Warming, soil moisture, and loss of snow increase *Bromus tectorum*'s population growth rate

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Abstract

Climate change threatens to exacerbate the impacts of invasive species. In temperate ecosystems, direct effects of warming may be compounded by dramatic reductions in winter snow cover. Cheatgrass (*Bromus tectorum*) is arguably the most destructive biological invader in basins of the North American Intermountain West, and warming could increase its performance through direct effects on demographic rates or through indirect effects mediated by loss of snow. 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 for the snowmelt treatment. We monitored cheatgrass population growth rate and the vital rates that determine it: emergence, 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 alter species composition and diversity (Parker et al., 1999; Hejda et al., 2009), fire regimes (D'Antonio and Vitousek, 1992), hydrology (Cavaleri and Sack, 2010), and biogeochemical cycles (Vitousek and Walker, 1989). Given the impacts of climate change and invasions when operating independently, understanding their potential interactions should be a high priority. Such interactions might drive rapid ecological changes, posing tremendous challenges to natural resource management.

In many temperate zones, winter snow cover plays a key role in regulating the function (Schimel et al., 2004; Monson et al., 2006) and structure (Harte and Shaw, 1995; Pauli et al., 2013) of ecosystems. Warming will dramatically reduce the depth and duration of winter snowpacks (Déry and Brown, 2007). Most experimental studies addressing the ecological role of snow on plants have been carried out in arctic, boreal, and alpine systems (Kreyling, 2010). However, loss of snow also can be ecologically important at lower latitudes and elevations by influencing soil processes and plant overwintering strategies (Kreyling, 2010).

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; Balch et al., 2013) by producing large amounts of flammable biomass (D'Antonio and Vitousek, 1992). Frequent fires negatively impact native, perennial plant species, decreasing natural habitat (West and Yorks, 2002) and endangering obligate consumer species (Dobkin and 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.

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 reductions in snow pack. Recent work at the upper end of cheatgrass' elevation range, where cheatgrass germinates after spring snowmelt, has shown that snow cover can decrease the population growth rate of cheatgrass (Griffith and Loik, 2010). However, in much of its range, cheatgrass typically germinates and establishes between fall and the end of winter (e.g. Mack and Pyke, 1983; Mack and Pyke, 1984; Pierson and Mack, 1990), provided sufficient moisture (Smith et al., 2008). If snow negatively impacts overwintering seedlings, loss of snow pack could play a significant role in exacerbating the invasion of cheatgrass, especially where the greatest reductions in snow depth and duration occur.

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, and (2) melting of snow will contribute to the positive effect of warming. We tested these hypotheses by monitoring population growth rate, a proxy for cheatgrass impact, and the vital rates that determine it: emergence, survival and fecundity. Emergence reflects how abiotic factors affect seed germination, survival reflects the effect of stress on established plants, and fecundity is a proxy for plant growth. Thus, 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 1460 m 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 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 and 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.

Table 1. Growing season (September through June) weather variables in the two years of the experiment

Growing season	Temperature (°C)	Precipitation (mm)	Snow fall (cm)	Mean 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

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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 and 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 25×25 cm quadrats consisting of a plastic mesh grid with 100 2.5×2.5 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 2.5×2.5 cm cell of the planted quadrats at the beginning of September. This is a density of 1600 seeds m^{-2}, much lower than cheatgrass dominated sites in the Great Basin where seed rain can range from 6000 (Young et al., 1969) to 17000 (Stewart and Hull, 1949) seeds m^{-2}. We planted cheatgrass at relatively low density to estimate population growth rate in the absence of intense intraspecific competition.

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, soil temperature at 5 cm depth, and air temperature at 5 cm above the ground surface. 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: *emergence*, 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 = emergence × survival × 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 where cheatgrass emerged 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 emerge 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. To check for differences between these two ways of accounting for naturally dispersed seeds, we fit models of λ using both of these estimations.

Our two estimates of λ, based on different methods of correcting for background emergence, yielded qualitatively identical figures (Figure 1, Figure S1) and model results (Table 2, Table S1). Henceforth, we refer to analyses of values of λ estimated by subtracting treatment-specific means of background emergence.

