. We addressed the third question using a 22-year long data set from an Idaho sagebrush steppe. We used this data to build population models of eight species. These models reproduced the effect of climate and of conspecific and heterospecific competition. We used models to simulate community dynamics under perturbed and unperturbed climate, and to estimate species' strength of stabilization. This allowed us to verify whether more rare species have stronger stabilization, and whether this translates into smaller indirect climate effects.

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CHAPTER 2

EXPERIMENTAL WARMING INCREASES CHEATGRASS (*BROMUS TECTORUM*)
POPULATION GROWTH RATE ALONG AN ELEVATION GRADIENT¹

Abstract

Cheatgrass (*Bromus tectorum*) is one of the most problematic invasive plant species in North America and climate change threatens to exacerbate its impacts. We conducted a two-year field experiment to test the effect of warming, competition, and ecotype on cheatgrass performance across an elevation gradient in northern Utah. We hypothesized that warming would increase cheatgrass performance, but that warming effects would be limited by competing vegetation and by local adaptation of cheatgrass ecotypes. The warming treatment relied on open top chambers, we removed vegetation to assess the effect of competition from neighboring vegetation, and we reciprocally sowed cheatgrass ecotypes from the three study sites. We quantified performance with per capita growth rate and its components (germination, survival and fecundity). Warming generally increased cheatgrass population growth rates at all elevations, and interactions with ecotype or competition were rare. Competition never offset warming effects. High elevation ecotypes performed best regardless of site. Our results indicate that in northern Utah, warming will increase cheatgrass densities in years with normal to high precipitation regardless of neighboring vegetation and cheatgrass ecotype. In this region, climate change

¹ Coauthored by Peter B. Adler.

is likely to increase the impacts associated with high cheatgrass density and biomass, such as shortened fire return intervals.

Introduction

Global change poses tremendous challenges to land management and conservation. Exotic invasive species have long been recognized as an important component of global change (Vitousek et al. 1997) and forecasting their interaction with other global change components represents an urgent research challenge. While considerable research has shown that increasing CO₂ and soil nutrients can favor invasive species (e.g. Huenneke et al. 1990, Smith et al. 2000), climatic change could have either positive or negative effects (Bradley et al. 2010) depending on an invader's autoecological characteristics (Bradley et al. 2009).

Cheatgrass (*Bromus tectorum*) is one of the most destructive plant invaders in North America and it is the greatest threat to the sagebrush steppe ecosystems of the Intermountain West (Mack 1981, Knapp 1996). This invasive, annual species promotes an uncharacteristically short fire return interval (3-5 yrs) that impedes the establishment and survival of native perennial vegetation. At present, cheatgrass invasions are more severe in warm, dry, low elevation sites than in colder and wetter high elevation sites (Suring et al. 2005). The temperature increases predicted for the 21st century (IPCC 2007) could increase cheatgrass density in its current range or allow cheatgrass to expand into higher elevations (Chambers et al. 2007, Bradley 2009), impacting additional native communities.

The extent and severity of the cheatgrass invasion may be controlled by abiotic conditions, community composition or both. Research based on climate envelope models (Bradley 2009, Bromberg et al. 2011) has addressed the role of abiotic conditions over large spatial scales, suggesting that warming will expand cheatgrass dominance into higher elevations. Field studies along elevation gradient also have provided valuable insights into the roles of temperature and community interactions. In particular, Chambers et al. (2007) suggested that at high elevations cheatgrass abundance is limited by both temperature and neighboring vegetation. In the Intermountain West, soil resources, aboveground productivity and biomass increase with elevation (Chambers et al. 2007), which might increase competitive pressure from perennial natives (Grime 1979). If warmer temperatures have positive direct effect on cheatgrass, strong competition might be especially important for limiting cheatgrass performance through indirect effects (Suttle et al. 2007).

Because genotype controls cheatgrass response to abiotic conditions, it should also determine its response to warming. Genotype can determine plant response to climate change (Rehfeldt et al. 2002, Banta et al. 2012) and genotypic diversity has been shown to promote plant invasions (Lavergne and Molofsky 2007). Consistent with this general knowledge, genotypic diversity within North America populations of cheatgrass is thought to have promoted the expansion of this species into new habitats (Young and Tipton 1990). This evidence suggests that short term cheatgrass response to warming could depend on available genotypes. For example, warming might have little effect if high elevation cheatgrass populations are not adapted to warmer temperatures. Therefore,

warming might improve cheatgrass performance only after the invasion of genotypes adapted to warmer temperatures.

We designed an experiment that builds on previous studies in three ways. First, we directly test the effect of warming on cheatgrass with a manipulative field experiment. This approach isolates the effect of temperature from other potentially confounding factors such as neighboring vegetation, precipitation, and soil characteristics. Second, we test the role of plant community interactions in limiting cheatgrass, and whether competition changes the effects of warming on cheatgrass. Third, we test whether variation among local cheatgrass seed sources (henceforth referred to as ecotypes) influences the response to warming. We conducted these manipulations of temperature, competition from resident vegetation, and local cheatgrass ecotypes across an elevation gradient in Northern Utah. We tested three hypotheses: (1) Experimental warming will increase cheatgrass per capita growth rates more at high than low elevations; (2) Competition will decrease cheatgrass population growth rate the most at high elevation and will reduce the effect of warming, resulting in significant interactions between warming and neighbor-removal treatments; (3) Cheatgrass seeds at any one location are adapted to local conditions. As a result, each cheatgrass seed source should perform best at its own site. Moreover, the effect of warming will be most positive for seeds adapted to lower, warmer elevations. We focused on the population growth rate because it is a synthetic measure of cheatgrass impact by integrating biomass through its effect on seed production and density. Moreover, by focusing on the contributions to growth from germination, survival and

fecundity, this demographic approach provides insights into the mechanisms determining experimental responses.

Methods

Experimental sites

We chose three sites that span an elevation gradient along the foothills of Northern Utah's Wasatch Mountains: Golden Spike National Monument ("low elevation"), Green Canyon Ecological Station ("mid elevation") and Hardware Ranch Wildlife Management Area ("high elevation"). All sites are located on flat areas dominated by the shrub *Artemisia tridentata*. Interspaces are dominated by the exotic perennial bunchgrass *Agropyron cristatum* at low elevation and by the short-lived exotic perennial grass *Poa bulbosa* at mid and high elevations. Data on the relative cover of the plant species found in shrub interspaces are summarized in Appendix A. The environmental characteristics for each site are summarized in Table 2-1. Values for the high elevation site might overestimate temperature and underestimate precipitation and snow cover because the reference meteorological station is located ~100 m lower in elevation than the experimental plots.

Cheatgrass life history

Cheatgrass is a winter annual grass characterized by very plastic growth and germination. Cheatgrass growth responds strongly to density (Rice and Mack 1991a), nitrogen levels (Monaco et al. 2003), and water availability (Rice et al. 1992). Cheatgrass

germination strongly depends on temperature (Roundy et al. 2007), moisture (Roundy et al. 2007), and nitrogen level (Evans and Young 1975). Over most of cheatgrass' range, the bulk of germination occurs at the end of summer or in early fall after the first rain, but plants can emerge anytime during the growing season (Mack and Pyke 1983). In general, cheatgrass has very high germination rates and <1% of its seed bank carries over after the second year following seed production (Smith et al. 2008).

Experimental design

At each site, we established 20 circular plots 85 cm in diameter in shrub interspaces. Two levels of a warming treatment (control and warming) were crossed with a neighbor removal treatment with two levels (control and removal of all vegetation). We randomly assigned plots to one of these four treatments combinations. We used open-top chambers (Molau and Molgaard 1996) to increase temperatures of warmed plots. The air temperature in experimental plots was monitored every 30 minutes in June of 2010 with DS1921G Thermochron iButton® data loggers installed 5cm above the ground surface and shaded by white styrofoam cups. We measured volumetric soil moisture of the upper 5 cm in May 2010 with an EC-5 Decagon soil moisture sensor, taking four readings per plot. We collected data in May and June because during this period cheatgrass produces most of its biomass. The neighbor removal treatment was carried out by spraying glyphosate (Roundup, Monsanto, St. Louis, Missouri, USA) in fall 2009 on a 1 m² area centered on the selected plots. We did not repeat the treatment the following year because in 2010 we planned to plant cheatgrass in late August. Therefore, spraying glyphosate in the fall

would have killed germinating cheatgrass. Moreover, there was little recolonization of the perennial grasses after just one growing season.

Within each plot we established four 20x20 cm quadrats (sub-plots), each containing 100 2x2 cm grid cells. We collected seeds at the end of the 2009 and 2010 growing seasons from cheatgrass populations naturally occurring at or in the immediate vicinity of the three experimental sites. We do not have data on genetic differences among these seed sources. However, these populations showed clear ecological differences: going from low to high elevation their average seed mass was 2.7 mg, 3.6 mg, and 4.0 mg, respectively. Seeds were planted in October and November 2009 and at the end of August 2010. Three quadrats were planted with cheatgrass seeds (one seed planted ~1 cm deep at the center of each grid cell), and one quadrat was left unplanted to check for germination from naturally dispersed seeds. Each quadrat was randomly assigned to be left unplanted or to be planted with seeds from one of the three sources. Germination and seedling survival were measured at least twice during the growing season: in 2009-2010, from April to June on a monthly basis and in 2010-2011 in May and June; the mid and high elevation sites were also sampled in October 2010. To estimate seed production, we counted the number of spikelets produced by the cheatgrass plants grown in each quadrat, and estimated the average number of seeds per spikelet by sub-sampling five mature plants per quadrat in 2011. ANOVA analyses showed that seeds per spikelet changed with site and treatment, but not with ecotype.

To measure cheatgrass performance, we calculated the geometric population growth rate as $\lambda = n_{t+1}/n_t$, where n_t denotes population abundance in year t . λ is a density-

independent measure of performance. In annual species, population abundance is equal to the number of viable seeds; because we planted 100 seeds per quadrat, we calculated the population growth rate of each quadrat as $\lambda = \text{seed production} / 100$. We also calculated the three vital rates that determine λ : *germination*, the probability that a seed germinates, *survival*, the probability that a germinated seedling survives to seed-set, and *fecundity*, the average number of seeds produced per surviving individual.

Our model for population growth assumes no carry over of seeds from one year to the next. This means that seeds planted at time t have either germinated or are considered dead at time $t+1$. This assumption is supported by work in natural populations showing germination rates as high as 96% (Smith et al. 2008). In addition, as part of a separate warming experiment at our mid-elevation site, we buried seed bags to test for germination and found that >99% of buried seeds germinated in both warming and control plots (Compagnoni unpublished data). Furthermore, even if our assumption of zero carryover leads to a small bias in our estimates of λ , it should not affect our treatment comparisons.

Although the seed bank is unlikely to play an important role in the population dynamics of this species, it is possible that dispersal from naturally occurring plants could contribute propagules to our study plots. We accounted for the effect of natural dispersal on our estimate of λ by subtracting the estimated average number of seeds produced in the unplanted quadrats in each treatment from the number of seeds harvested in the planted quadrats in each plot. We subtracted the average treatment-specific background seed production because of high variation in the plot-level data. We estimated treatment means by selecting the best model fitting the seed production data from the unplanted quadrats.

We used the best of four models according to Akaike Information Criterion (AIC). These models had the following predictor variables: warming only, removal only, warming plus removal, and warming plus removal and their interaction. We had two additional alternatives in estimating λ : subtracting the plot-specific seed production of unplanted quadrats to the seed production of planted quadrats, and estimating λ using data from planted quadrats only. A comparison of these three estimations of λ and a comparison of seed production in planted and unplanted quadrats can be found in Appendix C. We also used this method to account for any cheatgrass seed fall that escaped collection at the end of the first growing season (the one exception was the removal treatments at the mid elevation site, in which we removed fallen seed by hand).

Characterization of climatic range

To test where the temperature and precipitation of our sites fall within the cheatgrass range, we characterized the Great Basin climatic range of cheatgrass with the data set used in Bradley (2009). We define climatic range as the range of temperature and precipitation within which cheatgrass can attain dominance over the landscape.

Cheatgrass dominance on the landscape was estimated using a time series of satellite images. Inter-annual variability in biomass production was used to identify cheatgrass dominance because this metric is much larger in cheatgrass sites than in native shrublands (Bradley and Mustard 2006). Every 4 x 4 km pixel where cheatgrass is dominant was associated to monthly maximum and minimum temperature and total precipitation estimated by the PRISM database (Daly et al. 2002). We used monthly data to calculate

annual mean temperature and total precipitation. Plotting the kernel density estimates of these two measures represents the climate conditions where the species is most likely to reach high cover values. As shown in Bradley (2009), other climatic variables define cheatgrass range better; however, we chose annual values to provide a more intuitive representation of cheatgrass range.

Characterization of climatic variables

We calculated climatic and moisture values for the 2009-2010 and 2010-2011 growing seasons (September to June) to quantify inter-annual climatic variability and its anomalies with respect to historical data. Temperature means, total precipitation, and snowfall were calculated using data from the Utah State University weather station (source: Utah Climate Center, <http://climate.usurf.usu.edu/mapGUI/mapGUI.php>), three km away from the experiment's mid elevation site. We limited this analysis to our mid elevation site, the only one providing an uninterrupted, long-term data set which allowed comparing current temperatures to historical trends.

To estimate how temperature and precipitation translate into moisture, we calculated yearly soil moisture values using estimates of monthly soil moisture for the 344 climate divisions defined by the National Climatic Data Center in the conterminous United States (http://www.cpc.ncep.noaa.gov/soilmst/index_jh.html). We downloaded raw data for the division centered at longitude 40° 68' and latitude 112° 10'. This division is the closest to our sites among those provided in the dataset. We compared climatic and mois-

ture measures for the two years of the experiment to historical trends by calculating the 25th, 50th, and 75th quantiles of the observed values.

Finally, to characterize the effect of warming on the temperature and soil moisture of our plots, we used trends in average hourly temperature and May 2010 volumetric soil water measurements.

Analyses

We used linear mixed-effects models to test the effect of treatments on per-capita growth rate of cheatgrass. Population growth rate was log-transformed to meet normality assumptions. We modeled independent variances when Bartlett's test found a significant difference between removal and non-removal treatments. We treated temperature, removal, ecotype, and all their interactions as fixed factors and plot as a random factor. We fit six models, each corresponding to a unique combination of the two years and three sites. We modeled each site and year separately for two reasons. First, we did not have more than one replicate site per elevation. Second, the two years were not directly comparable because seeds were planted between October and November in 2009 and at the end of August in 2010: planting in August rather than November maximizes fall germination.

We also modeled the response of each vital rate. Because fecundity is constrained between 0 and infinity, we analyzed it with a linear mixed model after log-transforming the data to meet normality assumptions. We also modeled independent variance when Bartlett's test found a significant difference between removal and non-removal treat-

ments. We analyzed survival and germination using a generalized linear mixed model with a binomial distribution and logit link.

All hypotheses were tested using differences in population growth rate among treatments and sites. We tested hypothesis 1 by looking for a significantly positive effect of warming at high elevation and for a lack of significance at mid and low elevations. To address hypothesis 2, we verified whether the model coefficients that quantify the effect of neighbor removal increased with elevation and looked for significant warming x removal interactions. Finally, we tested hypothesis 3 by looking for significant differences among cheatgrass ecotypes and for significant warming x ecotype effects.

To understand which vital rates drove differences in population growth rate, we carried out a Life Table Response Experiment (LTRE), limiting our analyses to the warming and removal treatments. The LTRE calculated the contributions of our three vital rates (germination, survival, and fecundity) to the differences in growth rate (λ) caused by warming and removal. Closely following Caswell (2001), we calculated differences among treatments as:

$$\alpha^{(warming)} = \lambda^{warming} - \lambda^{control}$$

$$\beta^{(removal)} = \lambda^{removal} - \lambda^{control}$$

where $\alpha^{(warming)}$ estimates the effect caused by warming, and $\beta^{(removal)}$ estimates the effect of removal. The contributions of each vital rate to the above differences are:

$$\tilde{\alpha}^{(warming)} = \sum_i^3 (a_i^{warming} - a_i^{control}) \frac{\partial \lambda}{\partial a_i}$$

$$\beta^{(removal)} = \sum_i^3 (a_i^{removal} - a_i^{control}) \frac{\partial \lambda}{\partial a_i}$$

where a is a vital rate and the index i refers to one of the three vital rates: germination, survival or fecundity. The term $\frac{\partial \lambda}{\partial a_i}$ is the sensitivity of growth rate to a particular vital rate. The nominator and denominator of this expression refer to a population whose vital rates are the arithmetic mean of the two populations compared in the equation. We performed these analyses on 1000 bootstrap samples to provide an estimate of uncertainty. Because differences in λ induced by treatments vary widely in magnitude, so do the contributions to these differences. This hinders the graphical comparison of LTRE results among treatments, sites, and years. To solve this problem, we calculated the proportional contribution of each vital rate to λ differences. This constrains contributions between 0 and 1 and allows us to plot all graphs on the same scale.

Analyses were carried out with R version 2.14.0 (R Foundation for Statistical Computing, Vienna, Austria), linear mixed models and generalized linear mixed models were fit using the nlme and lme4 packages, respectively.

Results

Mean annual precipitation and temperature at our sites (Table 2-1) are within the climatic range of cheatgrass dominance. However, values are at the high end of the annual precipitation range and, at the high elevation site, close to the low temperature limit of dominance (Fig. 2-1).

The two years of the experiment (Table 2-2) were wetter and cooler than normal. Growing season temperatures were below the 50th percentile of the series, while precipitation was close to the median value the first year and above the 75th percentile the second. Estimated yearly soil moisture during the growing season was between the 25th and 50th percentile the first year, and above the 75th percentile of the series the second.

The warming treatment increased daily maximum temperatures by two degrees and daily minimum temperatures by one degree in June 2010. Warming was stronger at high elevation and during daytime (Fig. B1). Warming had no effect on soil moisture, but moisture did vary among sites (Table B2, Fig. B3): the lowest and highest moisture availabilities occurred at mid and high elevations, respectively.

Contributions from naturally dispersed seeds were small relative to the seed production of planted quadrats in the first year (Fig. C1). The contribution from unplanted seeds was larger the second year, indicating that substantial seed fall escaped harvest. Despite this, subtracting seed production of unplanted plots from seed production in planted plots had little qualitative effect on the estimates of λ in our experimental treatments (Figs. C2-4).

Warming significantly increased population growth rate in three out of six of the site-by-year combinations (Tables 2-3 and 2-4, Fig. 2-2). The three non-significant results came from the low elevation site in 2010 and from the low and mid elevation sites in year 2011. In these non significant cases, however, warming still increased cheatgrass population growth.

Removal of surrounding vegetation caused, on average, a tenfold increase in cheatgrass population growth rate. This increase was significant in four out of six site-by-year combinations (Tables 2-3 and 2-4). The effect of removal was larger at low and mid elevation in the first and second year, respectively (Table 2-5). The removal by warming interaction was significant only at the low elevation site in 2010. This occurred because warming decreased cheatgrass population growth rate in the removal plots (Table 2-5).

Seed ecotype significantly affected population growth rates in three out of six site-by-year combinations (Tables 2-3 and 2-4). Seeds collected at high elevation generally tended to have the largest growth rate, those from low elevation the lowest (Table 2-5). The ecotype-by-warming interaction was significant only the first year at the low site (Table 2-3). In this case warming increased the performance of seeds collected at low elevation (Table 2-5).

Vital rates responded differently to treatments. Germination was influenced most strongly by seed ecotype and removal (Fig. D1, Tables D1, D2). Survival varied little, but during the second growing season it significantly increased in warming treatments at mid and high elevations (Fig. D2, Tables D3, D4). Fecundity increased in response to removal in all cases except for the low and high elevation sites in 2011, and to warming at high elevation in 2011 (Fig. D3, Tables D5, D6). LTRE analyses (Fig. 2-3) show that treatments effects were generally driven by fecundity and, to a lesser extent, germination. However, higher survival was important in driving the positive response to warming at the mid and high elevation sites in 2011.

Discussion

Effects of warming

Our results suggest warming is likely to increase cheatgrass densities and impacts in Northern Utah. Warming had a significantly positive effect on cheatgrass growth rate in three out of six of our trials. Warming was also significant at the low site in the first year in non-removal plots, as shown by a significant warming x removal interaction (Table 2-3). Moreover, even when the effect of warming was non significant, it always increased cheatgrass population growth rate. We originally hypothesized that warming would increase cheatgrass population growth rates the most at high elevations. The results from our experiment provide support for this hypothesis in the second year. In this year, warming had a significantly positive effect at high elevation only: warming and its interactions were non-significant at lower elevations (Table 2-4). However, in the first year warming effects were significantly positive at all elevations. Warming generally increased cheatgrass performance regardless of neighboring vegetation and ecotype, suggesting its effects are not contingent on these factors. Our conclusion that cheatgrass will increase in density at higher elevations apparently contradicts data from our high site, where positive growth rates ($\lambda > 1$) were mostly restricted to removal plots (Fig. 2-2). However, the high elevation site's estimated average temperature was three degrees lower than the two other sites (Table 2-1). A magnitude of warming larger than that induced by our manipulations (1.6 °C) might allow a positive growth rate in undisturbed vegetation.

Warming increased cheatgrass population growth rates primarily by increasing fecundity, and secondarily by increasing survival (Fig. 2-3). The strong effect of warming on fecundity may reflect the fact that moisture was above average during our experiment and temperature was far from cheatgrass' upper tolerance (Table 2-1 and Fig. 2-1). The LTRE indicated that survival was also important in driving increased growth rate in warming plots at the mid and high elevations in 2011 (Fig. 2-3). This effect may result from decreased snow cover, which is known to influence the survival of fall-germinating individuals in this species (Rice and Mack 1991b, Griffith and Loik 2010). During the second growing season, snowfall was 50% higher than the previous one at the mid elevation site (Table 2-2) and seedlings were exposed to winter weather because August planting maximized fall establishment. We speculate that open top chambers decreased snow depth and persistence (personal observation), reducing mortality caused by snow-related pathogens (Klemmedson and Smith 1963, Meyers et al. 2008). If this hypothesis holds, future warming might increase cheatgrass growth rate at high elevations by decreasing snow cover.

Effects of removal

We found little evidence to support the hypotheses that competition effects increase with elevation or that they change under warming. First, the largest effects of competition were found at low and mid elevations rather than at high elevation (Table 2-5). Second, we found only one significant removal \times warming interaction, which occurred at the low site in 2010. In this case, warming had a stronger effect on growth rates

in plots with intact neighboring vegetation than in the removal plots (Table 2-5). This likely resulted from low early-season survival of high-elevation ecotype seeds in the warming plus removal plots: many seedlings were found dead on the first census in April. Because seeds that year were planted in late fall (mid November), germination most likely occurred in spring. Seedling mortality might have resulted from excessive heat stress in the removal plots, where the exposed bare ground would warm rapidly.

Our data suggests warming will increase cheatgrass performance regardless of neighboring vegetation. Competition did not increase with elevation and the lack of removal \times warming interaction indicates that neighbor vegetation is unlikely to offset or amplify the effects of warming, at least in the short term. Competition from perennial vegetation may limit cheatgrass (Anderson and Inouye 2001, Chambers et al. 2007), but it appears unlikely to alter the effects of warming.

Effects of ecotype

We expected the seeds from low elevations to respond most to the warming treatment and all seeds to perform best at their original site. On the contrary, the effect of seed origin on growth rate was usually independent of treatment and elevation. Ecotypes with the highest and lowest growth rates were generally the ones from high and low elevation, respectively (Fig. 2-2, Table 2-5). The warming \times ecotype interaction was significant only at the low elevation site in 2010 (Table 2-3) when warming increased the performance of low elevation seeds (Table 2-5). This interaction is the only evidence suggesting the low elevation ecotype might have an advantage under increased temperature.

