

Altered snowfall and soil disturbance influence the early life stage transitions and recruitment of a native and invasive grass in a cold desert

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Abstract Climate change effects on plants are expected to be primarily mediated through early life stage transitions. Snowfall variability, in particular, may have profound impacts on seedling recruitment, structuring plant populations and communities, especially in mid-latitude systems. These water-limited and frequently invaded environments experience tremendous variation in snowfall, and species in these systems must contend with harsh winter conditions and frequent disturbance. In this study, we examined the mechanisms driving the effects of snowpack depth and soil disturbance on the germination, emergence, and establishment of the native *Pseudoroegneria spicata* and the invasive *Bromus*

tectorum, two grass species that are widely distributed across the cold deserts of North America. The absence of snow in winter exposed seeds to an increased frequency and intensity of freeze–thaw cycles and greater fungal pathogen infection. A shallower snowpack promoted the formation of a frozen surface crust, reducing the emergence of both species (more so for *P. spicata*). Conversely, a deeper snowpack recharged the soil and improved seedling establishment of both species by creating higher and more stable levels of soil moisture availability following spring thaw. Across several snow treatments, experimental disturbance served to decrease the cumulative survival of both species. Furthermore, we observed that, regardless of snowpack treatment, most seed mortality (70–80 %) occurred between seed germination and seedling emergence (November–March), suggesting that other wintertime factors or just winter conditions in general limited survival. Our results suggest that snowpack variation and legacy effects of the snowpack influence emergence and establishment but might not facilitate invasion of cold deserts.

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Introduction

The majority of plant population mortality is associated with early life stage transitions of seed germination, seedling emergence, and seedling establishment (Fenner 1987; James et al. 2011). These early life stage transitions often regulate population growth rates (Silvertown and Charlesworth 2001), species range expansion (Clark et al. 2007), and community composition (Oster et al. 2009). As a consequence, early life stage transitions are expected to mediate climate change effects on plant species (Jeltsch et al. 2008;

Shevtsova et al. 2009). One aspect of climate change—snowfall change, exerts both positive and negative influences on plant populations and communities depending on snow depth, timing of snowmelt, and snowpack duration (Billings and Bliss 1959; Griffith and Loik 2010). In many ecosystems, seed germination and early seedling development occur during the winter underneath snow, and these key life stage transitions may be heavily influenced by snowfall variability. For example, colder winter temperatures induced by a shallow snowpack differentially affected the germination of 23 subarctic species and ultimately determined seedling survival (Milbau et al. 2009). Also, the flowering, seed dormancy, and establishment of alpine species were regulated by differences in snowfall levels that ultimately dictated community assembly (Bjork and Molau 2007). Despite the ecological importance of interactions between snowfall and plant population dynamics, only a few studies from a small number of systems have evaluated the effects of snowfall change on the population dynamics of co-occurring species. Such insights are critical for forecasting climate change effects on species distribution and abundance and identifying practical strategies to mitigate these impacts.

Through its effects on temperature, moisture, and nutrient availability, snowpack depth is an important environmental factor that may control seedling survival. Under a deep snowpack, germinating seeds may be insulated from cold atmospheric temperatures, can benefit from more moist soil conditions (Mondoni et al. 2012), and can receive inorganic nitrogen from bacteria that remain metabolically active continuously through the winter (Brooks et al. 1998). Conversely, under a shallow snowpack, seeds and seedlings must contend with freeze–thaw cycles (FTCs) where shifts in temperature regulate transitions of water between solid (ice) and liquid phases (Aanderud et al. 2011). As frozen soils repeatedly freeze and thaw, germinating seedlings are exposed to subzero conditions, drier soil conditions, and potential pulses of nutrients after soil thawing (Schimel and Clein 1996). If germinated seeds are stressed under these more variable conditions, the seeds may be more susceptible to soil pathogens, further restricting their emergence. Snowpack levels also dictate the degree that soil profiles are recharged with moisture following snowmelt (Hardy et al. 2001). As a deep snowpack melts, surface soils are buffered against drying and dramatic swings in soil moisture availability during critical periods of seedling establishment and survival. While snowpack change likely translates into a suite of effects on biotic and abiotic conditions for seedlings, the cumulative impact of these factors on early life stage transitions remains relatively unexplored (Kreyling 2010).

Snowpack change may differentially impact population dynamics of native and invasive species. In general, plants may avoid chilling, frost, and desiccation by overwintering

as seeds or acclimating/adapting to winter stresses associated with low atmospheric temperatures and FTCs (Kreyling 2010; Starr and Oberbauer 2003). However, differences in phenology, plasticity, and growth rate may allow species to be active in the winter—potentially capitalizing on more optimal soil conditions in early spring before other species germinate. Invasive species are prime examples of taxa that may be more successful in surviving under expected changes in snowpack conditions (Kunkel et al. 2009a), since they often possess higher levels of phenotypic plasticity than natives and faster growth rates (Davidson et al. 2011). Thus, invasive species may be able to exploit brief periods of increased resource availability and outcompete slower-growing native species (Grime et al. 1997). If invasive species are better at avoiding or tolerating critical stress periods associated with shallow snowpack, or exploiting changes in resource availability occurring under deeper snowpack, then these species may be favored as snowpack levels fluctuate. There is some precedence for this. Deeper snowpack led to the invasion of three out of six seeded exotic species in a mixed grass prairie (Blumenthal et al. 2008). Thus, snow variability may favor faster-growing and phenotypically flexible exotic species.