Table 2. Results of Tukey's HSD tests on population growth rate differences among treatments

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

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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 also used these data to calculate the 25%, 50% and 75% percentile of the historical climate record, the daily probability of snow presence, and average seasonal snow depth. We used the percentiles to compare the weather during the experiment to long term climate and the daily snow data to show the seasonality and length of the snow season. We quantified treatment differences in air temperature, soil temperature, and soil moisture by plotting daily averages and by calculating average values for the period between December 5th and June 15th.

Because we tested results averaged across the three ecotypes planted in each plot, before testing for treatment differences in population growth rate we verified that no ecotype × treatment interactions were significant. We did this because ignoring significant interactions could confound treatment effects. We tested for interactions with ecotype by fitting two year-specific models where we log-transformed λ and modeled it as a function of treatment, ecotype and their interactions, assuming normally-distributed errors.

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 emergence, survival, winter survival, and spring survival with a binomial distribution. We fit λ and fecundity data with a linear mixed model and emergence 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:

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

where a_i is one of the three vital rates and $\partial\lambda/\partial a_i$ 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 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. Snow cover is common, but intermittent, at our site between the end of December and the end of February (Figure 2a). Average daily snow cover peaks at the end of January, when average snow cover is 15cm (Figure 2b). During the experiment, the first year was by far the snowiest, with 81 days of snow cover and a peak snow depth of 41 cm. In the second year, there were 51 days of snow cover and a peak snow depth of 20 cm.

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 % lower than in the previous year. We found a negative correlation between soil moisture and the increase in temperature caused by warming treatments (Figure S2): the linear model fit on these data indicates that decreasing moisture by 0.1 % increases the effect of the infrared heaters by 4 ˚C (P = < 0.0001). Warming increased soil temperature (Figure S3) and decreased soil moisture at 5 cm depth, especially during the spring growing season (Figure S4). Interestingly, moisture at 20 cm depth was higher in warming treatments during the first growing season and in the first part of the second winter (Figure S4).
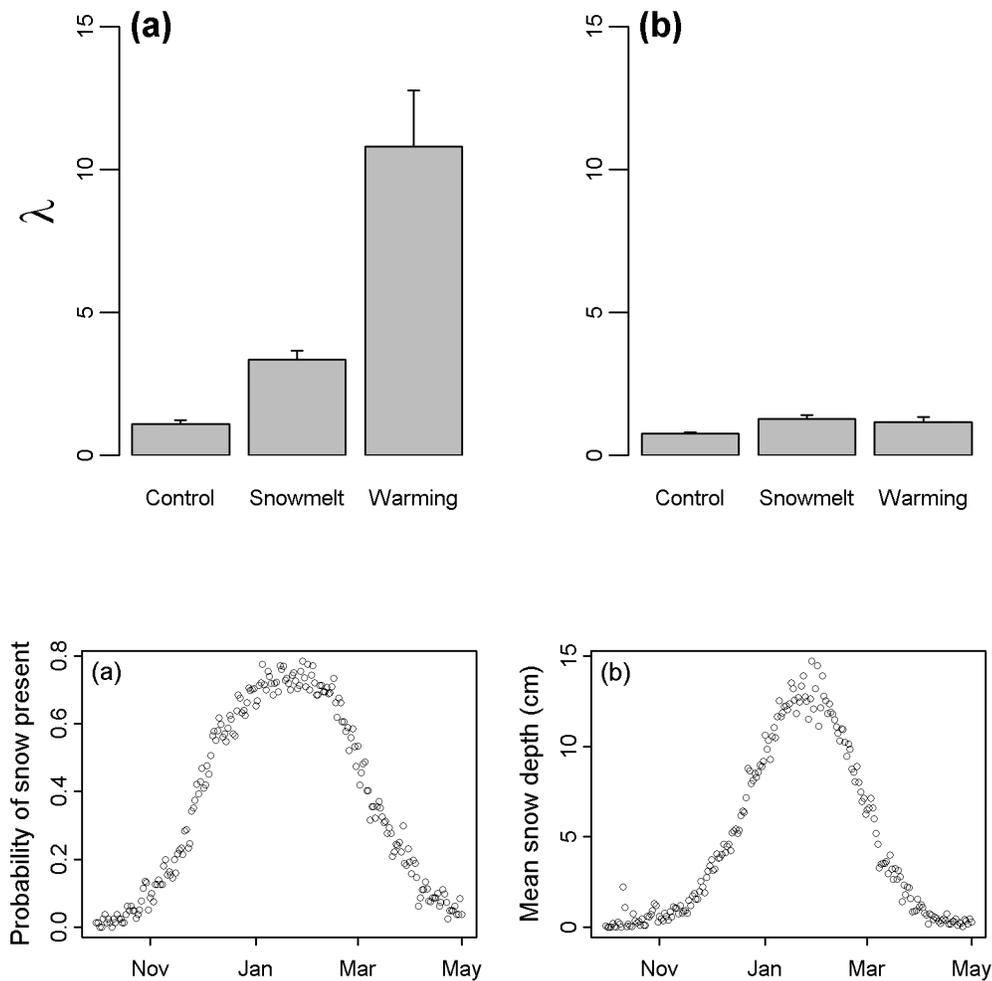
Figure 1