However, in this specific case the best performing ecotype was still the one from high elevation (Fig. 2-2). Collectively, these results indicate that at high elevations warming will express its full effects immediately, with no lag before colonization by ecotypes adapted to warmer growing seasons.

The poor performance of the low-elevation ecotype is puzzling. There are two ways to explain this pattern. First, the low elevation ecotype might be maladapted. Rice and Mack (1991b) found certain local cheatgrass populations performed worse at their own site than seeds from different locations. They proposed that maladapted genotypes persisted because their displacement was prevented by limited dispersal. Second, ecotype fitness might be determined by maternal effects. Cheatgrass seed weight correlates with fitness (Leger et al. 2009) and it is a plastic trait that increases in response to resource availability (Rice and Mack 1991a). Fitness of cheatgrass populations at low sites should be lower, because resources increase with elevation (Chambers et al. 2007), resulting in lighter seeds and lower fitness. Consistent with this line of reasoning, seed weight in our three populations increased with elevation (2.7 mg, 3.6 mg, and 4.0 mg, respectively).

Caveats

The limitations of our experiment constrain our ability to make quantitative predictions. Open-top chambers do not perfectly simulate warming: they increase temperatures the most during the day and during times of the year with high solar radiation, and they simulate only part of the effect that increased temperature has on snow cover. Moreover, during dry years or at the sites with lower water holding capacity, warming could

decrease cheatgrass population growth rate. During our experiment, moisture availability was never low compared to the historical mean, because the first growing season had average rainfall and low temperature, while the second had average temperatures and high precipitation. Because cheatgrass growth strongly depends on moisture availability (Stewart and Hull 1949), combining lower precipitation with higher temperature might decrease cheatgrass population growth rate. This is especially true at sites with lower average total precipitation (e.g. low elevation site, Table 2-1) or at sites that have lower available water supply due to their soil physical properties (e.g. mid elevation site, Table 2-1).

We cannot rule out the possibility of competition offsetting the positive effects of warming. Long term changes in the abundance of neighboring species could potentially increase the effect of competition on cheatgrass, or decrease it. This question can only be answered using long term data sets or experiments.

Conclusions

Our results suggest that warming will increase cheatgrass performance in years with normal to high precipitation regardless of elevation, neighboring vegetation, or cheatgrass ecotype. Warming likely will allow cheatgrass to extend its dominance into higher elevations that have yet to experience the brunt of the cheatgrass invasion. The fact that high elevation cheatgrass populations show the highest fitness indicates that dispersal of low elevation ecotypes is not needed for warming to express its full effect on cheatgrass performance. Federal land managers and private land owners responsible for

high elevation sagebrush habitats should anticipate allocating more resources to cheatgrass eradication and fire suppression.

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Table 2-1. Environmental variables of the three experimental sites (climate data come from the Western Regional Climate Center, <http://www.wrcc.dri.edu/climate-summaries/>; soil data come from the Web Soil Survey, <http://websoilsurvey.nrcs.usda.gov/app/WebS>

Site	Golden Spike	Green Canyon	Hardware Ranch
Climate Station name	Thiokol Plant	Logan USU	Hardware Ranch
Elevation (m)	1340	1460	1830
Latitude	41° 62' N	41° 77' N	41° 64' N
Longitude	112° 54' W	111° 79' W	111° 56' W
Soil type	gravelly loam	silt loam	cobbly silt loam
Available water supply (mm)	270.5	83.5	99.6
Average Temperature (°C)	8.5	8.9	5.15
Average Max. Temperature (°C)	16.7	15.0	15.1
Average Min. Temperature (°C)	0.3	2.8	-4.8
Average Total Precipitation (mm)	356.9	451.9	433.6
Average Total Snow Fall (cm)	56.1	149.6	162.1
Average Snow Depth (cm)	2.5	2.5	5.1

Table 2-2. Growing season temperature and precipitation recorded at the Utah State University.

Year	Temperature (°C)	Precipitation (mm)	Snow fall (cm)
2009-10	5.1	357.0	167.0
2010-11	5.9	644.7	250.1

Table 2-3. Results of mixed-effects ANOVA at the three sites in 2010 for the effects of treatments on cheatgrass population growth rates.

Treatment	Num. DF	Den. DF	F-value	p-value
Low elevation site				
Removal	1	16	9.1802	0.0080
Warming	1	16	2.3825	0.1422
Ecotype	2	32	3.1911	0.0545
Removal x warming	1	16	3.7914	0.0693
Removal x Ecotype	2	32	0.1078	0.8981
Warming x Ecotype	2	32	2.5724	0.0921
Removal x Warming x Ecotype	2	32	0.7210	0.4940
Mid elevation site				
Removal	1	16	44.9017	<0.0001
Warming	1	16	6.6236	0.0204
Ecotype	2	31	2.3370	0.1134
Removal x warming	1	16	2.1240	0.1644
Removal x Ecotype	2	31	0.9444	0.3998
Warming x Ecotype	2	31	1.9673	0.1569
Removal x Warming x Ecotype	2	31	0.9497	0.3978
High elevation site				
Removal	1	16	10.5453	0.0050
Warming	1	16	3.4101	0.0834
Ecotype	2	32	9.8574	0.0005
Removal x warming	1	16	0.0736	0.7897
Removal x Ecotype	2	32	6.0876	0.0057
Warming x Ecotype	2	32	1.7926	0.1828
Removal x Warming x Ecotype	2	32	2.1349	0.1348

Table 2-4. Results of mixed-effects ANOVA at the three sites in 2011 for the effects of treatments on cheatgrass population growth rates.

Treatment	Num. DF	Den. DF	F-value	p-value
Low elevation site				
Removal	1	16	0.5599	0.4652
Warming	1	16	0.0592	0.8108
Ecotype	2	30	2.7827	0.0779
Removal x warming	1	16	0.7046	0.4136
Removal x Ecotype	2	30	0.5095	0.6059
Warming x Ecotype	2	30	0.2540	0.7774
Removal x Warming x Ecotype	2	30	0.7082	0.5006
Mid elevation site				
Removal	1	16	32.7350	<0.0001
Warming	1	16	0.5892	0.4539
Ecotype	2	31	0.5369	0.5899
Removal x warming	1	16	2.4127	0.1399
Removal x Ecotype	2	31	0.4459	0.6443
Warming x Ecotype	2	31	0.7524	0.4796
Removal x Warming x Ecotype	2	31	0.2636	0.7700
High elevation site				
Removal	1	16	0.8615	0.3671
Warming	1	16	11.9893	0.0032
Ecotype	2	32	0.1622	0.8509
Removal x warming	1	16	2.1559	0.1614
Removal x Ecotype	2	32	0.8751	0.4266
Warming x Ecotype	2	32	1.8400	0.1752
Removal x Warming x Ecotype	2	32	0.3201	0.7283

Table 2-5. Coefficients of the linear models describing the effect of treatments on cheatgrass population growth rates. We present all site by year combinations.

Treatment	Low	Mid	High	Low	Mid	High
	2010	2010	2010	2011	2011	2011
Removal	2.38	1.03	0.79	-1.85	1.47	0.34
Warming	3.05	1.15	0.36	-0.13	-0.52	0.05
Ecotype (mid elevation)	0.37	1.30	-1.46	0.02	0.28	-0.16
Ecotype (high elevation)	1.79	0.34	0.44	0.34	0.35	-0.27
Removal x Warming	-1.08	3.19	1.51	2.16	1.58	1.71
Removal x Ecotype (mid elevation)	1.70	2.10	2.41	1.59	-0.27	-0.87
Removal x Ecotype (high elevation)	1.26	2.77	1.11	1.76	0.27	-1.04
Warming x Ecotype (mid elevation)	-0.93	-1.06	1.43	-0.18	0.60	1.91
Warming x Ecotype (high elevation)	-1.13	-0.42	0.63	-0.06	0.03	1.50

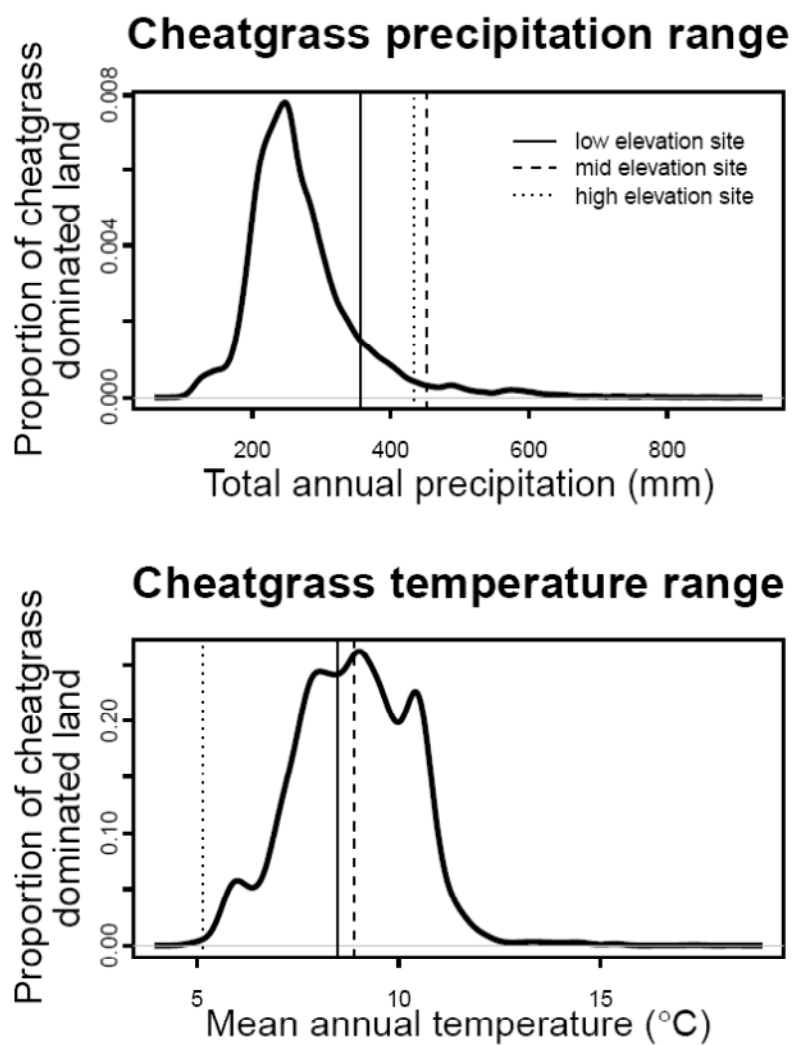


Fig. 2-1 Proportion of cheatgrass dominated land in the Great Basin as a function of annual precipitation (A) and temperature (B). Cheatgrass dominance was inferred from NDVI satellite images (data source: Bethany Bradley).

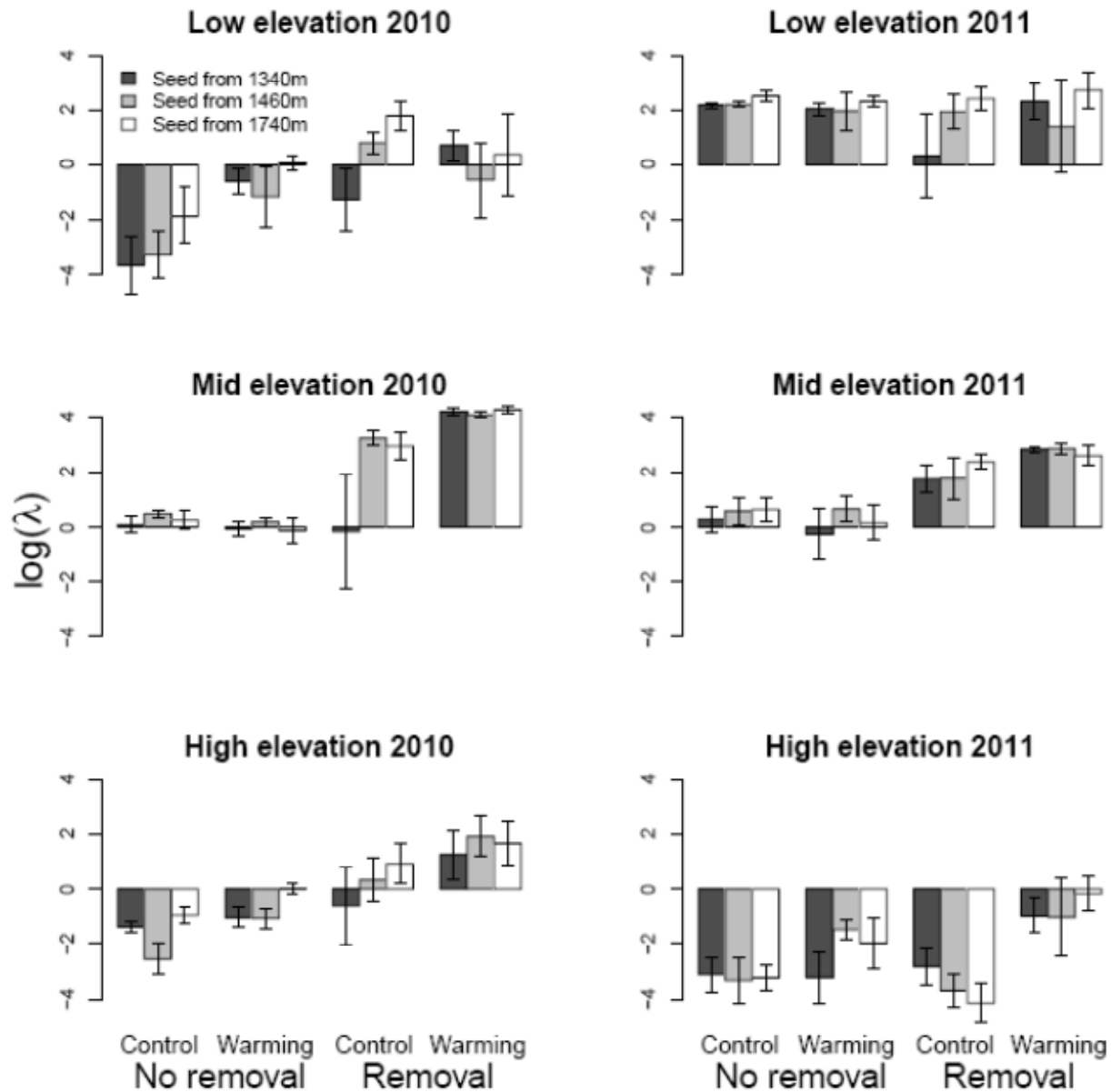


Fig. 2-2. Treatment, site and year specific differences in the log of cheatgrass population growth rate (λ). Below zero values denote negative population growth rates (untransformed λ is below 1). Error bars represent one standard error.

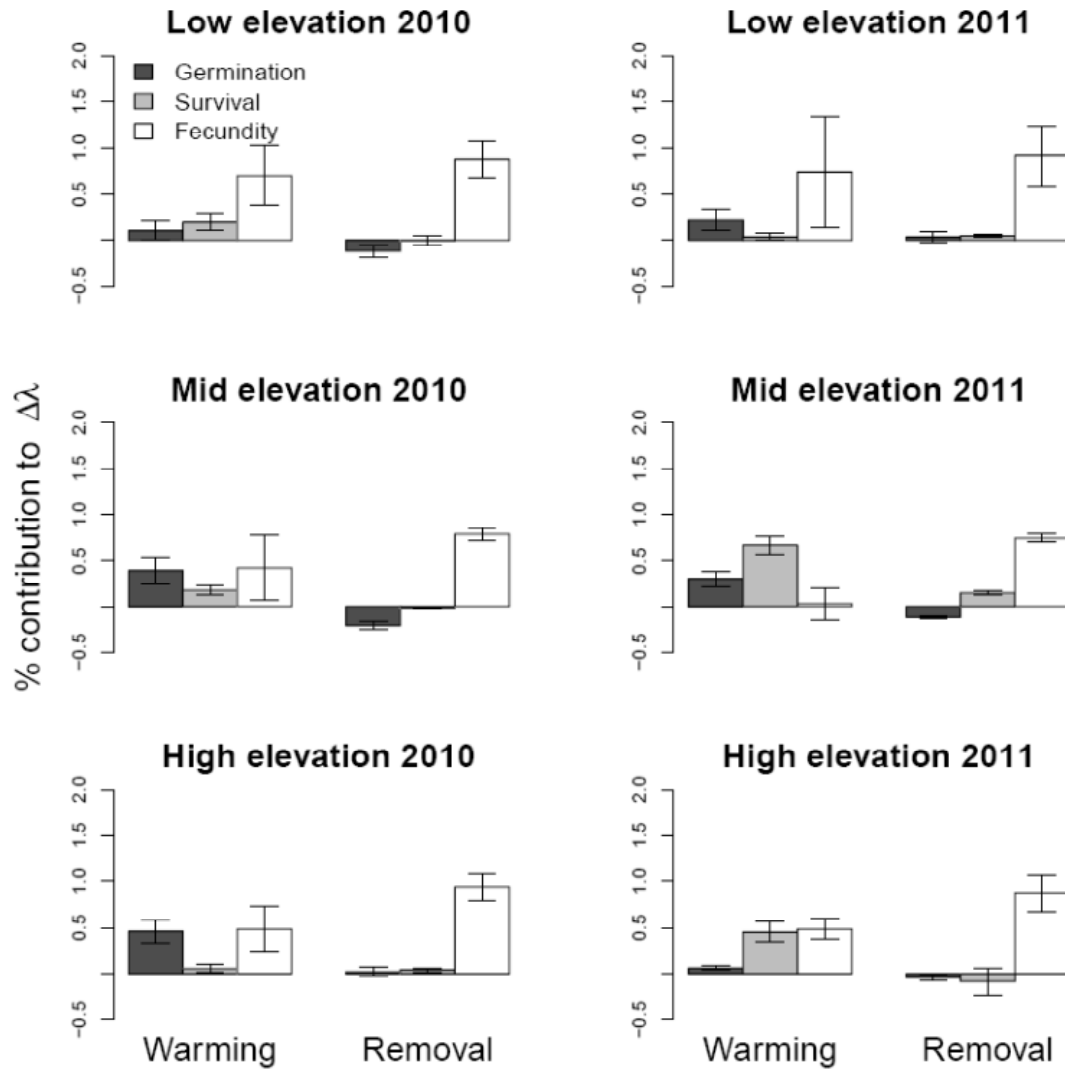


Fig. 2-3. Per-cent contribution of vital rates to differences in growth rate for the warming and removal treatments. Error bars represent one standard deviation.

CHAPTER 3

LOSS OF SNOW CONTRIBUTES TO THE POSITIVE EFFECT OF WARMING ON
BROMUS TECTORUM'S POPULATION GROWTH RATE

Abstract

Cheatgrass (*Bromus tectorum*) is arguably the most destructive biological invader in basins of the North American Intermountain West, and recent studies suggest climate warming might exacerbate its impacts at higher elevations. Warming could increase cheatgrass performance at high elevations through direct effects on demographic rates or through indirect effects mediated by loss of snow cover. We conducted a two-year experimental manipulation of temperature and snow pack to test whether 1) warming increases cheatgrass population growth rate and 2) reduced snow cover contributes to cheatgrass' positive response to warming. We used infrared heaters operating continuously to create the warming treatment, but turned heaters on only during snowfalls to create the snowmelt treatment. We estimated cheatgrass population growth rate and the vital rates that determine it: germination, survival and fecundity. Growth rate increased in both warming and snowmelt treatments. The largest increases occurred in warming plots during the wettest year, indicating that the magnitude of response to warming depends on moisture availability. Warming increased both fecundity and survival, especially in the wet year, while snowmelt contributed to the positive effects of warming by increasing survival. Our results indicate that increasing temperature will exacerbate cheatgrass impacts, especially where warming causes large reductions in the depth and duration of snow cover.

Introduction

Climate change (Parmesan, 2006) and biological invasions (Vitousek *et al.*, 1996) are greatly impacting the world's ecosystems. However, the effects of these global change agents are often studied in isolation. For example, climate change alters the function and structure of terrestrial vegetation (Cramer *et al.*, 2001), shifts species ranges (Root *et al.*, 2003), and will likely cause extinctions (Thomas *et al.*, 2004; Thuiller *et al.*, 2005). Plant invasions have large impacts at the community level (Parker *et al.*, 1999; Hejda *et al.*, 2009), thereby disrupting ecosystem processes such as the fire regime (D'Antonio & Vitousek, 1992), hydrology (Cavaleri & Sack, 2010), and biogeochemical cycles (Vitousek & Walker, 1989). However, few studies to date have examined interactions between climate change and biological invasions (e.g. Duke *et al.*, 2011). These interactions might lead to rapid ecological changes, posing tremendous challenges to natural resource management.

Cheatgrass (*Bromus tectorum*) is arguably the most destructive exotic plant invader in the North American Intermountain West (Knapp, 1996). This annual grass dramatically shortens the natural fire return interval (Whisenant, 1990) by producing large amounts of flammable biomass (D'Antonio & Vitousek, 1992). Frequent fires negatively impact native, perennial plant species, dramatically decreasing natural habitat (West & Yorks, 2002) and endangering obligate consumer species (Dobkin & Sauder, 2004). Currently, cheatgrass impacts are greatest in the lower elevation basins of the Intermountain West. Although cheatgrass is also present at higher elevations, it has not

reached sufficient abundance to cause large impacts (Suring *et al.*, 2005). Recent experimental (Chambers *et al.*, 2007) and modeling (Bradley, 2009) studies suggest warming might increase cheatgrass impacts at higher elevations. However, to our knowledge no study has directly tested this hypothesis with a manipulative field experiment (but see Chapter 1).

Understanding limitations on cheatgrass performance at high elevations, and predicting how these limitations may be altered by climate change, requires disentangling the effect of abiotic factors that co-vary with elevation, such as temperature, precipitation, and snow pack. If temperature has a direct, limiting effect on cheatgrass performance, then warming should favor cheatgrass at high elevations regardless of snow cover. However, because a small temperature increase can trigger large reductions in snow cover (IPCC, 2007), the direct effects of warming might be amplified or buffered by reduction in snow pack. Recent work at high elevations has shown that snow cover decreases the population growth rate of cheatgrass (Griffith & Loik, 2010; Concilio *et al.*, 2012). This suggests that loss of snow pack could play a significant role in exacerbating the cheatgrass invasion, and that warming effects should be greatest where future temperatures will dramatically decrease snow depth and duration.

Our objective was to experimentally test the effect of warming and loss of snow on cheatgrass population growth rates. We manipulated temperature and snow cover to evaluate the following hypotheses: (1) warming will improve cheatgrass performance; (2) melting of snow will contribute to the positive effect of warming. We tested these hypotheses by estimating population growth rate, a proxy for cheatgrass impact, and the

vital rates that determine it: germination, survival and fecundity. The vital rate data provide inference about the mechanisms driving responses to the warming and snowmelt treatments.

Methods

Site description

The Green Canyon ecological station is located in Logan, Utah, USA, at 41°76' N, 111°79' W and at 1460m above sea level. The site is located on a flat alluvial fan and soil is a silt loam (<http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>). Climate variables are summarized in Table 3-1. Within the region of the Western United States dominated by cheatgrass, the climate of this site is close to the median and upper bound of temperature and precipitation range, respectively (Compagnoni & Adler, *in review*). Vegetation is dominated by *Artemisia tridentata* ssp. *tridentata* in the shrub layer and by *Agropyron repens* and *Poa bulbosa* in the herbaceous layer.

Experiment

In September 2010, we implemented an experiment with three treatments replicated eight times: control, snowmelt and warming. Snowmelt and warming treatments were imposed with infrared heat lamps (Model HS-2420, Kalgo Electronics Co.; e.g. Harte & Shaw, 1995) installed 1.6 m above the ground surface. In warming plots, the lamps were left on from November until cheatgrass seed set, which occurred in May or June depending on phenology. In snowmelt plots, the lamps were turned on only

during snowfalls and were turned off immediately after the snow had been melted. Each plot contained four 20x20 cm quadrats consisting of a plastic mesh grid with 100 2x2 cm cells. We planted three of these quadrats with seed collected from three sites located along an elevation gradient. One of these sites was in the immediate vicinity of the experiment. The others were located within 60 km and 25 km of it, and 120 m lower and 370 m higher in elevation, respectively. We collected seed in both years during the month of June. Quadrats were randomly assigned to be planted with one of these three seed sources, and the fourth quadrat was left unplanted to determine background emergence. We planted one seed in each 2x2 cm cell of the planted quadrats at the beginning of September. Here we present results averaged across the three ecotypes. Discarding ecotype effects does not affect the results because statistical models including ecotype always yielded non-significant ecotype x treatment interactions (not shown).

Three plots in each of the control, snowmelt, and warming treatments were randomly chosen for soil moisture and temperature monitoring. We used Decagon Devices EC-5 and 5TM soil moisture sensors and ECT temperature sensors connected to Em50 digital/analog and Em5b analog data loggers to measure soil moisture at 5 cm and 20 cm depth and air temperature 5 cm above the ground. Data loggers operated from December through the end of June and recorded data every hour by saving the average of the values observed by sensors in the previous 60 minutes.

We estimated the geometric population growth rate (λ) of cheatgrass in each quadrat as $\lambda = n_{t+1}/n_t$, where n_t is the number of seeds in the population at year t . $n_t = 100$ because every quadrat is planted with exactly 100 seeds at the beginning of the growing

season. Therefore, λ = quadrat seed production / 100. Quadrat seed production was estimated by multiplying the number of cheatgrass spikelets harvested in each quadrat by the average number of seeds per spikelet. The latter was estimated by subsampling five individuals per quadrat. ANOVA tests showed that the number of seeds per spikelet varied with treatment but not with seed provenance.

We followed the fate of seeds planted in each cell of the plastic grids to estimate the three vital rates that determine cheatgrass population growth rate: *germination*, the percentage of cells where cheatgrass emerged, *survival*, the percentage of emerged individuals that survived until seed set, and *fecundity*, the average number of seeds produced per surviving individual. λ relates to vital rates through the formula λ = germination \times survival \times fecundity. We censused cheatgrass presence three times during the growing season: in November, at the end of March and at the end of the growing season. The last census was carried out at the beginning of June in 2011 and in mid May in 2012. We censused three times to minimize the risk of missing cells germinated in the spring, and to estimate seasonal survival rates.

Our estimate of λ assumes no carryover of seeds from one year to the next. Therefore, we consider dead those seeds that did not germinate the year we planted them. This assumption is supported by a buried bag experiment carried out in control and warming plots during the first growing season which showed that more than 99% of seeds germinated regardless of treatment. Even if the seed bank has little effect on population dynamics, natural dispersal could add seeds to our study plots. To account for contributions from naturally dispersed seeds, we subtracted the seed production in

unplanted quadrats from the seed production of planted quadrats. We did this in two ways. First, we subtracted treatment-specific averages of seed production in unplanted plots. These averages were the predicted values of a linear model explaining seed production in unplanted quadrats as a function of treatment. Second, we subtracted the plot-specific seed production in unplanted quadrats.

Analyses

Growing season (September through June) temperature, snow cover, precipitation and snow fall were measured at the Utah State University weather station, located 4 km from the experimental site (source: Utah Climate Center <http://climate.usurf.usu.edu/mapGUI/mapGUI.php>). We calculated the 25%, 50% and 75% percentile of the historical climate record to compare the weather during the experiment to long term climate. We quantified treatment differences in soil moisture, soil temperature, and air temperature by plotting daily averages and by calculating average values for the period between Dec. 5th and June 15th.

We tested treatment differences in population growth rate and vital rates using linear mixed-models and Tukey's Honestly Significant Difference (HSD) test for post-hoc comparisons. We log-transformed λ and fecundity and modeled them as normally-distributed variables. We modeled germination, survival, winter survival, and spring survival with a binomial distribution. We fit λ and fecundity data with a linear mixed model and germination and survival data with a generalized linear mixed-model with a logit link function. We modeled unequal variance for λ and fecundity because Bartlett

homogeneity of variance tests for these variables were significant among treatments. All models were fit using treatment as a fixed factor and plot as a random factor. Note that the plot effect was estimated with data from all three planted quadrats located within each plot.

We employed a Life Table Response Experiment (LTRE) to estimate the contribution of each vital rate to the differences in λ among treatments. Following Caswell (2001), we calculated treatment differences as:

$$\alpha^{(treatment)} = \lambda^{treatment} - \lambda^{control}$$

The contribution of each vital rate to the above differences was calculated as:

$$\alpha^{(treatment)} = \sum_i^3 (a_i^{treatment} - a_i^{control}) \frac{\partial \lambda}{\partial a_i}$$

where a_i is one of the three vital rates and $\frac{\partial \lambda}{\partial a_i}$ is the sensitivity of a population whose vital rates are the arithmetic average of the vital rates from the two treatments being compared. These formulas provide a deterministic value for each vital rate contribution. To estimate the standard deviation of these values, we performed analyses on 1000 bootstrap samples. Because differences in λ among treatments vary widely, so do the contributions to λ differences. To visually display values on the same scale, we constrained values between -1 and +1 by plotting the proportion of the contribution to the difference in λ . All analyses were carried out using R v 2.15 (R Development Core Team 2012); linear mixed

models were fit using libraries nlme and lme4, and Tukey tests were carried out using the multcomp library.

Results

Weather varied dramatically between the two growing seasons. The first year was cold and wet and the second year was hot and dry (Table 3-1). Compared to historical climate data, temperature was between the 25th and 50th percentile in the first year and above the 75th percentile in the second year. Precipitation was above the 75th percentile the first year and below the 25th percentile the second year.

The warming treatment increased air temperatures an average of 4.3 °C the first year and by 7 °C the second. The increase in the effect of infrared heaters in warming plots during the second year likely resulted from lower soil moisture decreasing evaporative cooling. Soil volumetric water content at 5 cm depth in the second year was on average 0.06 m³/m³ lower than in the previous year. We found a negative correlation between soil moisture and the increase in temperature caused by warming treatments (Fig. E-1): the linear model fit on these data indicates that decreasing moisture by 0.1 m³/m³ increases the effect of the infrared heaters by 4 °C (Table E-1). Warming also decreased moisture at 5 cm depth but increased it at 20 cm depth during the first growing season and in the first part of the second winter (Fig. E-2, Fig. E-3).

The effect of the snowmelt treatment on abiotic conditions was much smaller. Loss of snow increased surface temperature by ~1 °C and had little effect on average soil moisture.

Our two estimates of λ , based on different methods of correcting for background germination, yielded qualitatively identical figures (Fig. E-4) and model results (Table 3-2, Table E-2). Therefore, we focus on analyses of values of λ estimated by subtracting treatment-specific means of background germination.

Linear mixed-models testing the effect of treatments on λ were significant in both the first ($p < 0.0001$) and second year ($p = 0.0215$). Tukey's HSD contrasts show that the warming and snowmelt treatments significantly increased cheatgrass population growth rates in all but one case. Warming plots had significantly higher population growth rates than all other treatments in the first year, but not in the second when contrasts were non-significant (Fig. 3-1, Table 3-2). The snowmelt treatment significantly increased population growth compared to the control in both years (Fig. 3-1, Table 3-2).

Relative to controls, warming increased fecundity and survival in the first year but not the second (Fig. 3-2, Table E-3, Table E-4). Snowmelt increased survival in both years (Fig. 3-2, Table E-4) and caused a marginally significant increase in germination in the first year (Table E-5). The LTRE analysis indicated that warming effects were caused primarily by increased fecundity in both years and increased survival in the first year (Fig. 3-3). In contrast, the positive effect of the snowmelt treatment on cheatgrass population growth rate mostly resulted from increased survival (Fig. 3-3).

Discussion

H1) Warming will increase cheatgrass population growth rate

We found that warming increased cheatgrass population growth rate and that the magnitude of this increase depended on soil moisture. Warming effects were much stronger in the first year when soil moisture was high. In this year, warming increased cheatgrass population growth rate by 10 times. During the second year, low soil moisture likely limited growth and also amplified the effect of infrared heaters much more than we expected: December through June average temperature in warmed plots was up to ~4.5 °C higher than in the same plots the previous year. Despite such high temperatures cheatgrass still increased its population growth by 50% compared to controls, almost the same increase observed in snowmelt treatments (Fig. 3-1).

Warming increased per capita growth rates mostly through its effect on fecundity. Previous work suggests that warming may increase fecundity by increasing both photosynthetic rate and nitrogen uptake. Cheatgrass net photosynthesis increases with temperature to a peak at 25-30 °C (Rice *et al.*, 1992). In our warming plots, only 3-6% of the hourly temperature readings exceeded 30 °C. Even more dramatic warming would be necessary for temperature to negatively affect photosynthesis. Second, higher soil temperatures may increase cheatgrass nitrogen uptake rate (Leffler *et al.*, 2011). Both high photosynthesis and nitrogen uptake rates should promote biomass growth, and high biomass, which is tightly correlated with seed production in cheatgrass (Rice *et al.*, 1992), will increase the population growth rate.

H2) Loss of snow will contribute to the effect of warming

Our data strongly suggest that reduced snow cover contributes to the direct effects of warming by increasing survival. In the first year, survival doubled in both snowmelt and warming plots (Fig. 3-2), suggesting that part of the effect of warming was due to the increase in survival caused by the removal of snow. Increased survival might occur because conditions under snow are conducive to fungal growth (Schmidt *et al.*, 2009) and some of these fungi are pathogenic snow molds that cause cheatgrass death (Klemmedson & Smith, 1964; Meyers *et al.*, 2008). Regardless of the underlying mechanism, the positive effect of loss of snow on survival indicates that future increases in cheatgrass density could be largest where warming will cause the greatest decreases in the depth and duration of snow cover. We expect snow losses will be greatest where current average winter temperatures are only a few degrees below 0 °C. The snowpack at such sites is the most sensitive to temperature increase (IPCC, 2007).

We were surprised that survival was lower in warming than snowmelt plots in the second year (Fig. 3-2). Analysis of seasonal survival rates suggests this partly resulted from heat and moisture stress during spring. In this season warming plots were not only experiencing higher temperatures, but also lower soil moisture than control and snowmelt plots (Fig. E-2, Fig. E-3). Accordingly, spring survival in warming plots was lower than in snowmelt plots (Fig. E-5). However, we have no convincing explanation for why winter survival was significantly higher than controls in snowmelt but not warming treatments (Fig. E-5). The mortality in the warming treatment was unlikely an effect of

heat and moisture stress, because winter temperatures were too low to cause heat stress and winter soil moisture was higher in the warming treatment than in the control (Fig. E-2, Fig. E-3).

Conclusions

Our data strongly support the prediction that warming will exacerbate cheatgrass impacts in sites and years when moisture is not limiting. First, warming has a positive direct effect on cheatgrass fecundity, consistent with the assumption that temperature limits this species' performance at high elevations (Chambers *et al.*, 2007; Bradley, 2009). Second, warming indirectly increases cheatgrass survival by decreasing snow cover.

We expect that the effect of warming on cheatgrass will be greatest in areas that will experience a large decrease in snow cover. Large decreases in snow cover are expected where average winter temperatures are currently close to 0 °C, because the largest percent change in snow water equivalent occurs as temperature approach this value (IPCC, 2007). Areas that meet these criteria are not necessarily located at high elevation. Our experimental site is such an example: at 1460m of altitude, there is a consistent winter snow cover, and a December through February average temperature of -3.1 °C. Second, at high elevations snowpack is more likely to be deep, so even if large relative decreases in snow depth occur, they might not affect cheatgrass. Mid-elevation areas where snowpack may be lost entirely would be the areas of greater concern.

Managers of public and private lands located in such areas should anticipate increases in cheatgrass density and, in turn, fire size and frequency.

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Table 3-1 Growing season weather variables in the two years of the experiment.

Growing season	Temperature (°C)	Precipitation (mm)	Snow fall (cm)	Snow depth (cm)
2010-2011	5.9	645	250	4.2
2011-2012	7.3	327	130	1.2
Average	6.2	438	164	3.7

Table 3-2 Results of Tukey's HSD tests on population growth rate differences among treatments. Results refer to population growth rate values estimated subtracting treatment-specific means of seed production in unplanted quadrats.

Contrast	Estimate	z value	p value	
2011				
Snowmelt - Control	1.2830	3.6198	0.0009	***
Warming - Control	2.2198	6.2068	<0.0001	***
Warming - Snowmelt	0.9368	2.7490	0.0166	*
2012				
Snowmelt - Control	0.4984	3.0119	0.0069	**
Warming - Control	0.1324	0.4658	0.8841	
Warming - Snowmelt	-0.3661	-1.2912	0.3905	

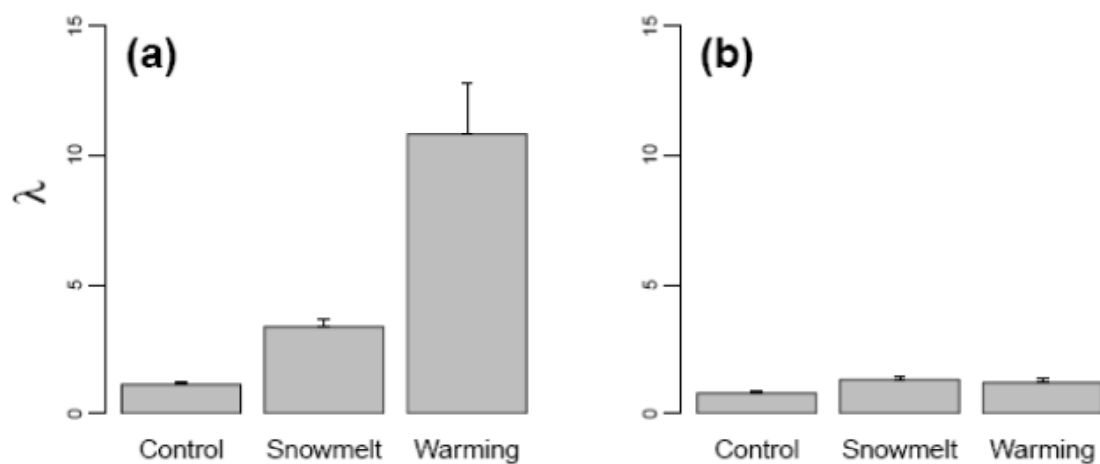


Fig. 3-1 Effect of treatments on cheatgrass population growth rate. Panels (a) and (b) refer to the first and second growing seasons, respectively.

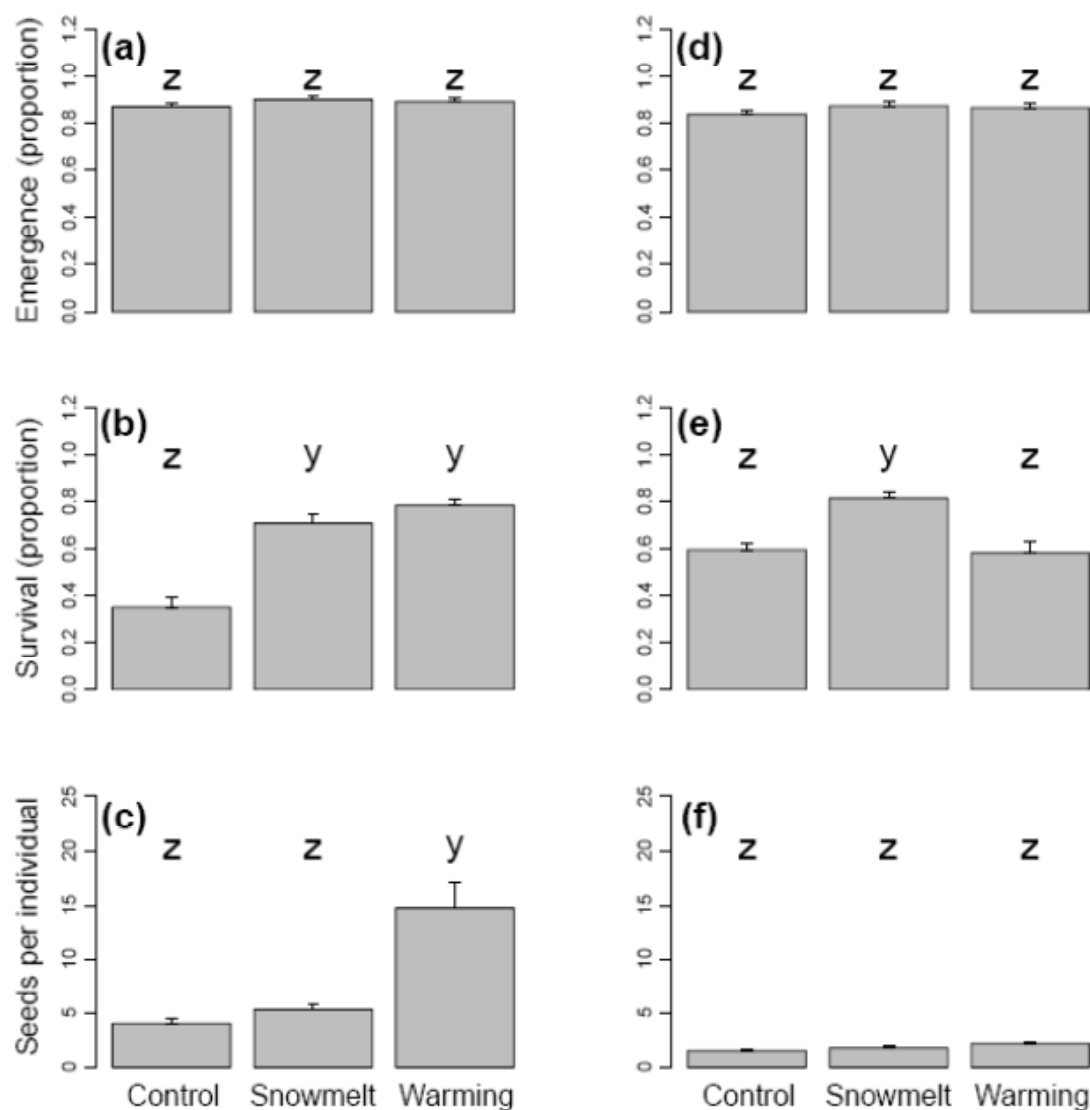


Fig. 3-2 Vital rates observed during the experiment. Vital rates from the first growing season are in panels (a-c), vital rates from the second are in panels (d-f). Letters z, y, and x identify statistically different groups based on Tukey's HSD contrasts. Tabular results of post-hoc contrasts for fecundity, emergence, and survival are respectively summarized in Table E-3, Table E-4 and Table E-5.

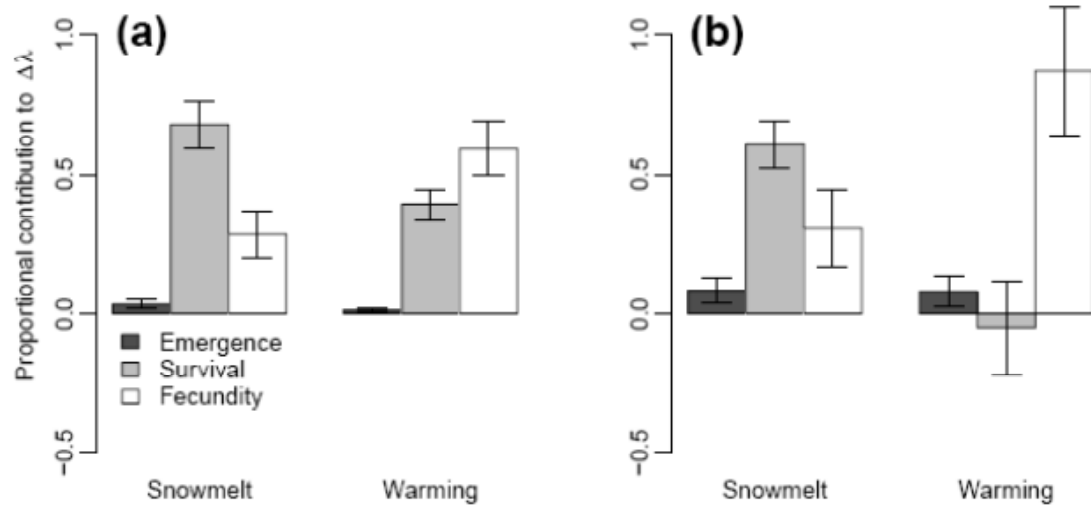


Fig. 3-3 LTRE results for the two years of the experiment. Panels (a) and (b) refer to the first and second growing seasons, respectively.

CHAPTER 4

ARE RARE PLANT SPECIES LESS SENSITIVE TO INDIRECT
EFFECTS OF CLIMATE CHANGE?²

Abstract

Climate change can affect species directly or indirectly. Indirect effects occur when climate causes changes in the abundance of neighbor species which then feedback to affect the focal species. Attempts to forecast the population effects of climate change would benefit from knowing which species are most vulnerable to indirect effects. Theory and limited empirical evidence show that species most strongly stabilized by niche differences should experience the weakest indirect effects of climate change in communities of competing species. If rare species are characterized by particularly strong niche differences, as suggested by recent work, then they might be less sensitive to indirect effects. We addressed the following questions: 1) Do less abundant species show larger stabilizing niche differences than more abundant species? 2) Does stabilization explain the absolute size of indirect effects? 3) Does stabilization also explain the size of indirect effects once they are scaled by population size? To address these questions, we added four relatively rare forb species to a pre-existing empirical model based on four abundant species in a sagebrush steppe community (one shrub and three grasses). We modeled four communities, each including one of the forbs and the original four species.

² Coauthored by Peter B. Adler

We estimated recruitment, survival, and growth as a function of climate and competitor (conspecific and heterospecific) density, and then simulated the models to estimate equilibrium abundances and to quantify niche differences. We also ran simulations using observed and perturbed climate in order to decompose the direct and indirect effects of altered climate. Consistent with our hypothesis, the less common forb species showed larger stabilizing niche differences than common species. Species with strong stabilizing niche differences experienced smaller absolute indirect effects. When analyzing proportional indirect effects, we found that forbs experienced stronger indirect effects than dominant species, but that within each group the size of indirect effects decreased with niche differences. In this community, rarity results from strong intraspecific density dependence rather than from competitive suppression by heterospecifics. Moreover, species relative abundance relates to the size of the absolute indirect effects of climate change. However, our partial evidence supporting the relationship between relative abundance and proportional indirect effects warrants further theoretical and empirical investigation.

Introduction

Land managers facing the challenges of global change are demanding reliable ecological forecasts (Clark et al. 2001). Most forecasts of climate change impacts on species ranges (Root et al. 2003) and abundances (Williams and Jackson 2007) model species responses as a function of climatic factors only (e.g. Guisan and Zimmerman 2000) even though environmental change may also affect biotic interactions (Tylianakis

et al. 2008, Gilman et al. 2010). Interspecific interactions can generate indirect climate effects that may amplify or buffer the direct effects of climate. Modeling such indirect effects requires data on species interactions, which are difficult to collect. Expensive multispecies modeling efforts would ideally focus on the species that are most likely to be affected by indirect effects.