Effect of treatments on cheatgrass population growth rate (λ).

Panels (a) and (b) refer to the first and second growing seasons, respectively. Bars show the size of cheatgrass population growth rate (λ).

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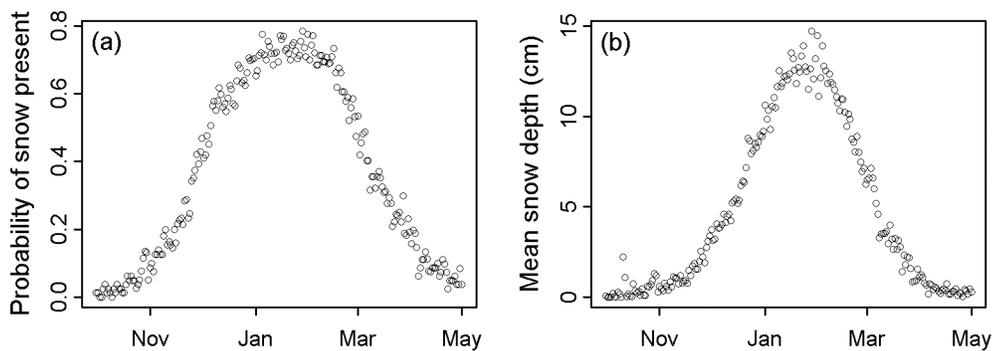
Figure 2

Daily values of probability of snow presence and average snow depth.

Panels (a) and (b) refer to probability of snow presence and average snow depth, respectively. Data comes from the Utah State University weather station, which is located 4 km from the experimental site.

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The effect of the snowmelt treatment on abiotic conditions was generally smaller. Loss of snow increased surface and soil temperature by ~1 °C and had little effect on average soil moisture. Soil temperatures in snowmelt treatments were lower than in control plots only for a week, during January 2011 (Figure S3).

Cheatgrass' population growth rate, λ, responded significantly to warming and/or snowmelt treatments in both the first ($F_{2,21} = 18.5039$, P = <0.0001) and second year ($F_{2,21} = 4.6343$, P = 0.0215) of the experiment. Tukey's HSD contrasts show that the warming and snowmelt treatments significantly increased cheatgrass population growth rates relative to controls 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 (Figure 1, Table 2). The snowmelt treatment significantly increased population growth compared to the control in both years (Figure 1, Table 2).

Vital rates also responded significantly to warming and snowmelt treatments. Relative to controls, warming increased fecundity and survival in the first year (Z = 4.1809, P = 0.0001 for fecundity; Z = 5.4699, P = <0.0001 for survival) but not in the second (Z = 1.4737, P = 0.2992 for fecundity; Z = −0.0552, P = 0.9983 for survival). Snowmelt increased survival in both years (Z = 4.4753, P = <0.0001 in 2011; Z = 3.7157, P = <0.0006 in 2012) and caused a marginally significant increase in emergence in the first year (Figure 3; Z = 2.1099, P = 0.0878). The LTRE analysis indicated that warming effects were caused primarily by increased fecundity in both years and increased survival in the first year (Figure 4). In contrast, the positive effect of the snowmelt treatment on cheatgrass population growth rate mostly resulted from increased survival (Figure 4).