A counter-intuitive hypothesis is that rare species should be the least affected by the indirect effects of climate change. The justification for this hypothesis depends on two assumptions. The first assumption is contrary to the common view that rare species are competitively suppressed by common species. It posits that species rarity arises from strong self-limitation rather than from a fitness disadvantage. This assumption is supported by recent studies on the strength of density dependence in forest communities. These studies show rare species are strongly self-limited and that heterospecific competition is uniformly low (Comita et al. 2010, Johnson et al. 2012). This implies that species rarity results from strong stabilizing niche differences, which measure the degree to which a species limits itself more than it limits others (Chesson 2000). These empirical results support the theoretical prediction that in rare species, long-term persistence is facilitated by strong stabilizing niche differences (Yenni et al. 2012). This follows the fact that the stronger stabilizing niche differences, the stronger the release from self-limitation after a decrease in abundance. As a consequence, strongly stabilized species are less likely to face stochastic extinction, because they regain equilibrium abundance faster than species whose rarity results from low fitness. These considerations suggest species abundance in stably coexisting species should be inversely correlated to

stabilizing niche differences. However, no study has yet directly tested the relationship between stabilizing niche differences and species relative abundance.

The second assumption is that the indirect effects of climate change should decrease with the strength of stabilizing niche differences. Indirect effects of climate change can arise from trophic and non-trophic interactions (Gilman et al. 2010). Theory suggests that indirect climate effects arising from non-trophic interactions such as competition should decrease with the strength of stabilizing niche differences (Adler et al. 2012). Simply put, strong stabilization results from low niche overlap, and low niche overlap implies weak species interactions. A recent empirical test confirmed the hypothesis that indirect climate effects decrease with the strength of stabilizing niche differences (Adler et al. 2012). If this finding held across communities, it would help determine which species require modeling of biotic interactions in climate change forecasts. However, Adler et al. (2012) was limited to four abundant species in a community. Extending the methods of this study to rare species would allow testing both of the assumptions necessary to support our main hypothesis: that rare species are the least affected by the indirect effects of climate change.

These tests would still fail to address an important problem: if a species has low abundance, it will likely experience small indirect effects. Therefore, it would be useful to also predict the size of the indirect effects of climate change scaled by population size. These proportional indirect effects are particularly relevant to rare species for which relatively small changes can dramatically increase the chance of stochastic extinction. Theoretical predictions from the two-species model used in Adler et al. (2012) suggest

proportional indirect effects depend on stabilizing niche differences, on fitness inequality among the two species and on the strength of interspecific interactions (Appendix F). These results suggest stabilizing niche differences should relate to the size of proportional indirect effects. However, this relationship should be weak, because proportional indirect effects depend on other factors as well.

The objective of this study was to test whether the indirect effects of climate change decrease with species rarity. To address this objective, we added species of lower abundance to the Adler et al. (2012) model and tested three hypotheses: 1) Less abundant species are more strongly stabilized by niche differences, 2) the stronger the stabilizing niche differences, the smaller the indirect effects of climate change, 3) the stronger the stabilizing niche differences, the smaller the proportional indirect effects of climate change.

Methods

Our analyses were carried out in four steps (Fig. 4-1): (1) We extracted demographic information (survival, growth and recruitment) from our original vegetation data. (2) We used demographic information to build statistical models that correlate vital rates with climate and interspecific interactions. (3) We used vital rates to build population models of multiple interacting species. (4) We perturbed multispecies population models to obtain estimates of full, direct and indirect climate effects. Moreover, we perturbed models to estimate species' stabilization strength.

Demographic data

Our data were collected at the U.S. Sheep Experiment Station (USSES) in Dubois, Idaho (44.2° N, 112.1° W). The site is located at an elevation of 1500m, average yearly temperature is 13° C and average annual precipitation is 270 mm. The vegetation is dominated by three-tip Sagebrush (*Artemisia tripartita*) and by three grasses: Bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread grass (*Hesperostipa comata*) and Sandberg bluegrass (*Poa secunda*). In this study, we also consider four less abundant forbs: arrowleaf balsamroot (*Balsamorhiza sagittata*), tapertip hawksbeard (*Crepis acuminata*), longleaf phlox (*Phlox longifolia*) and spiny phlox (*Phlox hoodii*).

26 quadrats of size 1-m², located within and outside of grazing exclosures, were sampled between 1926 and 1956 using pantographs. These produce maps of plant location and size which were digitized using ArcGIS (Zachmann et al. 2010). This data provides spatially explicit measurements of canopy cover for shrubs, basal cover for grasses and stem location for forbs. We used this data set to estimate the recruitment and survival of individuals of all species, as well as the growth of individuals belonging to species recorded as polygons (the forbs were mapped as points, meaning we have no size information). We identified and tracked the fate of individuals using two functions (Lauenroth and Adler 2008): one for plants recorded as point locations (forbs) and one for plants recorded as polygons (grasses and shrubs). The algorithm for point features assigns survival to individuals observed in year t within a 5 cm radius of a conspecific location in year t-1. Individuals falling out of such radius are considered new recruits. By

tracking survival and recruitment, this function also estimates the age of individuals. The algorithm for polygon features adds a 5 cm buffer around polygons in year $t-1$ and considers overlapping polygons in year t as a surviving part of the genet. When a polygon in year t overlaps with more than one genet in year $t-1$, it is assigned to the genet for which the overlap is largest. This function allows genets to fragment when a single polygon separates into smaller polygons or coalesce when two genets merge into one.

Forb survival modeling

We first fit forb survival models because they differed from pre-existing shrub and grass models. We fit survival models only, because forbs lacked size and therefore growth information. For the same reason, we modeled survival as a function of age rather than size. Following the methods by Adler et al. (2012), we selected the best survival model in three preliminary steps before fitting a final, mixed-effect model including all selected variables.

In the first step, we selected the best model including the effect of individual age, species interactions, and spatio-temporal variability. Moreover, we selected the best Gaussian distance decay parameter for forb neighborhood effects. The modeling of interspecific interactions depends on this decay parameter. Decay parameters for the shrubs and grasses had been estimated previously by Adler et al. (2010), but we did not have estimates for forbs. We modeled the survival of each individual from year t to year $t+1$. Survival was a function of individual age, crowding, spatial location and year. We calculated crowding as a function of the distance, size and species identity of each plant

surrounding a focal individual (Appendix G). Even if we lacked size information for forbs, we modeled forb crowding using location and assuming every individual had size 1-cm². Assuming an arbitrary size should not bias model behavior because interaction coefficients scale based on the abundance measure chosen. Finally, we accounted for spatial and temporal variability by modeling the effect of quadrat group and year.

Quadrats were grouped in areas that shared similar abiotic and biotic factors, such as grazing exclosures. We fit seven candidate model structures that included various combinations and interactions among these predictor variables (Appendix G). Each of these seven model structures was fit multiple times using a sequence of candidate distance decay parameter values for forbs. The model with lowest AIC value indicated the best model structure and the best Gaussian distance decay parameter value.

The estimation for forbs distance decay parameter slightly differed from that of the shrub and the grasses. Adler et al. (2010) estimated the decay of shrub and grasses interaction effects in single species models. However, estimation for forbs was done through models including interactions from all four dominant species. We did this because using single species forb models led to unreasonable estimates of the distance decay parameters.

In the second step of model selection, we chose the best age predictor for survival. This posed two challenges. First, we only knew the age of the individuals for which we observed birth and survival. Therefore, we had no age information at the start of an uninterrupted time series. This occurs in five years: at the start of the data set and after each one of the four gaps in data collection. However, we decided to increase our data set by assuming individuals in these five years were 1 year old. We compared the models in

Table G-1 fit on the extended data set and on the data set with known ages only. There were little differences in sample-size adjusted deviance among these two models. Second, for survival correlates nonlinearly with age: survival is lowest at age 1, dramatically increases in year 2, and slightly increases thereafter. To model this pattern, we compared AIC values of models using age, inverse age ($1/\text{age}$), and several modifications of the age structure. First, we changed age structure so that all individuals older than 1 year were considered 2 year olds. In other words, we ignored the age structure of individuals older than 1 year. We also ignored the age structure of individuals older than 2, 3, 4, and 5 years of age. We chose inverse age as predictor, because models using this variable produced the lowest AICs.

In the third model building step, we selected the best model including seven climatic variables and their interaction with individual age. We chose what we assumed to be the most important climatic factors for vital rate transitions in this sagebrush steppe ecosystem: annual precipitation in year $t-1$, fall to spring precipitation in year t and $t+1$ and spring temperature in year t and $t+1$. Because individual survival refers to the transition from year t to year $t+1$, year $t-1$ refers to the year preceding this transition. In addition, we included the interactions between fall through spring precipitation and spring temperature in year t and $t+1$. Finally, we included the interaction term between each climatic covariate and individual size. We used AIC values to select the best model in a stepwise backward fashion. We included the variables selected in these three model building steps in a final mixed-effect model (Appendix G).

Shrub and grasses vital rates modeling

We modeled growth and survival of the shrub and grasses by adding one forb species at a time to the models described by Adler et al. (2012). Model selection was identical to that of forb survival, but we characterized individuals of the shrub and grasses by their size instead of age (Appendix G). We fit shrub and grass models including only one forb species at a time, meaning each species-specific survival, growth and recruitment model was fit four times. This implies we simulated the dynamics of this system using four models, each including the four dominants plus one forb. We chose this approach because the forbs occur at low densities, making it difficult to estimate their effects on each and run one simulation with all eight species.

We modeled recruitment by fitting a model that included the effect of species interactions, spatial and temporal variability, and climatic factors. We modeled recruitment at the quadrat level because recruits' parents cannot be identified. Species interactions were incorporated in a Ricker (1954) model based on conspecific and heterospecific abundance in each quadrat. Forb abundance was measured as density, the abundance of other species as absolute cover. We fit four recruitment models each of which included five species: one forb, plus the shrub and the grasses.

Population models

We used the estimated vital rates to build integral projection models (IPMs). Because these models are demographically deterministic, they are ideal to simulate equilibrium abundances and low density growth rates. We ran IPMs of five interacting species: the

four common species plus one forb. Thus, we had four IPMs, each defined by a different forb. These models simulated interacting populations as a function of the state of individuals, species interactions, climate, and year. The state of individuals is defined by age in forbs, and by size in the other species. Interactions are quantified by mean field approximations of intra and interspecific crowding. These approximations assume patterns are random except for intraspecific patterns of shrubs and grasses. Data shows conspecifics of these species are more regularly distributed in space than expected at random (Fig. G-1). Therefore, our mean field approximation of conspecific crowding for these species uses a no-overlap rule, which prevents individuals of the same species from overlapping in space (Adler et al. 2010, 2012).

IPMs represent each population by a density function $n(u_j, t)$. For shrubs and grasses, this function gives the number of individuals in each size class u_j at time t . In time $t+1$ the size structure transitions from u to v . IPM calculates this transition as:

$$n(v_j, t + 1) = \int_{K_j}^{U_j} [P_j(v_j, u_j, \bar{w}_u) + R(v_j, u_j, \bar{w})] n(u_j, t) du$$

where j refers to one of the four species of shrub and grasses, L and U are the lower and upper size limits of a species' size distribution, P is a kernel that projects survival and growth, and R projects recruitment. Forbs differed from shrubs and grasses because their population was age rather than size structured. Forb populations were divided in age-specific density functions. These give the number of individuals in one size class only, because we assume all forbs have size 1-cm². Forb abundance at time $t+1$ was obtained as follows:

$$n_0(v, t + 1) = \sum_{A=0}^m R(v, u, \bar{w}) n_A(u, t)$$

$$n_A(v, t + 1) = P_{A-1}(v, u, \bar{w}_u) n_{A-1}(u, t)$$

where A identifies age class and varies from 0 to m , which is maximum age – 1. Note that unlike models for shrubs and grasses, forb models project density rather than cover.

Simulations

We used these models to simulate the effect of climate perturbation on species' equilibrium abundances. We ran a series of simulations to calculate the full, direct and indirect effect of climate perturbation on each species. The full effect was the difference between equilibrium % cover in perturbed and unperturbed climate simulations. To estimate direct effects, we simulated the target species' population under perturbed climate, while simulating the other populations in unperturbed climate. These simulations estimated the response of the target species to climate alone, because heterospecific competition is the same observed in unperturbed climate. Last, we calculated indirect effects as the difference between full and direct effects.

At each time step in these simulations, we drew climate variables and random year effects independently from the set of 22 observed years. We preserved patterns of climate correlations by using, at every time step, the climate variables observed in a single year. Climate perturbations included increases 1% increases in precipitation and/or temperature and a 10% increase in climate variability. Such small perturbations avoid extrapolation beyond the range of values used to fit the models. To estimate equilibrium cover, we ran models for 2250 time steps and averaged cover after discarding the first

250 time steps. For the shrub and grasses, equilibrium cover estimates slightly differed according to which forbs were included in the models. We present the averaged equilibrium cover of shrubs and grasses across the four forb-specific models.

We estimated the proportional indirect effects of climate change first, and then calculated the absolute indirect effects. Proportional differences can be calculated and compared even though the forb populations were modeled as density and the shrub and grasses as cover. To rescale the abundances into a common currency, and convert proportional indirect effects to absolute indirect effects, we multiplied the proportional change by the species cover observed in contemporary, natural communities. We estimated these cover values using data from an experiment located in the immediate vicinity of the permanent quadrats. Given the proximity, the cover values observed at that site should be very similar to those found in the long-term quadrats. However, because the experimental site is grazed, in contrast to many (but not all) of the historical quadrats, the cover of *B. sagittata* is very low. For this species, we estimated cover using photos taken between 2007 and 2012 of thirteen of the historical quadrats located in a livestock exclosure. These are a subset of the quadrats mapped between 1926 and 1956 that provide the data for this study. In the discussion section, we consider how sensitive our results are to uncertainty about the abundance of *B. sagittata*.

Stabilizing niche differences

We also used simulations of IPMs to calculate species' negative frequency dependence, a measure of stabilizing niche differences (Adler et al. 2007). Negative

frequency dependence determines how fast a species' growth rate decreases when its relative frequency increases. The low density population growth rate represents the greatest average growth rate of a species, which occurs when its abundance is close to zero but its competitors are near their equilibrium abundances. We calculated the low density population growth rate by running IPMs where focal species were returned to 0.01% cover after each time step. As in simulations of perturbed climate, we ran models for 2250 time steps and discarded the initial 250 runs. We took the geometric mean of these 2000 low density population growth rates. Species relative abundances (i.e. equilibrium frequencies) were calculated using the same contemporary cover observations used to calculate the full, direct and indirect effects of climate.

Hypothesis tests

We directly tested our three hypotheses by fitting linear regressions. We used species relative abundance as a predictor of stabilization strength (hypothesis 1), and stabilization strength as a predictor of absolute indirect effects (hypothesis 2) and proportional indirect effects (hypothesis 3). We log-transformed the relative abundances, stabilization strengths, and the absolute magnitude of indirect climate effects in order to make relationships linear.

Results

1) Less abundant species are more strongly stabilized by niche differences

We measured stabilization in terms of negative frequency dependence (Fig. 4-2). We found there is a significant, strong relationship between species relative abundance and the strength of their stabilizing niche differences (Fig. 4-3, Table 4-1).

2) The stronger the stabilizing niche differences, the weaker the absolute indirect effects of climate change

There were two patterns in the direct responses of species to climate perturbation. First, responses to increased temperature and precipitation were similar only among grasses (Fig. 4-4). These species generally responded positively to increased precipitation and temperature. The only exception was the negative response of *P. spicata* to increased temperature. Second, increased variability consistently decrease plant abundance. In all other cases, species responses to the increase in temperature and precipitation appeared individualistic (Fig. 4-4).

Consistent with theory, the absolute indirect effects of climate significantly decreased with the strength of stabilizing niche differences (Fig. 4-2) and this relationship was nonlinear (Fig. 4-5A). The indirect effects of climate change were generally negative, with no systematic differences between shrubs, grasses and forbs (Fig. 4-4). The only positive indirect effects were observed for *C. acuminata* and *A. tripartita*. In *C. acuminata*, indirect effects were generally positive, in *A. tripartita* they were positive only under increased variability.

3) The stronger the stabilizing niche differences, the weaker the proportional indirect effects of climate change

Treating all species together, we did not find a significant relationship between stabilizing niche differences and the proportional indirect effects (Fig. 4-2, Table 4-1). However, the expected relationship holds within the two main species groups: shrub and grasses, and forbs. The shrub and grasses experienced weaker proportional indirect effects than the forbs (Fig. 4-5B).

Discussion

1) Less abundant species are more strongly stabilized by niche differences

Our data supports the hypothesis that low abundance in stably coexisting species results from strong stabilization rather than low fitness (Yenni et al. 2012). This hypothesis suggests that in a stochastic environment, strongly stabilized rare species persist because they have high growth rates at low density. This characteristic decreases extinction probability, because species will regain their equilibrium abundance faster. Without strong stabilization, these dynamics would make species with low fitness prone to stochastic extinction, regardless of the fact that they coexist in deterministic models.

2) The stronger the stabilizing niche differences, the weaker the absolute indirect effects of climate change

The absolute indirect effect of climate perturbation significantly decreases with the strength of stabilizing niche differences (Fig. 4-3, Table 4-1). Consistent with theoretical predictions and with a previous empirical test carried out on the four dominant species (Adler et al. 2012), this decrease is nonlinear (Fig. 4-5A). The fact that this

relationship holds for our four additional forbs provides further empirical support for this theory.

The few patterns in the direct response to climate perturbation can be explained by the ecology of individual species and by demographic principles. First, grasses responded positively to precipitation. Accordingly, a previous study carried out on this data set found *H. comata* and *P. spicata* respond positively to precipitation (Dalglish et al. 2011). Second, assuming growth rates are normally distributed, the negative response of plants to increased variability is expected because this perturbation should decrease long-term growth rates (Tuljapurkar et al. 2003). The fact that indirect effects of climatic variability are usually negative suggests demographic fluctuations do not promote coexistence in this community. If the storage effect (Chesson 2000) were operating, indirect effects should have counteracted the negative direct effects of variability. Instead, we found the indirect effects of increased variability were negative. Consistent with this observation, previous work show climatic variability has little effect on the coexistence of shrubs and grasses in this community (Adler et al. 2009). While the explanations above address qualitative patterns, it is puzzling that the full effects of climate are so large (Fig. 4-5). Because climate perturbations were very small, this suggests plant abundances in this system are very sensitive to climate change.

Indirect climate effects are generally negative for all species except for *C. acuminata*, and for *A. tripartita* in the case of increased variability. There is no single species or group of species whose direct responses can explain the indirect effects experienced by *C. acuminata*. However, the indirect effects on *A. tripartita* might in part

be driven by the direct response of grasses. Climate perturbations increase the abundance of *H. comata* and *P. secunda*, so increased competition by these species might explain the negative indirect effects on *A. tripartita*.

3) The stronger the stabilizing niche differences, the weaker the proportional indirect effects of climate change

The proportional indirect effect of climate perturbation did not significantly decrease with the strength of stabilizing niche differences (Fig. 4-3). However, the relationship holds within the two main functional groups: shrubs and grasses, and forbs (Fig. 4-3, Fig. 4-5B). We speculate the difference between these groups might result from fitness differences. In particular, according to our derivation (Appendix F), fitness inequality should increase the proportional indirect effects of species with relatively low fitness. Therefore, it might be that forbs have, on average, lower fitness than the shrub and grasses.

Caveats

Unexplained variation in the relationship between indirect effects and stabilization (Fig. 4-3) could reflect three main sources. First, these discrepancies might result from one of the assumptions made by the theoretical model presented by Adler et al. (2012). The model assumes the magnitude of climate change response is similar across species. However, this does not hold, because the magnitude of direct responses to climate is clearly individualistic (Fig. 4-4). For example, if certain species did not respond to temperature perturbation, this would decrease the potential magnitude of

indirect effects on the remaining species. Second, limited to the absolute indirect effects of climate, the abundance data we used to quantify species relative frequency might not perfectly match the community data our model is based on. Even if the site where we collected abundance data were located nearby the mapped quadrats, its community might still have slightly different relative abundances due to the apparent effect of grazing on *B. sagittata*. For example, where present, this species' average cover is 8.5%. If competition by *B. sagittata* decreased *P. spicata*'s abundance by 2%, these species' ranking of stabilization would switch. *P. spicata* would become more stabilized than *B. sagittata*, removing one of the main deviations from the expected pattern (Fig. 4-4).

Conclusion

Our finding that the magnitude of indirect climate effects co-varies with species abundance might be crucial to climate change forecasting. If indirect climate effects decrease with species abundance, prioritizing which species require modeling of interspecific interactions becomes surprisingly simple. This would be dramatically easier than the empirical estimation of stabilization strength we performed, which relies on unique long-term data and complex models. However, our evidence is definitive only for a relationship between species abundance and absolute indirect effects. Our mixed results on the relationship with proportional indirect effects warrant further theoretical and empirical investigation. Ecological forecasts would benefit the most from knowing what species will experience the largest proportional indirect effects. This is especially true for rare species which are the most prone to stochastic extinction.

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Table 4-1. Results from linear models testing our three hypotheses.

Test	Response	Estimate	Std. Error	t value	Pr(> t)	
H1	Relative abundance	1.2033	0.2053	5.8605	0.0011	**
H2	Absolute indirect effect	0.9375	0.2100	4.4634	0.0043	**
H3	Proportional indirect effect	0.2300	0.2351	0.9782	0.3657	NS

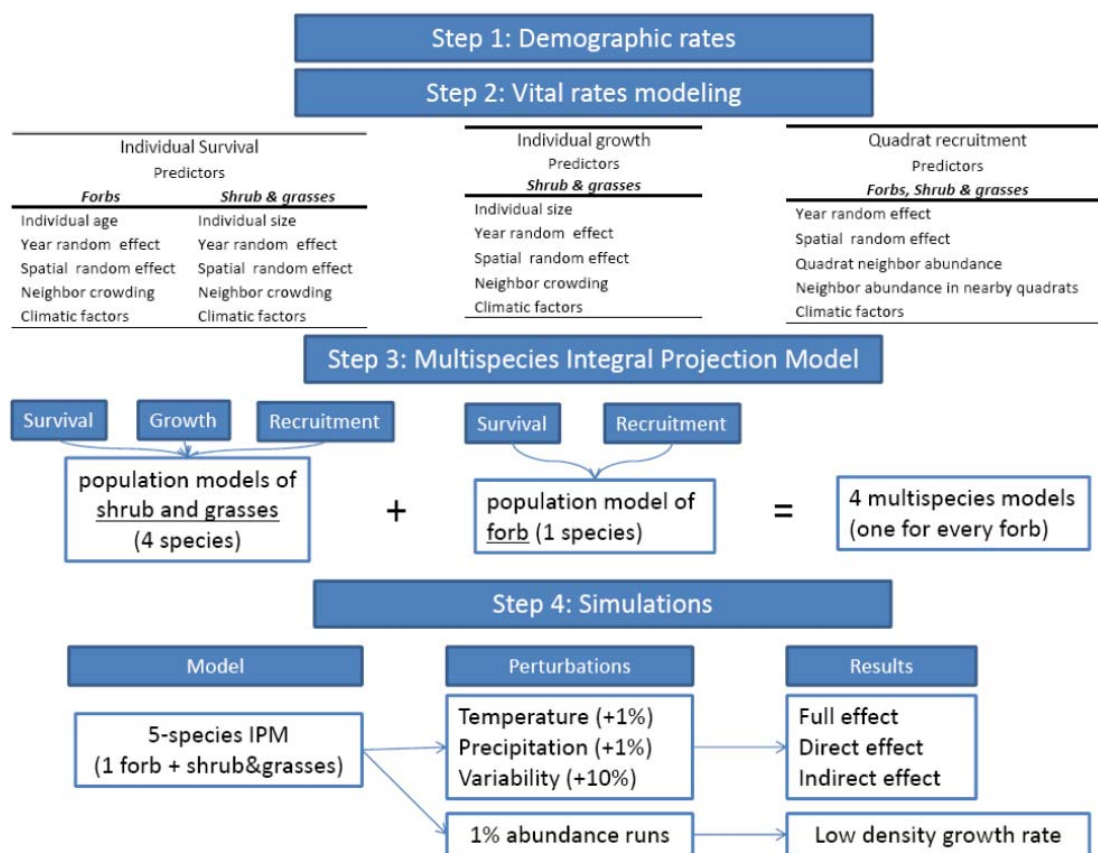


Fig. 4-1. The four analytical steps of this study.

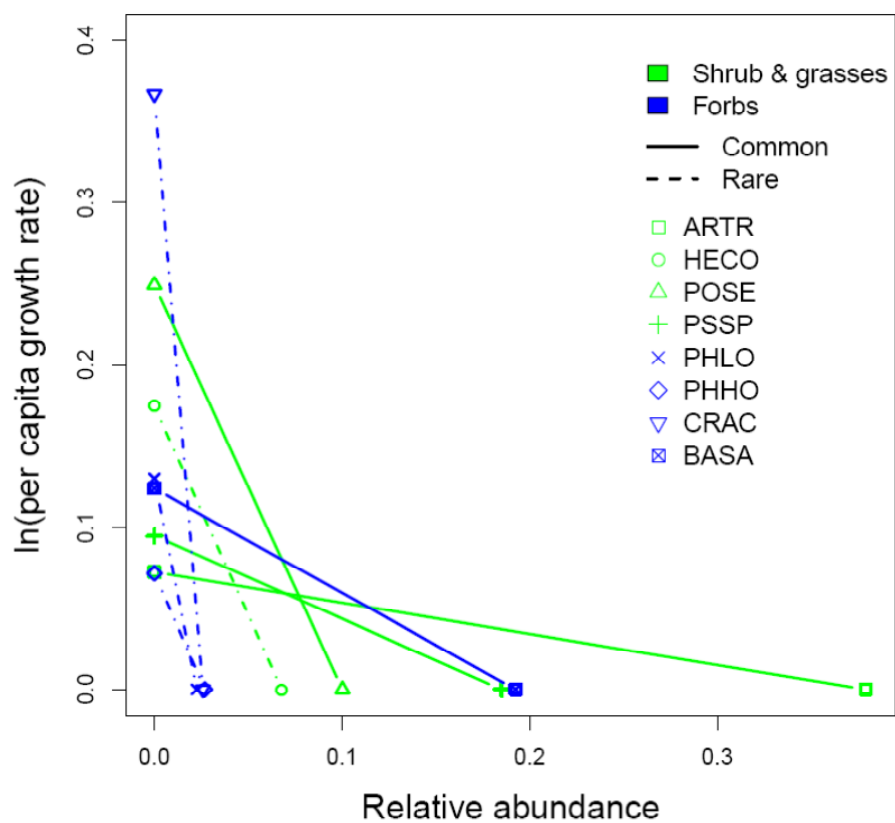


Fig. 4-2. The strength of stabilization for the eight species of this study.

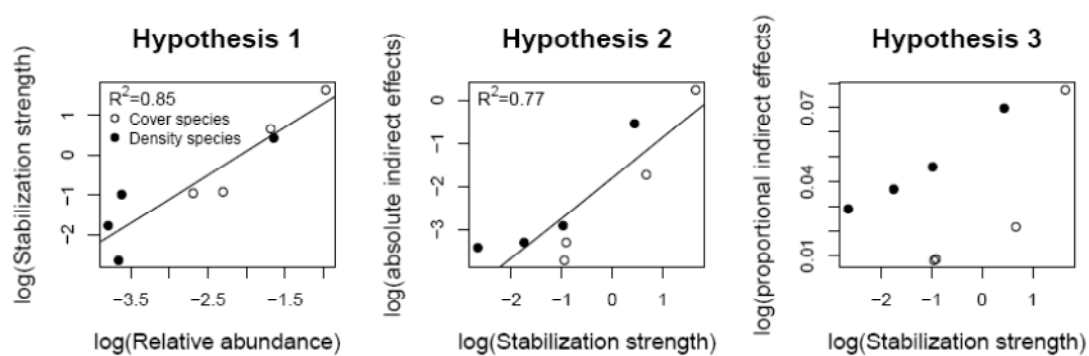


Fig. 4-3. Relationships between the variables used to test hypothesis 1, 2 and 3.

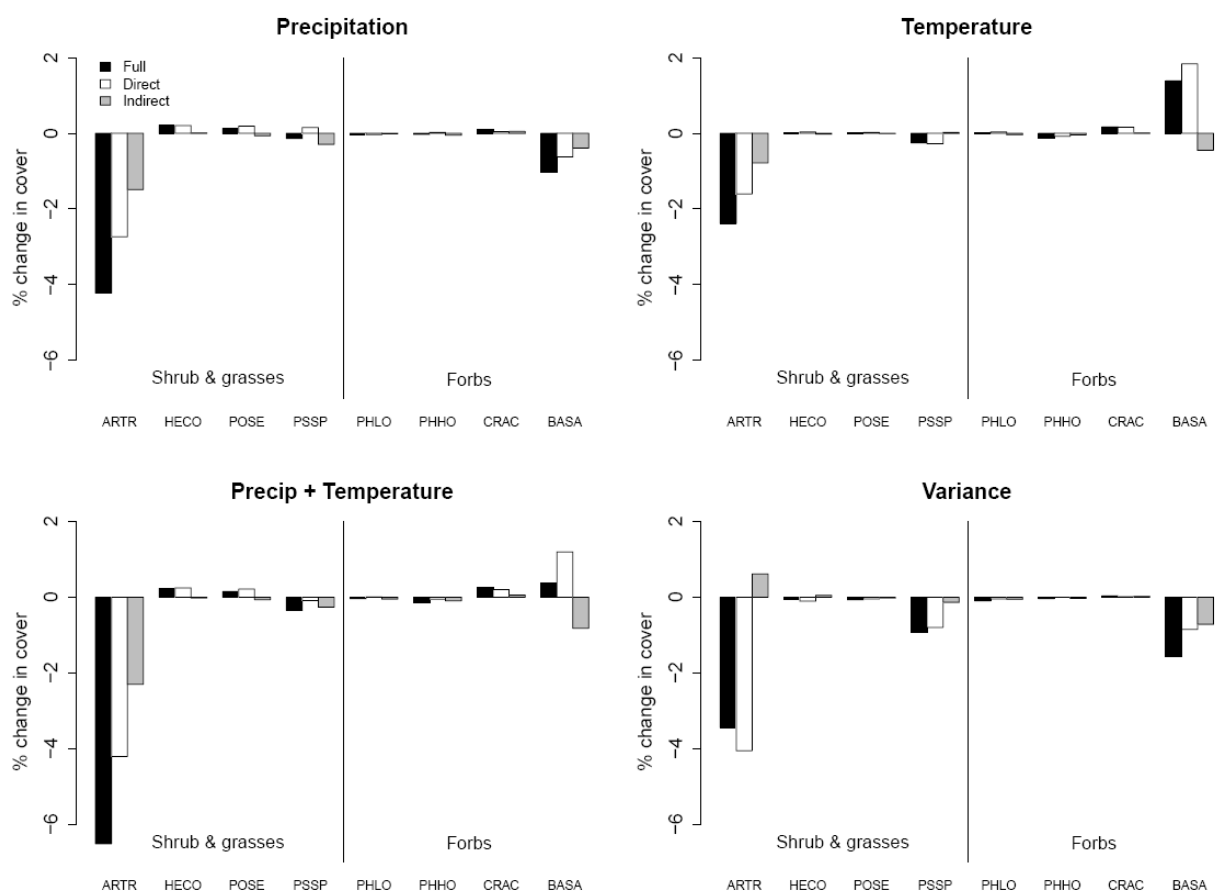


Fig. 4-4. Full, direct and indirect effects of climate perturbation on shrubs, grasses and forbs.

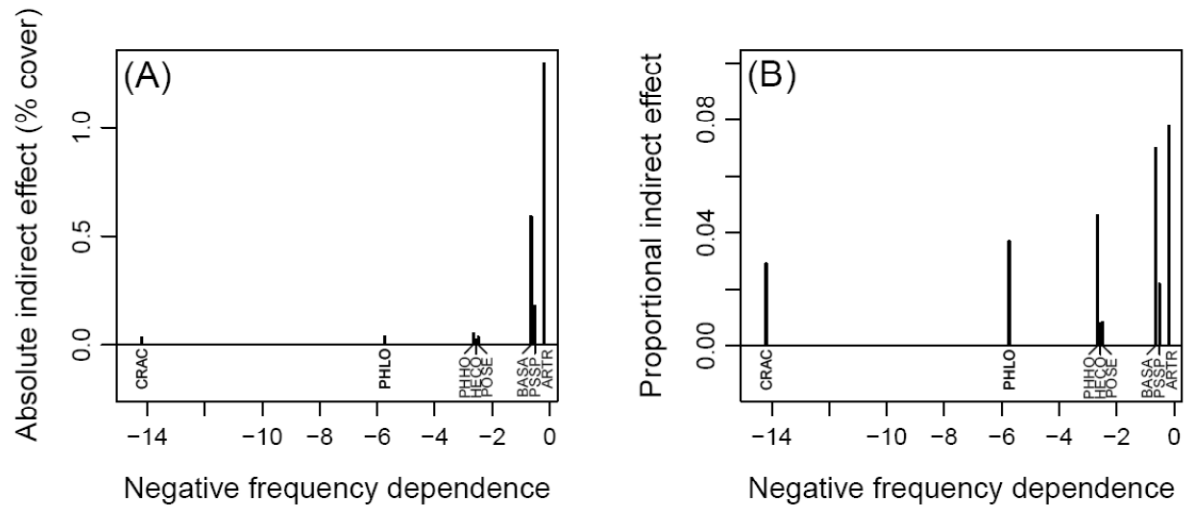


Fig. 4-5. Magnitude of absolute (A) and proportional (B) indirect effects as a function of stabilization strength

CHAPTER 5

CONCLUSION

Our work shows some of the advantages that demographic approaches provide when studying the effect of climatic change on plant communities. We chose the Sagebrush steppe of North America to conduct three climate change studies. First, we used a manipulative experiment to test the hypothesis that in the Sagebrush steppe of Northern Utah, warming increases cheatgrass population growth rate. We used a second field experiment to test the hypothesis that melting snow contributes to the positive effects of rising temperature. Third, using a long-term data set, we build multispecies population models designed to test the hypothesis that rare species are the least prone to the indirect effects of climate. Our results support all of our initial hypotheses. Decomposing population growth rate into its components always proved useful. It showed what demographic mechanisms underlie cheatgrass responses to experimental treatments. Moreover, it was the foundation of our multispecies population models.

Our field experiments provided four insights, all of which indicate that warming improves cheatgrass success in the Sagebrush steppe. First, warming increases cheatgrass population growth rate regardless of elevation. However, warming effects decrease with drought to the point of being non-significant in hot, dry growing seasons such as the one of 2011-2012. Second, snowmelt can contribute to the positive effects of warming by increasing cheatgrass survival. This is supported by the fact that in our experiments warming increased both survival and growth, but snowmelt manipulations only increased

survival. Third, neighbor removal does not influence warming effects. At least in the short term, cheatgrass response to warming should be independent of competing vegetation. Fourth, cheatgrass' positive response to warming is independent of ecotype. High elevation ecotypes performed best regardless of site and treatment.

Our third study provides support for the hypothesis that rare species are the least affected by the indirect effects of climate change. This hypothesis is based on two assumptions. First, species rarity results from strong stabilizing niche differences (Yenni et al. 2012). These are the demographic proxy for niche overlap. Second, the indirect effects of climate change decrease with the strength of stabilizing niche differences (Adler et al. 2012). We found support for both of these assumptions, implying that ecological forecasts of climate change should consider interspecific interactions for common species only.

These results indicate four potential avenues for future research. First, forecasts should model the indirect effect of climate on cheatgrass. Neighbor removal experiments address the effect of competition in current communities. However, in the long run warming will change community abundances. Moreover, cheatgrass is a common species, and the results from our modeling study suggest it should experience strong indirect climate effects. Second, the fact that high elevation cheatgrass ecotypes consistently perform best suggests testing whether this results from maternal or genetic effects. Data from our field experiments show high elevation cheatgrass produce heavier seeds. We hypothesize high elevation seeds do better because of size, but it is not know if this is driven by maternal investment or long-term selection on the genetic variation for seed

size. Third, our novel finding that snowmelt boosts cheatgrass survival suggests testing whether snow kills cheatgrass through the action of snow molds. These pathogens have been proposed as a potential factor of cheatgrass death several decades ago (Klemmedson and Smith 1964). However, no study has directly tested this hypothesis and its relevance to cheatgrass demographic rates. Forth, our finding that rare species are the least affected by indirect climate effects demands that this pattern be tested across different communities and ecosystems. This is because our results cannot test whether these patterns are a general property of plant communities or unique to our study system.

Our work adds to the currently small but promising literature regarding the demographic effects of climate change on plants (Doak and Morris 2010, Salguero-Gomez et al. 2012). We feel our field results make an important contribution to the understanding of warming effects on the cheatgrass life cycle and on its future impacts on Sagebrush steppe ecosystems. Moreover, the main finding of our modeling study warrants further investigation. Confirming that species interactions can be ignored when modeling climate effects on rare species would be an ecological forecasting breakthrough that could save vast amounts of time and money.

References

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- Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in

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Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). *The Botanical Review* 30:226–262.

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APPENDICES

Appendix A - Vegetation of Experimental Sites

Table A-1. Relative cover estimation of the plant species observed at each site

Species	Relative abundance (%)
1340m	
Argopyron cristatum	41
Bromus tectorum	28
Artemisia tridentata	13
Sysimbrium altissimum	6
Bare ground	6
Litter	4
Lactuca serriola	3
1460m	
Poa bulbosa	43
Convulvulus arvensis	19
Bromus tectorum	10
Tragopogon dubius	9
Medicago sativa	6
Bromus japonicus	6
Artemisia tridentata	6
Erodium cicutarium	2
1830m	
Poa bulbosa	39
Wyethia amplexicaulis	19
Myosotis spp.	15
Poa glaucifolia	6
Melica bulbosa	6
Achillea millefolium	4
Danthonia californica	4
Taraxacum officinale	3
Bare ground	3
Rock	1

Appendix B - Effects of Warming on Plot Temperature and Moisture

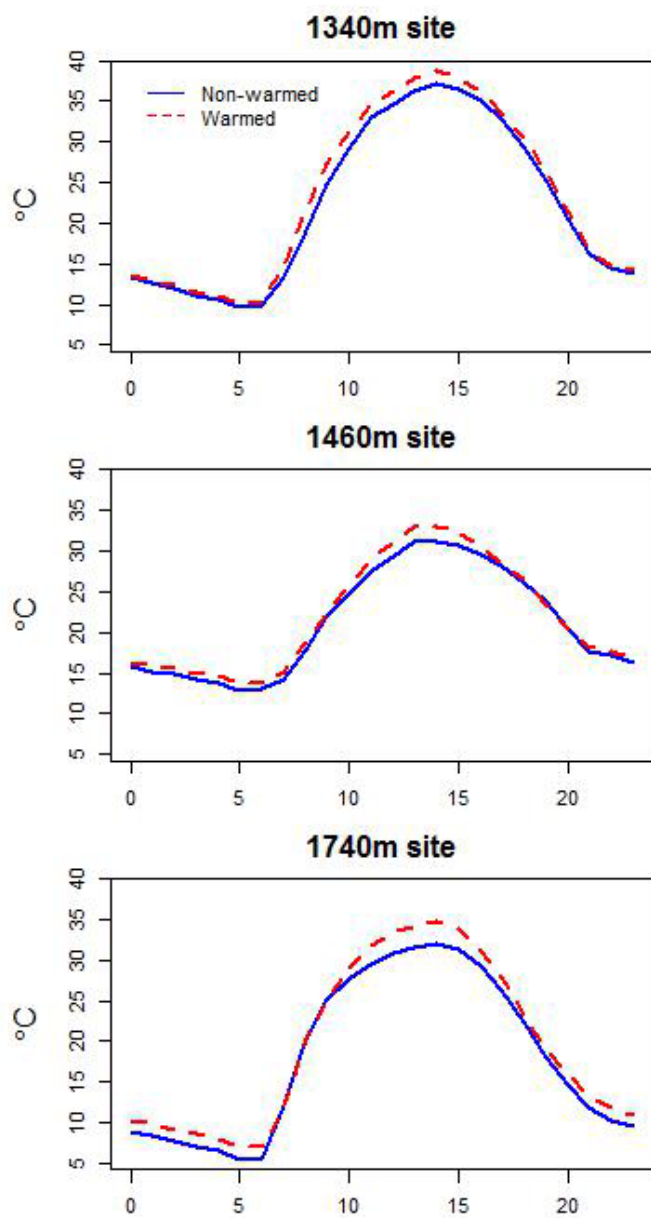


Figure B-1. Average hourly temperatures for the month of June 2010 in warmed and non-warmed plots.

Table B-1. Mixed effect ANOVA of May 2010 soil moisture.

Factors	Num. DF	Den. DF	F-value	p-value
Intercept	1	180	1248.62	<0.0001
Elevation	2	54	106.33	<0.0001
Warming	1	54	0.64	0.4255
Elevation:Warming	2	54	2.37	0.1027

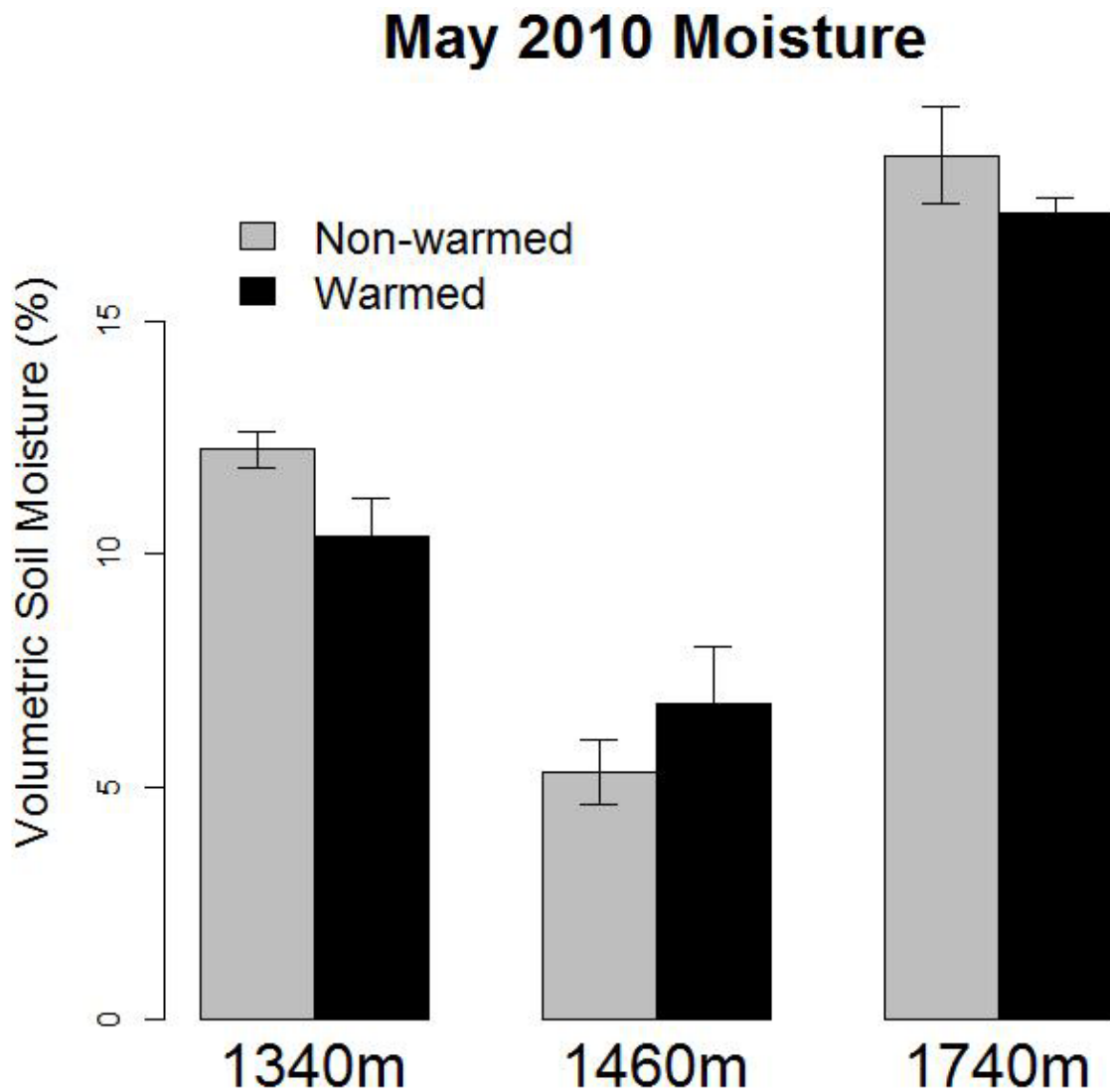


Figure B-2. Volumetric soil moisture in the upper 5cm of soil in control and warming plots at the three sites in May 2010.

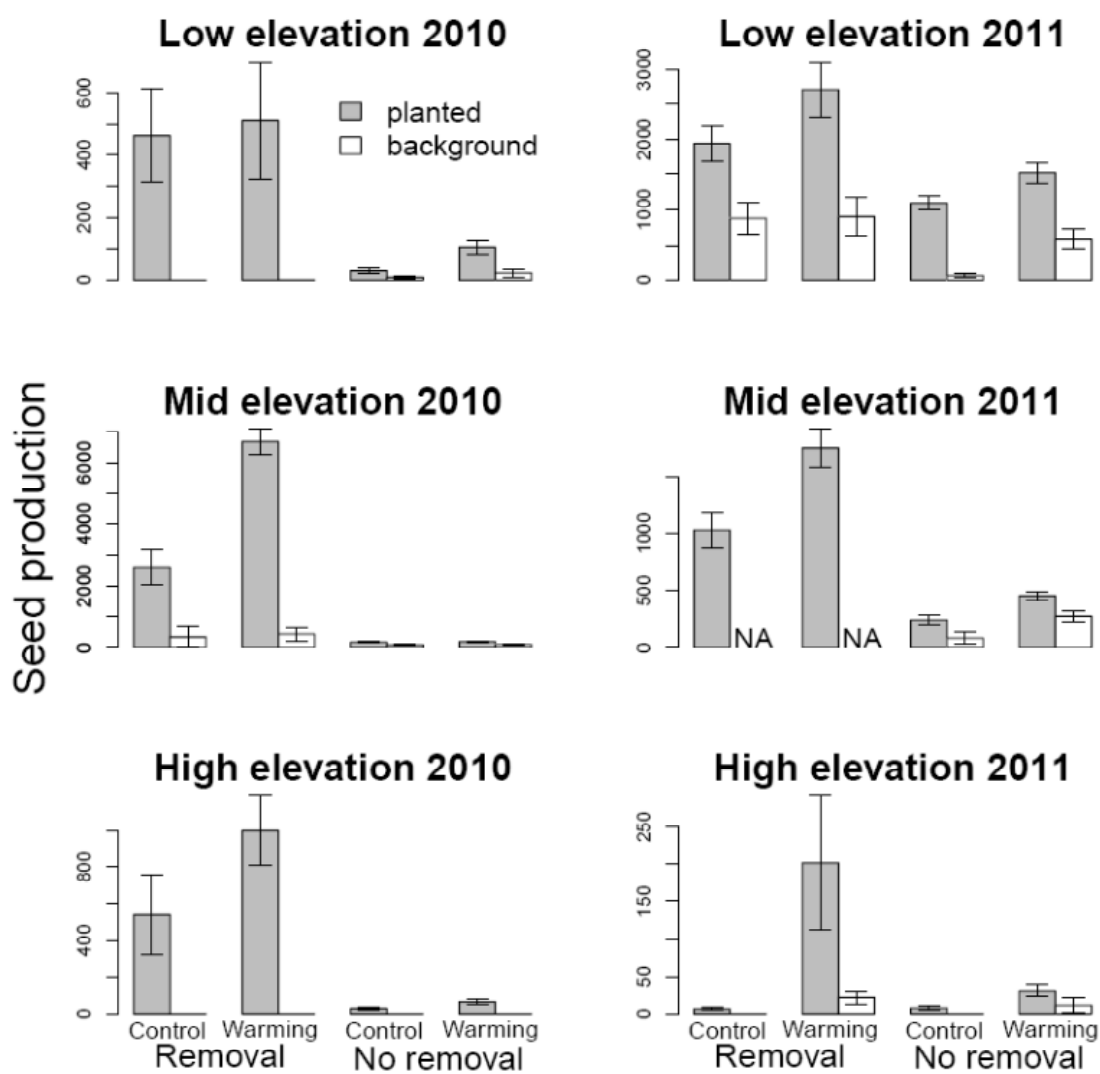
Appendix C- Unplanted Quadrats Seed Production and Estimation of λ 

Figure C-1. Comparison of seed production in planted and unplanted quadrats.