Including ecotype in the models of λ did not change the effect of treatments. Ecotype × treatment interactions were not significant ($F_{4,42} = 1.3186$, P = 0.2788 in 2011; $F_{4,42} = 0.2022$, P = 0.9357 in 2012) because ecotype effects were generally equal across treatments: high elevation ecotypes had higher λ regardless of treatment (Figure S5).
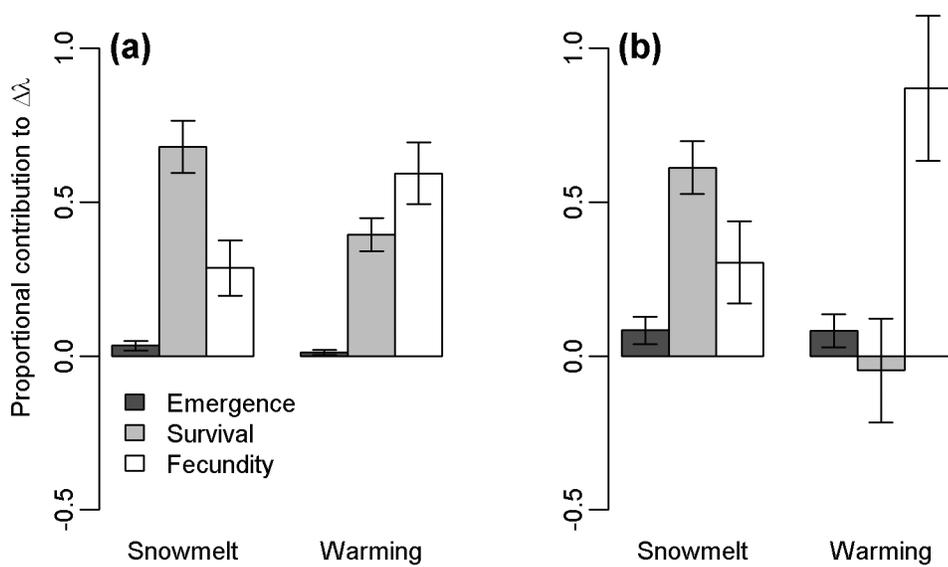
Discussion

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 ten-fold. 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 (Figure 1).

In the first year, 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. First, cheatgrass net photosynthesis increases with temperature to a peak at 25–30 °C (Rice et al., 1992). In the first year, only 0–3% of the hourly air temperature readings in warming treatments exceeded 30 °C. Because leaf and air temperatures are usually decoupled, the temperature of cheatgrass' leaves might have exceeded 30 °C. However, abundant soil moisture in the first year should have promoted high transpiration rates (Melgoza et al., 1990; Rice et al., 1992), cooling leaves via evaporative heat exchange (Lambers et al., 2008). 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 because high biomass is tightly correlated with seed production in cheatgrass (Rice et al., 1992), high biomass should correlate with the population growth rate.

An interaction between temperature and cheatgrass pathogens might offer an alternative explanation to differences in soil moisture for the interannual variability in the effects of warming. However, we are doubtful that our manipulations increased the prevalence or virulence of *Ustilago bullata* (head smut) and *Pyrenophora semeniperda* (black fingers of death), the pathogens currently known to limit cheatgrass populations in the field (Meyer et al., 2008). The head smut preferentially infects seedlings germinating at high temperatures (Meyer et al., 2008), but we initiated warming in November, after the bulk of cheatgrass seedlings had emerged. The black fingers of death infects cheatgrass seeds that become dormant because of low moisture or temperature (Finch et al., 2013). This pathogen should decrease emergence, but differences in population growth rate among years were driven by fecundity (Figure 3).

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

Our data show that reduced snow cover contributes to the direct effects of warming by increasing cheatgrass seedling survival. In the first year, survival in both snowmelt and warming plots was two-fold higher than survival in control plots (Figure 3), suggesting that part of the effect of warming was due to the increase in survival caused by the removal of snow. While the head smut and black fingers of death appear unlikely to have played a role in our study, lower survival in control plots might have resulted from a different pathogen. In particular, conditions under snow are conducive to fungal growth (Schmidt et al., 2009) and some of these fungi are pathogenic snow molds capable of causing cheatgrass mortality (Klemmedson and Smith, 1964; Meyer 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.