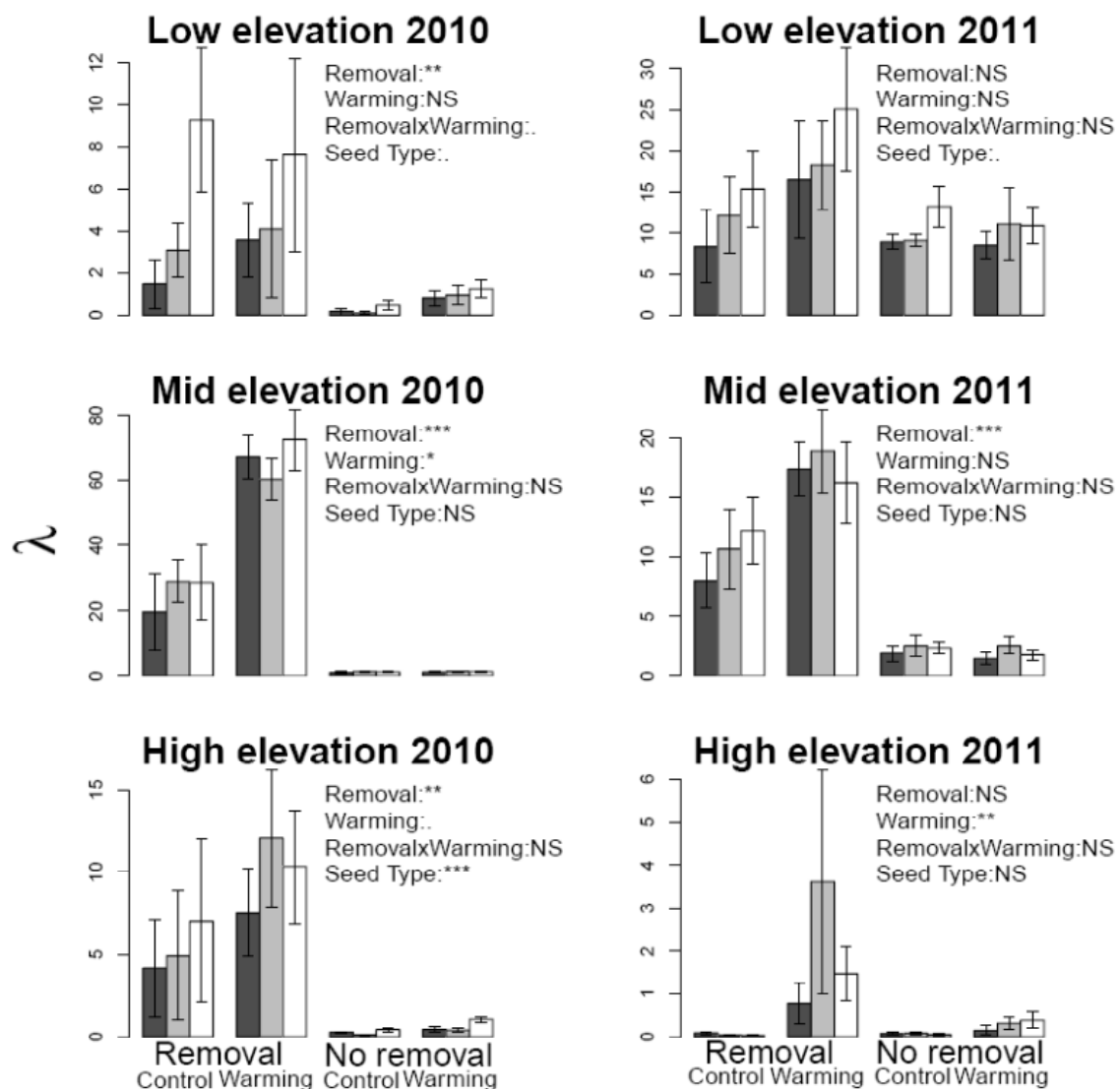


Figure C-2. λ calculated subtracting the seed production of treatment-specific means of unplanted quadrats to the seed production of planted quadrats.

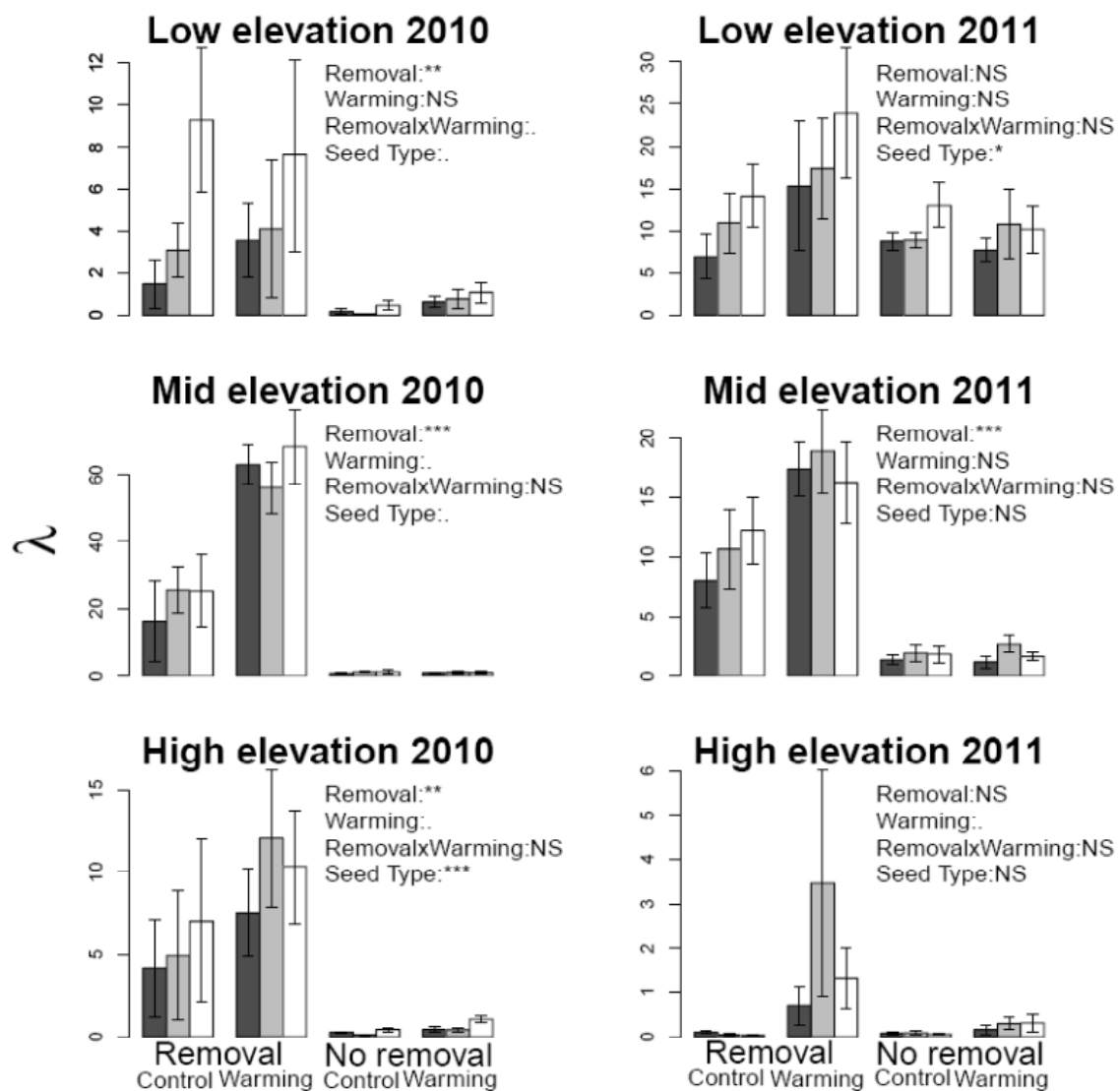


Figure C-3. λ calculated subtracting the plot-specific seed production of unplanted quadrats to the seed production of planted quadrats.

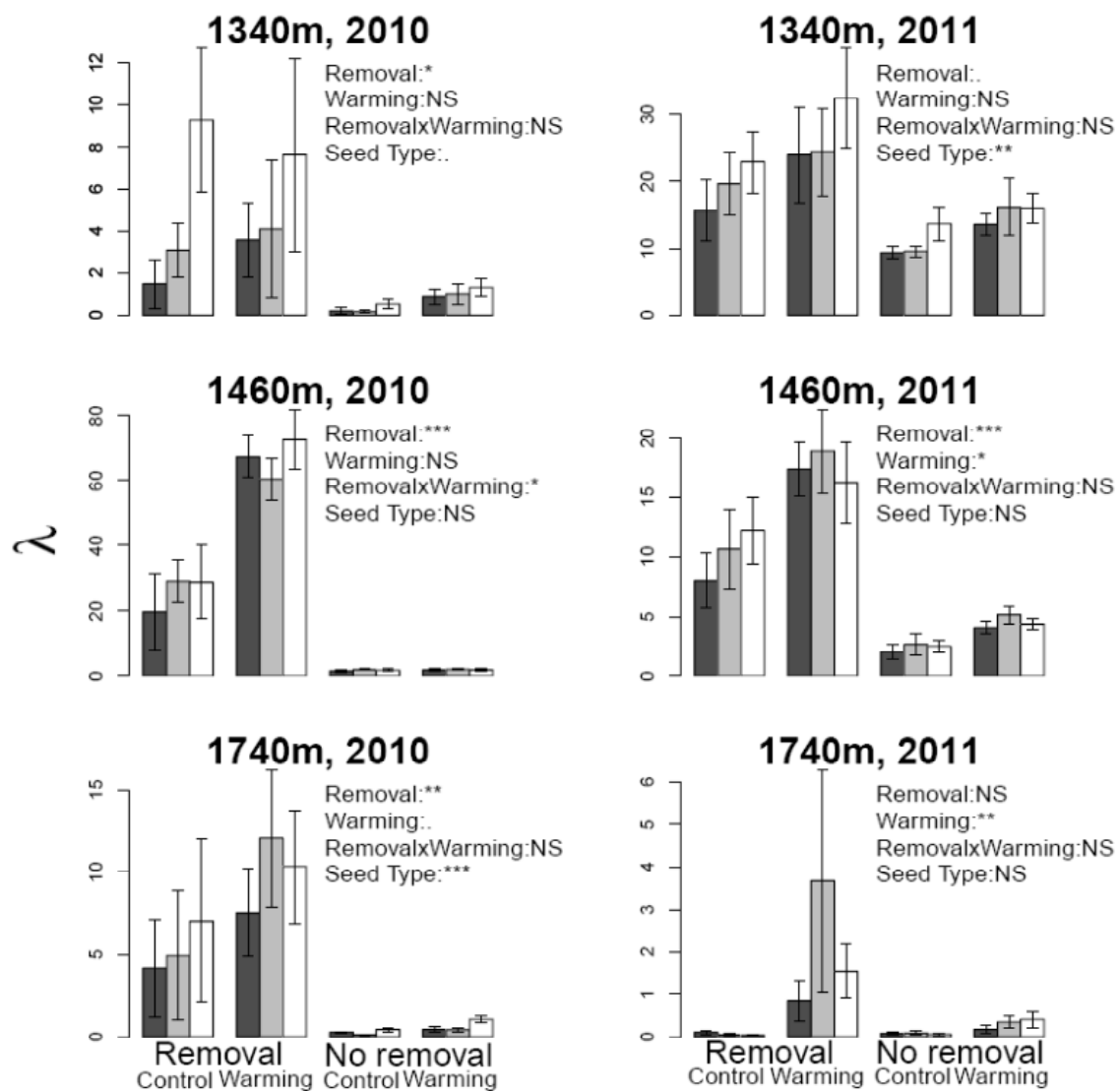


Figure C-4. λ calculated exclusively using the seed production of planted quadrats.

Appendix D - Vital Rates

Table D-1. Results of generalized linear mixed-models fit on 2010 germination data.

2010				
Treatment	Estimate	Std. Error	z value	p-value
1340 m elevation site				
Removal	-0.93324	0.42273	-2.208	0.02727
Warming	-0.28682	0.41148	-0.697	0.485773
Ecotype2	-1.16998	0.21201	-5.518	3.42E-08
Ecotype3	1.18549	0.15017	7.894	2.92E-15
Removal:Warming	1.48578	0.58814	2.526	0.011529
Removal: Ecotype2	1.89329	0.29371	6.446	1.15E-10
Removal: Ecotype3	0.38488	0.24223	1.589	0.112085
Warming: Ecotype2	0.31514	0.29929	1.053	0.292361
Warming: Ecotype3	-0.76501	0.22773	-3.359	0.000781
Removal: Warming: Ecotype2	-0.66136	0.39063	-1.693	0.090446
Removal: Warming: Ecotype3	0.09419	0.32925	0.286	0.774813
1460 m elevation site				
Removal	2.4091	0.7288	3.306	0.000947
Warming	1.0741	0.7249	1.482	0.138399
Ecotype2	-0.6723	0.1672	-4.02	5.81E-05
Ecotype3	0.2849	0.1649	1.728	0.083926
Removal:Warming	-1.0978	1.0273	-1.069	0.285224
Removal: Ecotype2	-0.1666	0.2307	-0.722	0.470356
Removal: Ecotype3	-0.603	0.2319	-2.6	0.009318
Warming: Ecotype2	0.4903	0.217	2.259	0.023868
Warming: Ecotype3	-0.1095	0.216	-0.507	0.612108
Removal: Warming: Ecotype2	0.2059	0.3135	0.657	0.51129
Removal: Warming: Ecotype3	0.5242	0.3175	1.651	0.098695
1830 m elevation site				
Removal	-0.6988	0.4119	-1.697	0.089755
Warming	0.4456	0.4038	1.103	0.26986
Ecotype2	-0.6054	0.1577	-3.839	0.000124
Ecotype3	0.5992	0.138	4.343	1.40E-05
Removal:Warming	0.4379	0.5775	0.758	0.448339
Removal: Ecotype2	0.7375	0.2329	3.167	0.001539
Removal: Ecotype3	0.3001	0.2099	1.43	0.152837
Warming: Ecotype2	0.5139	0.2077	2.475	0.013328
Warming: Ecotype3	-0.5364	0.1921	-2.792	0.005242
Removal: Warming: Ecotype2	-0.724	0.3077	-2.353	0.01864
Removal: Warming: Ecotype3	0.811	0.289	2.806	0.005013

Table D-2. Results of generalized linear mixed-models fit on 2011 germination data.

2011				
Treatment	Estimate	Std. Error	z value	p-value
1340 m elevation site				
Removal	-0.53803	0.30653	-1.755	0.079221
Warming	0.85024	0.33452	2.542	0.011032
Ecotype2	-0.13006	0.16994	-0.765	0.44409
Ecotype3	-0.02986	0.17263	-0.173	0.862654
Removal:Warming	0.10293	0.45938	0.224	0.822718
Removal: Ecotype2	0.07553	0.225	0.336	0.737106
Removal: Ecotype3	0.56605	0.23643	2.394	0.01666
Warming: Ecotype2	-1.50656	0.25993	-5.796	6.79E-09
Warming: Ecotype3	-0.66007	0.27456	-2.404	0.016212
Removal: Warming: Ecotype2	1.27771	0.35348	3.615	0.000301
Removal: Warming: Ecotype3	-0.09348	0.37123	-0.252	0.801193
1460 m elevation site				
Removal	2.0524	0.5964	3.442	0.000578
Warming	0.2939	0.5662	0.519	0.603763
Ecotype2	-1.0861	0.1472	-7.376	1.63E-13
Ecotype3	-0.3241	0.1498	-2.164	0.030464
Removal:Warming	0.152	0.8561	0.178	0.859055
Removal: Ecotype2	-0.4776	0.2846	-1.678	0.093255
Removal: Ecotype3	-0.2078	0.3099	-0.671	0.502385
Warming: Ecotype2	1.1525	0.2195	5.251	1.51E-07
Warming: Ecotype3	0.9155	0.2335	3.921	8.82E-05
Removal: Warming: Ecotype2	-1.0997	0.4293	-2.561	0.010426
Removal: Warming: Ecotype3	-0.6443	0.4834	-1.333	0.182547
1830 m elevation site				
Removal	1.2635	0.1953	6.47	9.81E-11
Warming	1.2623	0.1953	6.465	1.02E-10
Ecotype2	-1.2166	0.1353	-8.992	< 2e-16
Ecotype3	0.5962	0.1567	3.805	0.000142
Removal:Warming	-1.0859	0.3055	-3.555	0.000378
Removal: Ecotype2	-1.0141	0.2233	-4.541	5.60E-06
Removal: Ecotype3	-1.0962	0.2533	-4.328	1.51E-05
Warming: Ecotype2	-0.279	0.2261	-1.234	0.217123
Warming: Ecotype3	-0.8116	0.2606	-3.114	0.001845
Removal: Warming: Ecotype2	0.5877	0.3442	1.707	0.087758
Removal: Warming: Ecotype3	1.1348	0.3979	2.852	0.004343

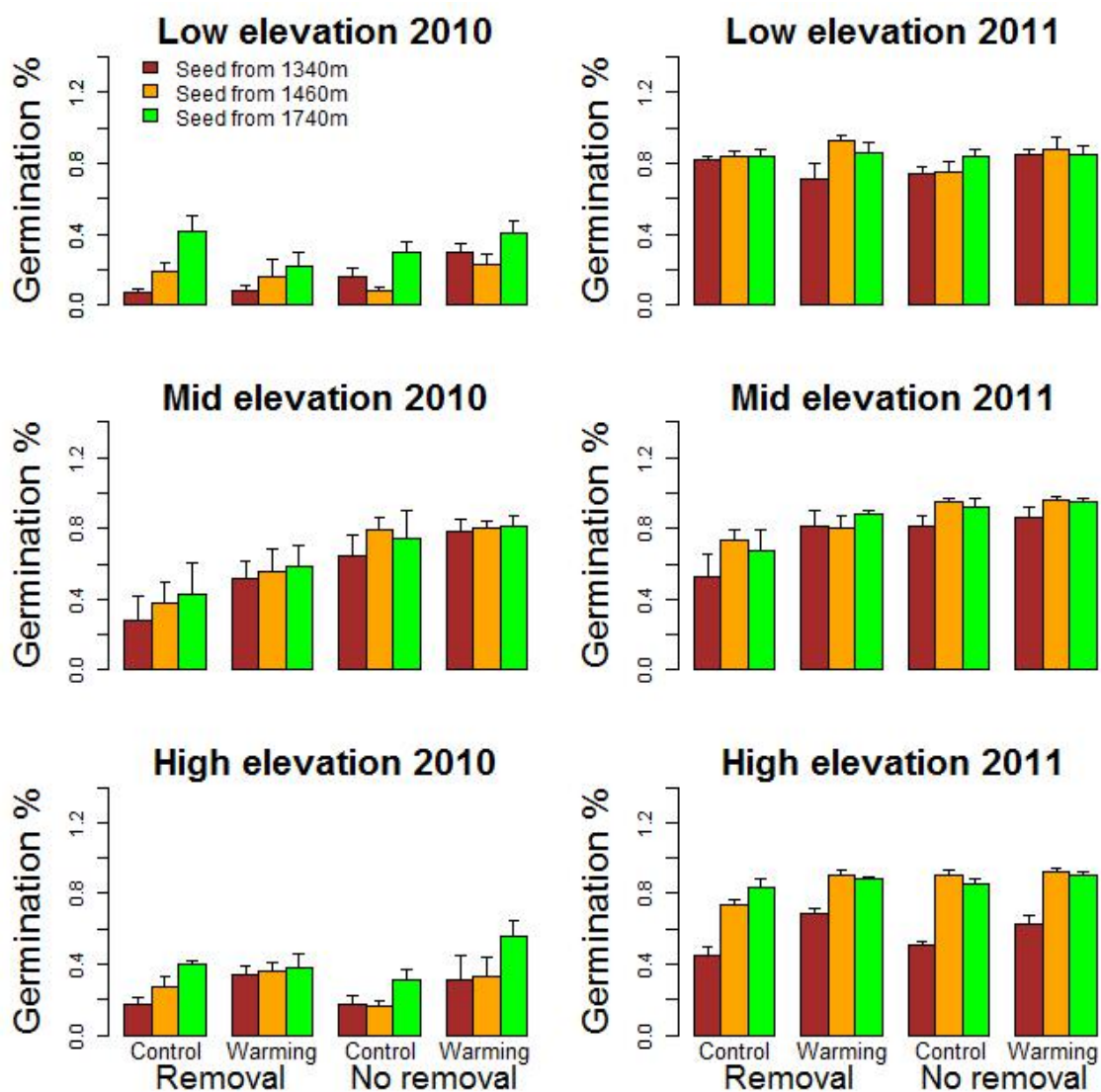


Figure D-1 Percentage of germinating cells by site, year, and treatment.

Table D-3. Results of generalized linear mixed-models fit on 2010 survival data.

2010				
Treatment	Estimate	Std. Error	z value	p-value
1340 m elevation site				
Removal	-0.9541	0.6133	-1.556	0.11979
Warming	-0.8227	0.5716	-1.439	0.15006
Ecotype2	-0.4686	0.4308	-1.088	0.27663
Ecotype3	-0.1069	0.2619	-0.408	0.68329
Removal:Warming	2.0418	0.8353	2.444	0.01451
Removal: Ecotype2	1.2688	0.6032	2.103	0.03543
Removal: Ecotype3	1.2188	0.4706	2.59	0.0096
Warming: Ecotype2	1.2453	0.6049	2.058	0.03954
Warming: Ecotype3	1.2195	0.4258	2.864	0.00419
Removal: Warming: Ecotype2	-2.0951	0.7856	-2.667	0.00766
Removal: Warming: Ecotype3	-1.8045	0.6343	-2.845	0.00444
1460 m elevation site				
Removal	0.1361	0.3727	0.365	0.715
Warming	0.2595	0.3953	0.656	0.5117
Ecotype2	-0.2365	0.3157	-0.749	0.4538
Ecotype3	0.2991	0.313	0.956	0.3392
Removal:Warming	0.0458	0.5222	0.088	0.9301
Removal: Ecotype2	-0.3571	0.3785	-0.944	0.3454
Removal: Ecotype3	0.4815	0.4071	1.183	0.2369
Warming: Ecotype2	1.01	0.4667	2.164	0.0304
Warming: Ecotype3	0.4874	0.4518	1.079	0.2806
Removal: Warming: Ecotype2	-0.877	0.5577	-1.573	0.1158
Removal: Warming: Ecotype3	-1.4566	0.5697	-2.557	0.0106
1830 m elevation site				
Removal	-1.05999	0.57308	-1.85	0.06437
Warming	0.7914	0.58683	1.349	0.17746
Ecotype2	0.61808	0.45652	1.354	0.17577
Ecotype3	0.06225	0.31544	0.197	0.84355
Removal:Warming	-0.0998	0.80854	-0.123	0.90177
Removal: Ecotype2	-0.26359	0.56604	-0.466	0.64146
Removal: Ecotype3	0.89959	0.4473	2.011	0.04431
Warming: Ecotype2	-1.53568	0.5686	-2.701	0.00692
Warming: Ecotype3	-0.59323	0.46787	-1.268	0.20482
Removal: Warming: Ecotype2	1.02617	0.71944	1.426	0.15377
Removal: Warming: Ecotype3	0.5213	0.63246	0.824	0.4098

Table D-4. Results of generalized linear mixed-models fit on 2011 survival data.

2011				
Treatment	Estimate	Std. Error	z value	p-value
1340 m elevation site				
Removal	-0.226	0.3815	-0.592	0.5536
Warming	0.7611	0.4307	1.767	0.0772
Ecotype2	0.8335	0.3714	2.244	0.0248
Ecotype3	0.748	0.3612	2.071	0.0383
Removal:Warming	0.1204	0.6028	0.2	0.8416
Removal: Ecotype2	-0.7125	0.4727	-1.507	0.1317
Removal: Ecotype3	-0.4582	0.4661	-0.983	0.3255
Warming: Ecotype2	-1.344	0.5346	-2.514	0.0119
Warming: Ecotype3	-0.7276	0.5458	-1.333	0.1825
Removal: Warming: Ecotype2	0.8095	0.7056	1.147	0.2513
Removal: Warming: Ecotype3	-0.1032	0.7108	-0.145	0.8846
1460 m elevation site				
Removal	-1.63872	0.46932	-3.492	0.00048
Warming	1.04816	0.50827	2.062	0.039187
Ecotype2	-0.90153	0.2207	-4.085	4.41E-05
Ecotype3	-0.05915	0.22337	-0.265	0.791154
Removal:Warming	0.57345	0.68719	0.834	0.404015
Removal: Ecotype2	0.73674	0.26408	2.79	0.005273
Removal: Ecotype3	-0.27615	0.26359	-1.048	0.294796
Warming: Ecotype2	0.66781	0.36283	1.841	0.065687
Warming: Ecotype3	0.24484	0.3778	0.648	0.516946
Removal: Warming: Ecotype2	-1.41929	0.4259	-3.332	0.000861
Removal: Warming: Ecotype3	-0.25129	0.43876	-0.573	0.566833
1830 m elevation site				
Removal	0.5935	0.7435	0.798	0.4248
Warming	1.8364	0.7316	2.51	0.0121
Ecotype2	0.8011	0.3345	2.395	0.0166
Ecotype3	-0.3737	0.3541	-1.055	0.2913
Removal:Warming	-0.2097	1.0162	-0.206	0.8365
Removal: Ecotype2	-0.556	0.4274	-1.301	0.1933
Removal: Ecotype3	0.4778	0.4266	1.12	0.2628
Warming: Ecotype2	-0.9482	0.3829	-2.476	0.0133
Warming: Ecotype3	0.1389	0.3955	0.351	0.7253
Removal: Warming: Ecotype2	-0.0841	0.5049	-0.167	0.8677
Removal: Warming: Ecotype3	-0.343	0.489	-0.702	0.483

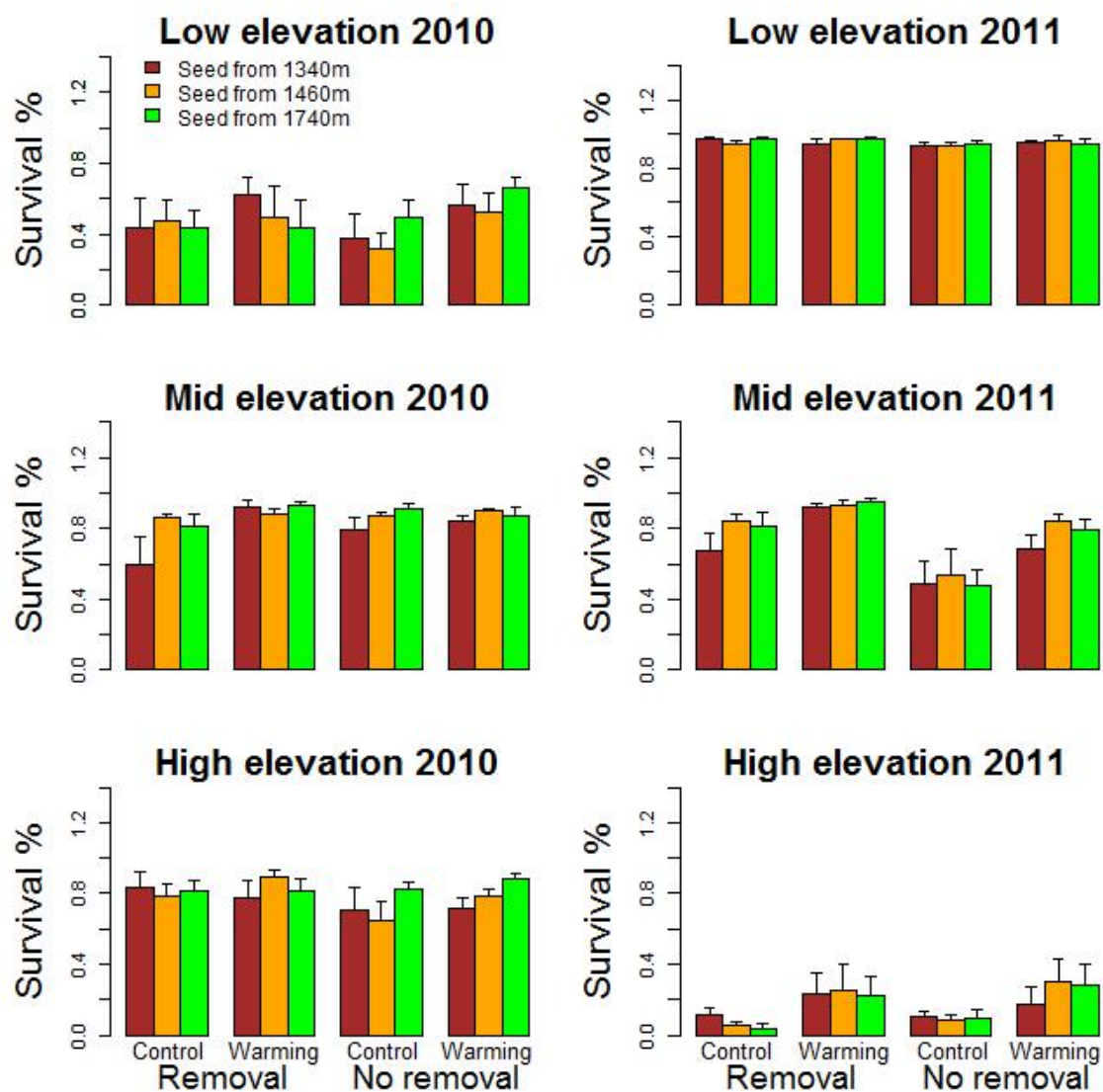


Figure D-2. Percentage of surviving individuals by site, year, and treatment.

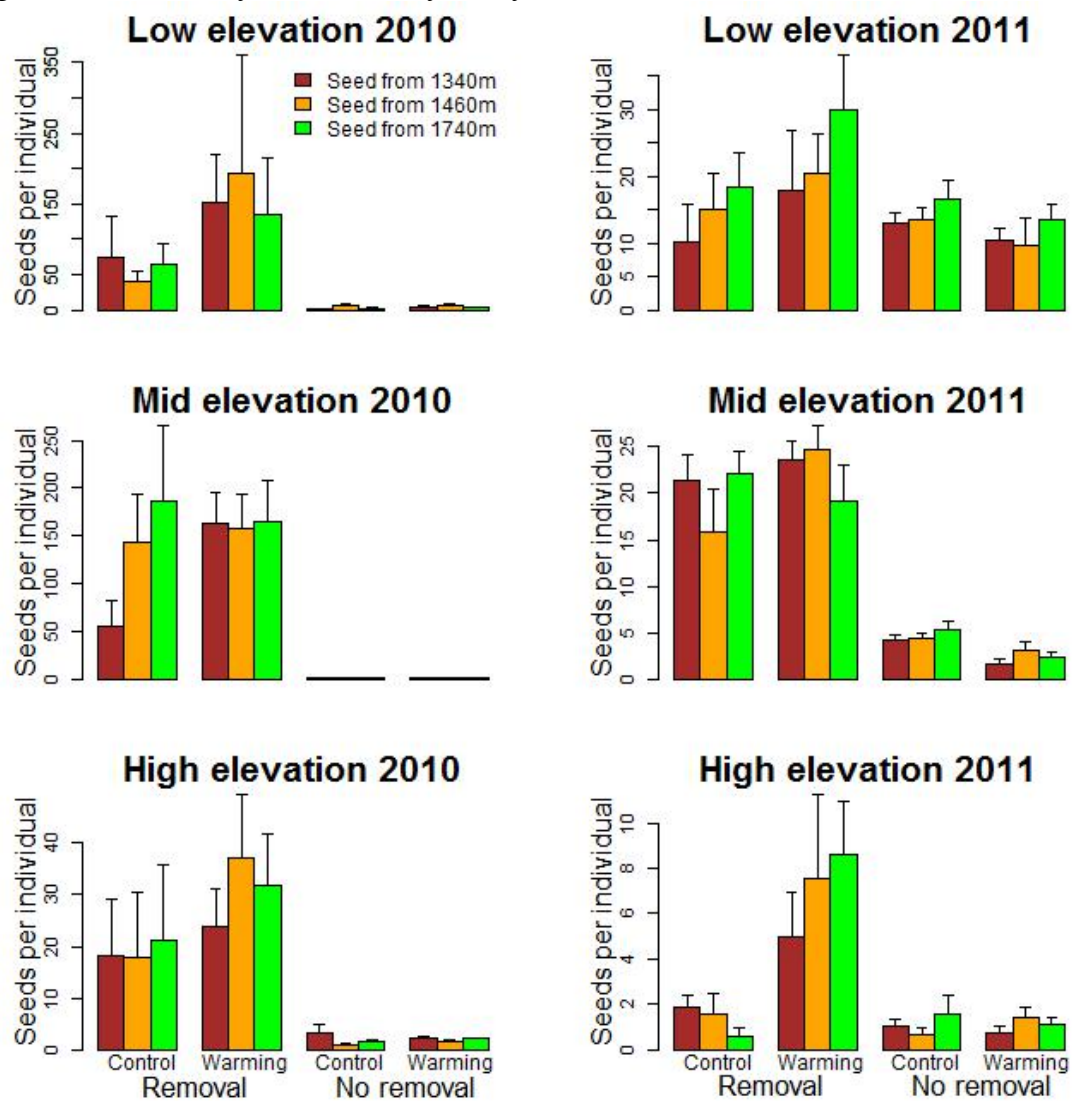
Table D-5. Results of linear mixed-models fit on 2010 fecundity data.

2010				
Treatment	Num. DF	Den. DF	F-value	p-value
1340 m elevation site				
Removal	1	16	8.8249	0.0090
Warming	1	16	1.3276	0.2661
Ecotype	2	32	0.3760	0.6896
Removal x warming	1	16	1.8523	0.1924
Removal x Ecotype	2	32	0.2248	0.7999
Warming x Ecotype	2	32	2.9745	0.0653
Removal x Warming x Ecotype	2	32	0.1468	0.8641
1460 m elevation site				
Removal	1	16	60.9664	<0.0001
Warming	1	16	0.0028	0.9588
Ecotype	2	32	0.9315	0.4044
Removal x warming	1	16	4.9462	0.0409
Removal x Ecotype	2	32	3.1543	0.0562
Warming x Ecotype	2	32	2.3187	0.1147
Removal x Warming x Ecotype	2	32	1.7404	0.1917
1830 m elevation site				
Removal	1	16	18.0331	0.0006
Warming	1	16	2.4592	0.1364
Ecotype	2	32	4.1626	0.0247
Removal x warming	1	16	1.6289	0.2201
Removal x Ecotype	2	32	1.3768	0.2669
Warming x Ecotype	2	32	1.4237	0.2557
Removal x Warming x Ecotype	2	32	0.4524	0.6401

Table D-6. Results of linear mixed-models fit on 2011 fecundity data.

2011				
Treatment	Num. DF	Den. DF	F-value	p-value
1340 m elevation site				
Removal	1	16	0.4729	0.5015
Warming	1	16	0.8826	0.3615
Ecotype	2	32	1.9469	0.1593
Removal x warming	1	16	0.4436	0.5149
Removal x Ecotype	2	32	1.3700	0.2686
Warming x Ecotype	2	32	1.4620	0.2468
Removal x Warming x Ecotype	2	32	0.0390	0.9618
1460 m elevation site				
Removal	1	16	55.4150	<0.0001
Warming	1	16	0.1987	0.6617
Ecotype	2	32	0.1065	0.8993
Removal x warming	1	16	8.0148	0.0120
Removal x Ecotype	2	32	1.8967	0.1666
Warming x Ecotype	2	32	2.1449	0.1336
Removal x Warming x Ecotype	2	32	0.6442	0.5318
1830 m elevation site				
Removal	1	16	2.2325	0.1546
Warming	1	16	4.7542	0.0445
Ecotype	2	32	0.0067	0.9934
Removal x warming	1	16	4.7035	0.0455
Removal x Ecotype	2	32	0.8828	0.4235
Warming x Ecotype	2	32	0.9199	0.4088
Removal x Warming x Ecotype	2	32	2.6864	0.0835

Figure D-3. Fecundity differences by site, year, and treatment.



Appendix E - Supplementary Figures and Tables for The Snowmelt Experiment

Table E-1. Results of the linear model relating the increase in temperature caused by warming treatments to soil moisture at 5 cm depth.

Factors	Estimate	Std. Error	t value	p value	
Intercept	13.7347	0.4430	31.0026	<0.0001	***
Moisture	-39.7197	2.2995	-17.2728	<0.0001	***

Table E-2. Results of Tukey's HSD tests on population growth rate differences among treatments. Results refer to population growth rate values estimated subtracting plot-specific seed production in unplanted quadrats.

Contrast	Estimate	z value	p value	
2011				
Snowmelt – Control	1.2813	3.7914	0.0004	***
Warming – Control	2.1356	5.7487	<0.0001	***
Warming – Snowmelt	0.8543	2.4114	0.0419	*
2012				
Snowmelt – Control	0.4999	3.0238	0.0064	**
Warming – Control	0.1219	0.4227	0.9034	
Warming – Snowmelt	-0.3780	-1.3142	0.3772	

Table E-3. Results of Tukey's HSD tests on differences in fecundity among treatments.

Contrast	Estimate	z_value	p.value	
2011				
Snowmelt - Control	0.2900	1.1327	0.4934	
Warming - Control	1.1187	4.1809	0.0001	***
Warming - Snowmelt	0.8288	2.9519	0.0087	**
2012				
Snowmelt - Control	0.1240	1.0454	0.5437	
Warming - Control	0.2411	1.4737	0.2992	
Warming - Snowmelt	0.1172	0.7013	0.7597	

Table E-4. Results of Tukey's HSD tests on differences in survival among treatments.

Contrast	Estimate	z_value	p.value	
2011				
Snowmelt - Control	1.747802	4.475319	<0.0001	***
Warming - Control	2.139018	5.469919	<0.0001	***
Warming - Snowmelt	0.391216	1.000928	0.5763	
2012				
Snowmelt - Control	1.1907	3.7157	0.0006	***
Warming - Control	-0.0176	-0.0552	0.9983	
Warming - Snowmelt	-1.2082	-3.7672	0.0005	***

Table E-5. Results of Tukey's HSD tests on differences in germination among treatments.

Contrast	Estimate	z_value	p.value	
2011				
Snowmelt - Control	0.3089	2.1099	0.0878	
Warming - Control	0.2099	1.4461	0.3173	
Warming - Snowmelt	-0.0990	-0.6658	0.7833	
2012				
Snowmelt - Control	0.3025	1.7320	0.1932	
Warming - Control	0.2828	1.6176	0.2382	
Warming - Snowmelt	-0.0197	-0.1114	0.9932	

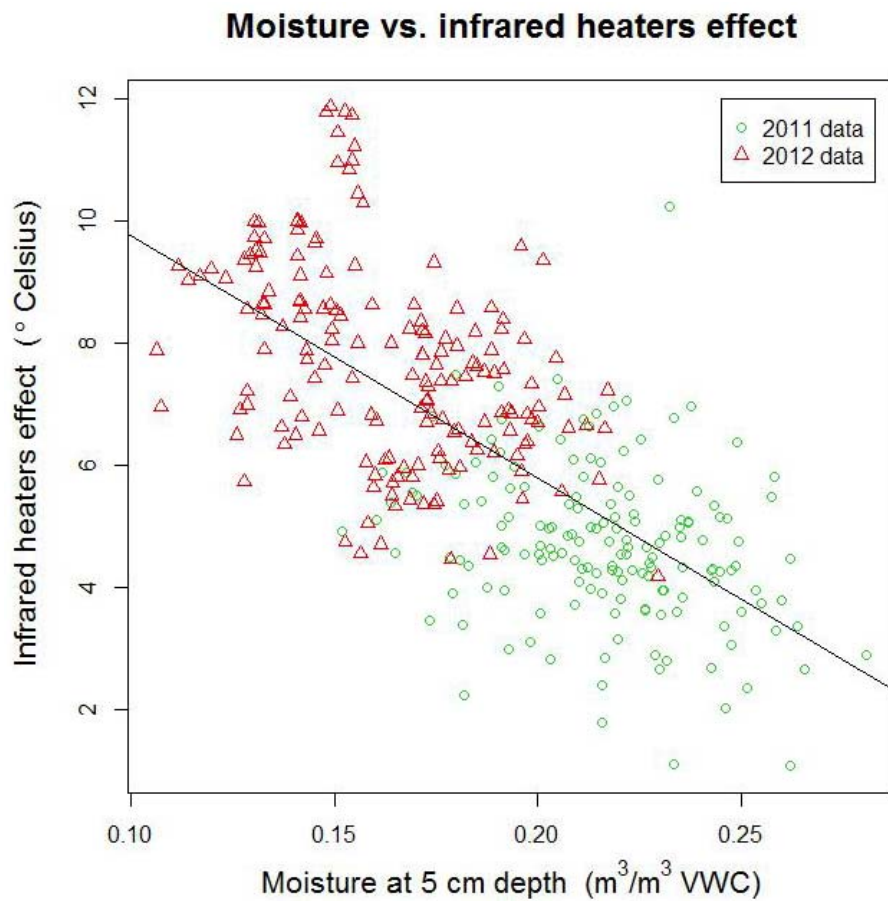


Figure E-1. Daily average temperature increase caused by infra red heaters versus soil moisture at 5 cm depth.

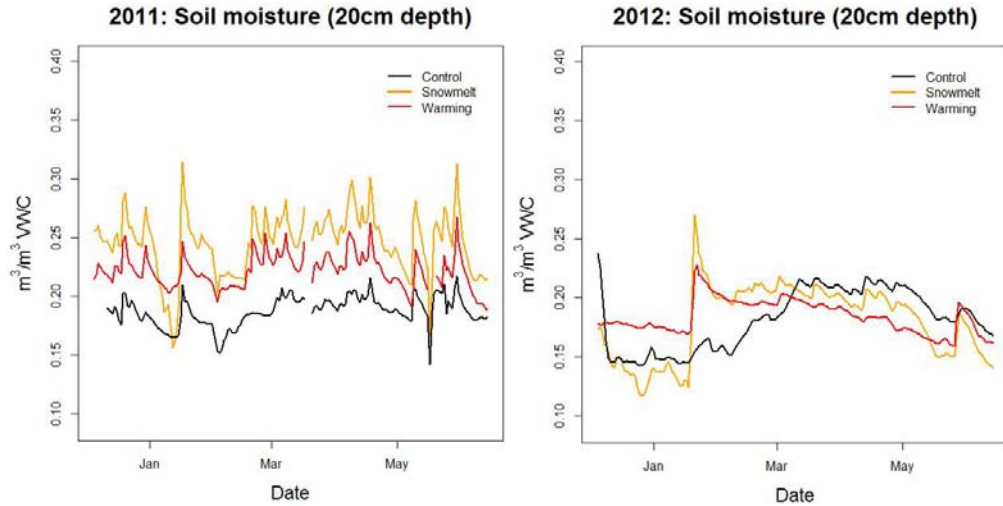


Figure E-2. Differences in volumetric water content at 20 cm depth among warming, snowmelt, and control plots between mid December and mid June.

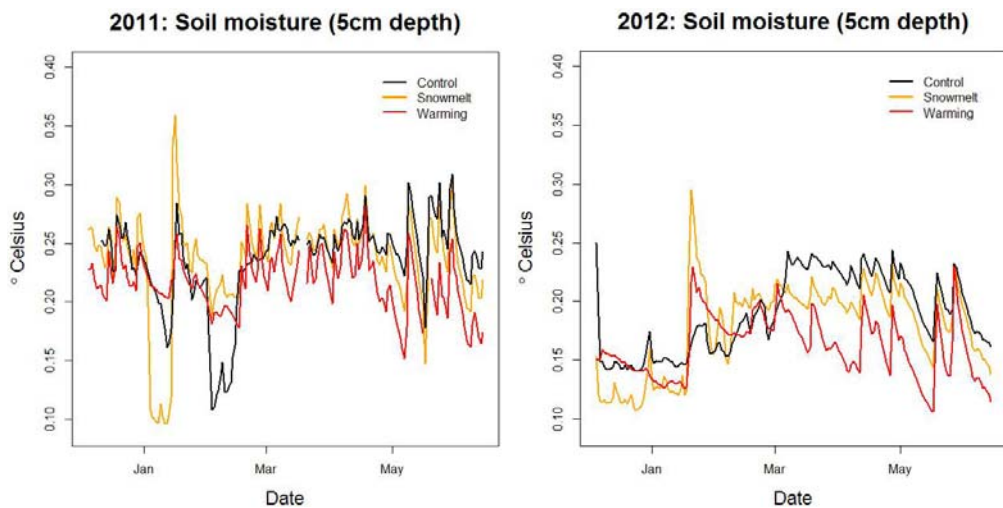


Figure E-3. Differences in volumetric water content (VWC) at 5 cm depth among warming, snowmelt, and control plots between mid December and mid June.