Our results imply that snow should limit cheatgrass population growth rate at sites where a significant proportion of plants overwinter as seedlings rather than seeds. This should be common across cheatgrass' range, as indicated by several observational studies that found the bulk of cheatgrass seedlings generally emerges between fall and winter (Mack and Pyke, 1983; Mack and Pyke, 1984; Pierson and Mack, 1990). Moreover, warming has the potential to increase the proportion of fall germinating seeds, because fall germination is often limited by temperature rather than moisture (Roundy et al., 2007).

In portions of its range where cheatgrass overwinters as seed and emerges after snowmelt, changes in snow cover should have smaller ecological effects. Consistent with this interpretation, a recent study carried out at high elevations found that the effect of snow on cheatgrass is neutral (Concilio et al., 2013). An earlier study from the same site showed that snow cover had both negative and positive effects on cheatgrass (Griffith and Loik, 2010). However, to explain the positive correlation between snow cover and cheatgrass performance, Griffith and Loik (2010) suggest that high snow years prevent cheatgrass from germinating in fall and winter, thereby preventing mortality during winter. This hypothesis is consistent with our results showing that snow increases winter mortality of seedlings.

We were surprised that survival was lower in warming than snowmelt plots in the second year (Figure 3). 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 (Figures S4). Lower soil moisture in the second year should have resulted in lower transpiration rates, and therefore lower leaf evaporative cooling of cheatgrass leaves. Because air

temperatures were much higher in the second year, the chance that cheatgrass plants suffered heat stress is much higher than in the previous year. This is a potential explanation for why spring survival in warming plots was lower than in snowmelt plots (Figure S6). However, we have no convincing explanation for why winter survival was significantly higher than controls in snowmelt but not warming treatments (Figure S6). The mortality in the warming treatment was unlikely an effect of heat because winter temperatures were too low. Drought stress is also unlikely, because in the second winter, soil moisture was higher in the warming treatment than in the control (Figure S4).

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 temperatures 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 1460 m of altitude and a December through February average temperature of -3.1 °C. Second, at high elevations snowpack is more likely to remain deep even under higher temperatures. 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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Supplementary material

- **Figure S1. Comparison between two methods for estimating population growth rate.**
  Population growth rate was estimated by subtracting seed production in unplanted quadrats to the seed production in planted quadrats. "Mean correction" shows population growth rates calculated by subtracting the treatment-specific mean of seed production in unplanted quadrats. "Plot correction" shows population growth rates calculated by subtracting the plot-specific values of seed production in unplanted quadrats. doi:10.12952/journal.elementa.000020.s001
- **Figure S2. Average daily air temperature increase caused by infra-red heaters is related to soil moisture at 5 cm depth.**
  The daily air temperature increase is the difference between temperatures in warming and control treatments. Temperatures were pooled across the three replicates per treatment which were equipped with a data logger. doi:10.12952/journal.elementa.000020.s002
- **Figure S3. Treatment differences in soil temperature recorded at 5 cm depth.**
  Data are for the period from mid December to mid June. doi:10.12952/journal.elementa.000020.s003
- **Figure S4. Treatment differences in volumetric water content (VWC) at 5 and 20 cm depth.**
  Data are for the period from mid December to mid June. doi:10.12952/journal.elementa.000020.s004
- **Figure S5. Effect of treatments and ecotypes on cheatgrass population growth rate (λ).** doi:10.12952/journal.elementa.000020.s005
- **Figure S6. Winter and spring survival rates by treatment and year.**
  Letters denote statistically significant Tukey's HSD contrasts. In particular, snowmelt vs. control (x), warming vs. control (y), and warming vs. snowmelt (z). Bars represent survival rate. doi:10.12952/journal.elementa.000020.s006
- **Table S1. Results of Tukey's HSD tests on treatments differences among "plot corrected" population growth rates.**
  Results from a model fit with population growth rate data calculated by subtracting the plot-specific values of seed production in unplanted quadrats to the seed production in planted quadrats. (DOC) doi:10.12952/journal.elementa.000020.s007

Data accessibility statement

The following dataset was generated:
- Plant demographic data: Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.63872

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