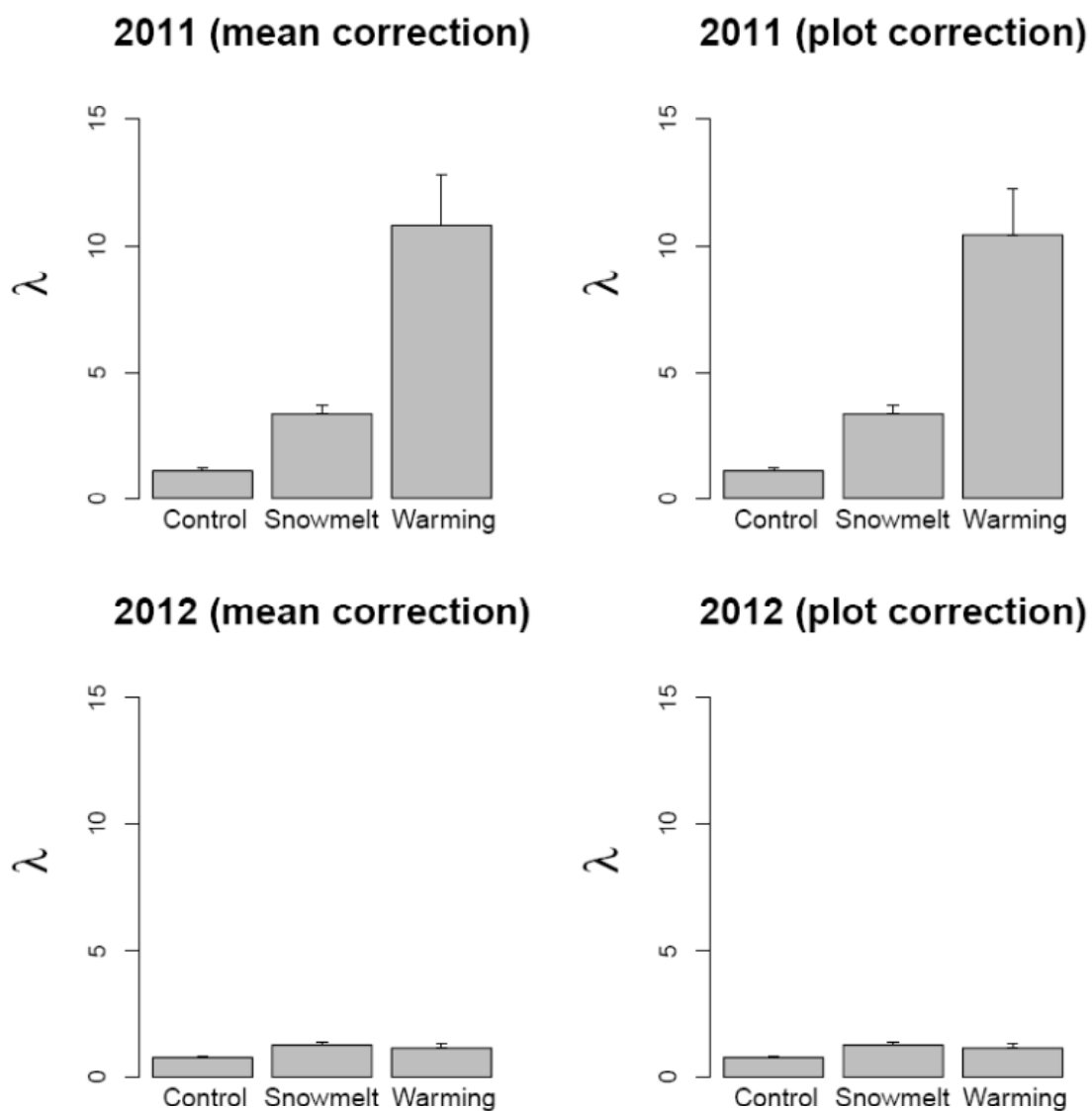


Figure E-4. Comparison between values of population growth rate estimated subtracting treatment-specific averages (left column) and plot-specific values (right column) of seed production in unplanted quadrats.

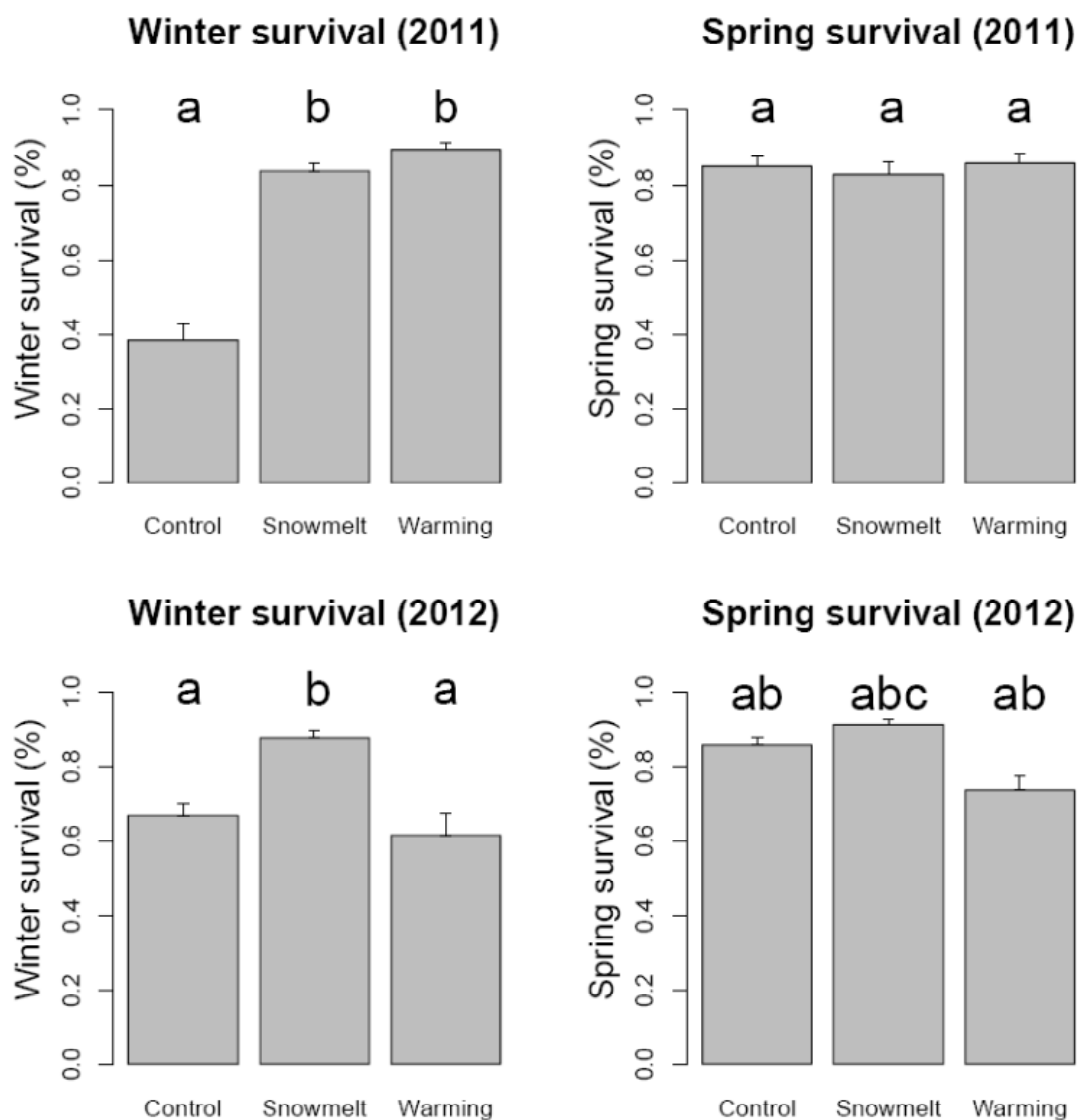


Figure E-5. Winter and spring survival rates by treatment and year. Letters refer to groups that significantly differ according to Tukey tests.

Appendix F – Proportional indirect effects of climate

Our objective was to identify the expression that determines the size of proportional indirect effects in the two-species annual plant model (Watkinson 1980) employed by Adler et al. (2012). The following two-equation system determines the model:

$$N_{1,t+1} = \frac{\lambda_1 N_{1,t}}{1 + \alpha_{11} N_{1,t} + \alpha_{12} N_{2,t}}$$

$$N_{2,t+1} = \frac{\lambda_2 N_{2,t}}{1 + \alpha_{22} N_{2,t} + \alpha_{21} N_{1,t}}$$

Where $N_{i,t}$ is the abundance of species i at time t , λ_i is its intrinsic rate of increase, and α_{ij} is the per capita competitive effect of species j on species i . The absolute indirect effect of climate change on species 1 is the sensitivity of that species' equilibrium abundance to an infinitesimal change in its competitor's λ . Adler et al. (2012) showed that:

$$\frac{\partial N_1^*}{\partial \lambda_2} = \frac{-\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}$$

Where N_1^* is the equilibrium abundance of species 1. To calculate the *proportional* indirect effects of climate change, we scaled this absolute indirect effect by N_1^* . The simplified expression is:

$$\frac{1}{N_1^*} \frac{\partial N_1^*}{\partial \lambda_2} = \frac{-\alpha_{12}}{\alpha_{22}(\lambda_1 - 1) - \alpha_{12}(\lambda_2 - 1)}$$

The proportional indirect effects experienced by species 1 do not exclusively depend on the strength of stabilizing niche differences. They depend on fitness differences with

species 2, and on the inter and intra specific effects of species 2. The presence of inter and intraspecific effects of species 2 on species 1 suggests stabilizing niche differences still have a role in determining proportional indirect effects. However, we cannot weight the importance of stabilizing niche differences relative to other factors in determining the size of proportional indirect effects.

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Appendix G – Detailed methods

Survival and growth models

We modeled survival and growth as a function of individual plants' state, crowding by surrounding species, climatic variables, random variation among years and random variation among spatial locations. The state of individual plants is given by size in shrubs and grasses and by age in forbs. Individual crowding is calculated separately for each neighboring species using the formula:

$$w_{ijm,t} = \sum_k e^{-\alpha_{jm} d_{ijkm,t}^2} u_{km,t} (1)$$

Where $w_{ijm,t}$ is the crowding experienced by individual i of species j from species m in year t . Every individual k of species m exerts an effect that depends on u , its size, on d , its distance from the focal plant and on α , the decay of neighbor competitive effect with distance. This formula assumes a Gaussian competition kernel whereby the decrease in competitive effects is proportional to the square of distance. Note that because we do not have size information on forbs, for these species we assume u is equal to 1 cm².

Neighborhood crowding values are identical for both survival and growth. This is because a previous study (Adler et al. 2010) showed α values for survival and growth are almost equal. Survival probability was modeled with a combination of the following terms:

$$\text{Logit}(S_{ijg,t}) = \eta_{j,t}^S + \Phi_{jg}^S + \beta_{j,t}^S m_{ij,t} + \omega_j^S w_{ij,t}^S + \Omega_j^S w_{ij,t}^S u_{ij,t} + \gamma^S C_t + \Gamma^S C_t u_{ij,t} (2)$$

Here, S superscripts indicate the coefficients refer to the survival model. $\eta_{j,t}^S$ is a time-dependent intercept, Φ_{jg}^S is the group effect, $\beta_{j,t}^S$ is the coefficient describing the

effect of individual state, $m_{ij,t}$ refers to individual state (age for forbs, size for the shrub and grasses), ω is the vector of species-specific competition coefficients that describe the effect of crowding \mathbf{w} , Ω are coefficients that describe the interaction between crowding and individual state, γ determines the effect of \mathbf{C} , the climate variables, and Γ are the coefficients for the interaction between individual state and the climate variables. The terms of the growth model (referred to as G) are the same:

$$u_{ijg,t+1} = \eta_{j,t}^G + \Phi_{jg}^G + \beta_{j,t}^G u_{ij,t} + \omega_j^G \mathbf{w}_{ij,t}^G + \gamma^G \mathbf{C}_t + \Gamma^G \mathbf{C}_t u_{ij,t} + \varepsilon_{ij,t}^G \quad (3)$$

Because growth models are fit for shrub and grasses only, individual state corresponds to size, $u_{ij,t}$. $\varepsilon_{ij,t}^G$ refers to variance, which we model as a nonlinear function of predicted size:

$$Var(\varepsilon_{ij,t}^G) = ae^{bu_{ij,t+1}} \quad (4)$$

We fit equations in two steps: first, equation (3) under the assumption of equal residuals, then equation (4) with non-linear least square regression performed on the squared residuals of the predicted values.

We used these models to select predictors unrelated to climatic variables. We considered two questions. First, what parameters should vary through time? Our equations allow the intercept, η , size, β , and crowding coefficients to vary through time. Second, should there be an interaction between individual size and crowding effect? To address these questions, we fit the seven models presented in Table G-1. We fit these models using the `glm()` function in R and assuming all predictors were fixed effects. To meet normality assumptions for the state variable of the four dominants, we fit models

with the natural logarithm of individual size values. The model with lowest AIC indicated the predictor variables to include in the final mixed-effect model. Note that in these models we assume that α varies with neighbor species, not focal species (Adler et al. 2010).

We used the predictors selected in this step with the exception of $\eta_{j,t}$ to choose climate variables in survival and growth models. Climate variables were chosen in a stepwise backward fashion. Last, we fit the final mixed-effect models (see methods section). We fit equation (2) with `glmer()` and equation (3) with `lmer()`, both contained in the lme4 R package. Last, we checked the correlation between the climate coefficients and random year effects. These correlations were consistently below 0.5, showing random year effects are independent of climatic variables.

Recruitment

We modeled recruitment employing the same variables used in Adler et al. (2012). We used a hierarchical Bayesian approach to predict new recruits based on plant abundances within and outside focal quadrats. We modeled recruits at the quadrat level because we could not identify recruits' parents. The number of species j new recruits y observed at quadrat q in year $t+1$ follows a negative binomial distribution:

$$y_{jq,t+1} \sim \text{NegBin}(\lambda_{jq,t}, \theta)$$

Where λ is the expected number of recruits and θ is the dispersion parameter. We calculated λ with the following Ricker (1954) model:

$$\lambda_{jq,t+1} = N'_{jq,t} e^{(\eta_t^R + \phi_g^R + \omega^R N'_{qt} + \gamma^R C_t)}$$

Where N' is the effective abundance, and R identifies recruitment specific coefficients. Abundance values were measured as absolute cover for shrubs and grasses, and as absolute density for forbs. The effective cover accounted for the effect of species abundances in the focal quadrat and in the adjacent ones:

$$N'_{jqt} = p_j N_{jqt} + (1 - p_j) \bar{N}_{jgt}$$

Here, p is the ‘mixing fraction’. This is a proportion by which species abundances in the focal quadrat determine new recruits relative to the average abundances of the surrounding quadrats (the group). We fit a mixed-effect model using WinBUGS (Lunn et al. 2000) where group and year were random effects. We used five climate variables, the same used in survival and growth models except for the two temperature x precipitation interactions. We used uninformative priors and ran 20,000 Markov Chain Monte Carlo simulations with a 10,000 burn in period. We checked for the convergence of two parameter chains based on whether Brooks and Gelman’s (1998) potential scale reduction factor (\hat{r}) values were <1.1 .

Table G-1. Model structures compared to select variables unrelated to climate. Notation follows text, except for ω_j , which represents coefficients for interactions not mentioned in the text.

$Response_{ijg,t} = \Phi_{jg} + \beta_{j,t}u_{ij,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t} + \omega_j w_{ij,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t} + \omega_j w_{ij,t} + \Omega_j w_{ij,t}u_{ij,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t} + \omega_j w_{ij,t} + \gamma_{j,t}u_{ij,t}\eta_{j,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t} + \omega_j w_{ij,t} + \gamma_{j,t}u_{ij,t}\eta_{j,t} + \Omega_j w_{ij,t}\eta_{j,t}$
$Response_{ijg,t} = \eta_{j,t} + \Phi_{jg} + \beta_{j,t}u_{ij,t} + \omega_j w_{ij,t} + \gamma_{j,t}u_{ij,t}\eta_{j,t} + \Omega_j w_{ij,t}u_{ij,t}$

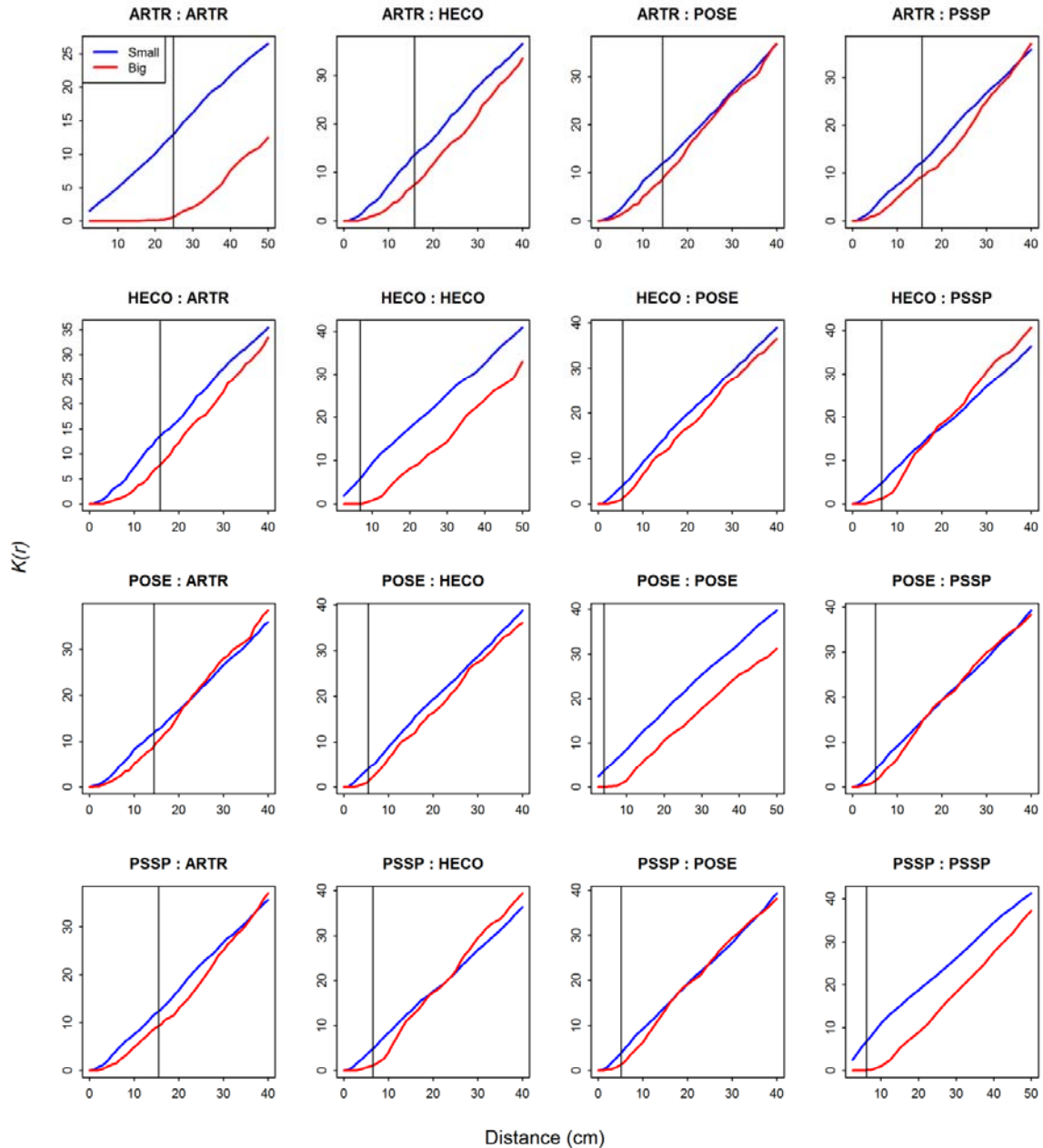


Figure G-1. $K(r)$ values of observed genet data. The K statistic calculates the cumulative density of neighbor individuals observed around focal plants. A 1:1 line represents a random pattern, deviation above and below the line represent, respectively, clustered and regular patterns. The vertical bar shows the median radius or large genets: those whose radius is above the 33% of size distribution. Graph titles, show focal species code first, followed by its neighbor species. Species codes are: ARTR=*A. tripartita*, HECO=*H. comata*, POSE=*P. secunda*, PSSP=*P. spicata*.

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Curriculum Vitae

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- 2008: M.S. in Forest Ecology, University of Washington, Washington, Seattle.
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Scholarships

2006-2007 Fulbright scholarship (\$16000).

2006-2008	College of Forest Resources Fellowship – 2 year Tuition waiver and 3 quarters of Research Assistantship (University of Washington).
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Skills:

Solid R programming skills, experience with Matlab and C++.

Publications

Compagnoni, A., and C. B. Halpern. 2009. Properties of native plant communities do not determine exotic success during early forest succession. *Ecography* 32:449-458.

Compagnoni, A., and P. B. Adler. *Submitted*. Experimental warming increases cheatgrass (*Bromus tectorum*) population growth rate along an elevation gradient.

Zachmann, L., A. Compagnoni, M. Hooten, D. Peters, and P. B. Adler. *In revision*.

Density-dependence and climate, more than community composition, drive plant population dynamics.

Theses:

Compagnoni A. (2004). “Successional dynamics and conservation of biodiversity in the rangelands of the Stura di Demonte valley”. Bachelor of Science Thesis. University of

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Compagnoni A. (2008). “Controls on plant species invasions during early secondary succession: the roles of plant origin and community properties”. Master of Science Thesis. University of Washington, College of Forest Resources. Seattle, Washington.

Compagnoni A. (*in preparation*). “Climate change and plant demography in the Sagebrush steppe”. Ph.D. Thesis. Utah State University, S.J. and Jessie E. Quinney College of Natural Resources, Logan, Utah.

Work experience

- | | |
|------------|---|
| 2007 | Field assistant for studies on the temporal variability of understory vegetation (HJ Andrews LTER site) and on meadow restoration and dynamics (for the Bunchgrass experiment, http://depts.washington.edu/bgridge/). P.I. for both projects: Charles B. Halpern.

Tasks: Plant (cover and biomass) and soil sampling on permanent plots. |
| 2005 –2006 | Consulting firm Geostudio: Project consultant (drafting of environmental impact assessments and of restoration projects); |

Consulting firm Ecolabel: Field botanist;

Field Botanist within the EU founded Interreg-III research project
 “*Messa in Rete dei Parchi Naturali Regionali del Massiccio del
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 natural parks);

Service

Reviewer for: *Western North American Naturalist*, *International Journal of Wildland
 Fire*, *Philosophical Transactions of the Royal Society B*, *Journal of Arid Environments*,
Biological invasions

Utah State University Ecology Center Student Committee: Member (2009-2011) and
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Presentations

Compagnoni, A. and P.B. Adler. 2011. "Climate warming and cheatgrass (*Bromus
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Compagnoni, A. and P.B. Adler. 2011. "Climate change and cheatgrass (*Bromus
 tectorum*) invasion in the Sagebrush ecosystems of Northern Utah". Intermountain

Graduate Research Symposium, Logan, Utah.

Compagnoni, A. and P.B. Adler. 2012. "Climate change and cheatgrass (*Bromus tectorum*) invasion in the American Intermountain West". Max Planck Institute for Demographic Research, Rostock, Germany.

Compagnoni, A. and P.B. Adler. 2012. "Warming and reduced snow cover improve cheatgrass (*Bromus tectorum*) performance in the Intermountain West". Ecological Society of America, Portland, Oregon.

Grants and awards (internal USU sources):

2012. ESA student travel award from the U.S. Department of Defense's Strategic Environmental Research and Development Program (SERDP)

2012. "Climate warming effects on cheatgrass (*Bromus tectorum*): do maternal effects matter?". Utah State University graduate student senate. \$824.

2011. "Will climate change exacerbate cheatgrass (*Bromus tectorum*) invasion?". Utah State University Ecology Center. \$2800.

2011. Plant population ecology section student travel award. Plant Population Ecology Section of the Ecological Society of America. Austin, Texas.

2011. Selected attendees for the 3rd Stanford Workshop in Biodemography, Stanford, USA.

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Workshops attended:

2011. 3rd Stanford Workshop in Biodemography, Stanford, USA.

2011. Sensitivity Analysis, Ecological Society of America, Austin, Texas.

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Teaching experience:

2009. Wildland Ecosystem (WILD 3800, TA)

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2007-2008 Vice-President.

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