Systems that are vulnerable to the effects of snowpack change are also likely to be modified by soil disturbances, which can directly affect resources like soil moisture. The cumulative effects of soil disturbance and snowpack change may result in more pronounced differences in seedling demography during winter. For example, soil disturbance may decrease soil moisture and increase soil compaction, which can decrease the penetrability of the soil surface, potentially slowing or preventing the emergence of germinated seed and increasing the time that germinated seeds are susceptible to desiccation and attack by fungal pathogens (Chambers 1995; O'Hanlon-Manners and Kotanen 2004). The spread and abundance of invasive plants across biomes is also closely related to changes in disturbance regimes that increase resource availability (e.g., Seabloom et al. 2003). Lower tissue construction costs and corresponding greater relative growth rates generally allow invasive species to exploit increases in soil nutrient availability that occur following soil disturbance. For example, degradation of soil structure and subsequent increases in bulk density following disturbance modifies the spatial and temporal heterogeneity of soil moisture, which may differentially impact the demographies of native and invasive plant populations (Brooks et al. 1996; Meelis and Aveliina 2007).

In this study, we evaluated the effects of snowpack variability and soil disturbance on the early life stage transitions of the exotic annual grass *Bromus tectorum* (L.) and the native perennial grass *Pseudoroegneria spicata* [(Pursh) A. Löve] in a cold desert shrubland. We compared the germination, emergence, and establishment of these two

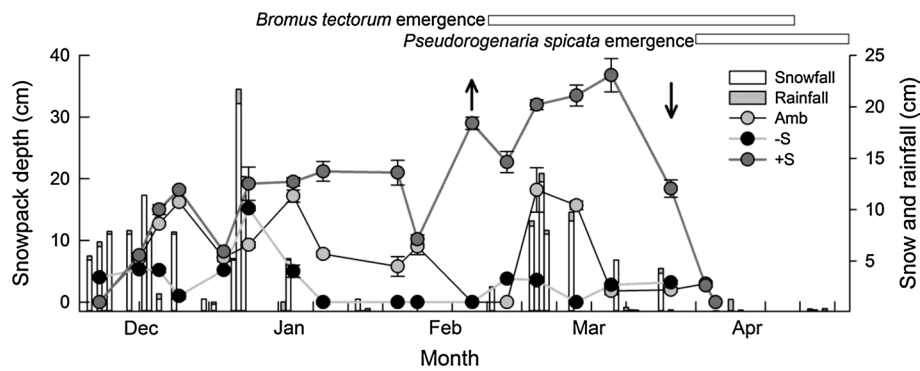


Fig. 1 Seasonal patterns of snowfall, rainfall and snowpack in the three snow manipulations during the winter and into spring. Values are either daily totals (snowfall and rainfall) or mean \pm SEM ($n = 5$)

grasses in a replicated field experiment where snowpack levels were directly manipulated over 8 months during the winter and spring. We also created a disturbance and fungicide treatment to evaluate interactions among snowpack, soil disturbance, potential fungal pathogens, soil penetration resistance, and nitrogen mineralization on grass species survival. Finally, we investigated snowpack-induced fluctuations in soil temperature, moisture, and FTCs to characterize the environmental conditions experienced by the two grass species.

We expected that snowpack reduction would increase soil penetration resistance and decrease nitrogen mineralization (Brooks et al. 1998). We also expected that snowpack reduction would reduce germination of both grasses due to a reduction in soil water and temperatures (Walck et al. 2011), and that snowpack reduction would decrease seedling establishment, as soil moisture is essential for early transition success in arid environments (Castro et al. 2005). Disturbance was expected to exacerbate the negative effects of snow removal on establishment because disturbance destroys soil structure, subsequently increasing penetration resistance and decreasing emergence probability (Chambers 1995). Finally, since the exotic *B. tectorum* has an earlier phenology than *P. spicata* (Hardegree et al. 2010) and was expected to largely escape the more stressful soil conditions that follow snow removal and disturbance, we expected the native species to be more vulnerable to the snow removal and disturbance treatments compared to the exotic species.

Materials and methods

Study site

The experiment was conducted at the Northern Great Basin Experimental Range in eastern OR, USA ($43^{\circ}22'N$,

of snowpack. The *upward pointing arrow* indicates when 15 cm of snow were added to the plus snow (+S) plots (3 Feb). The *downward pointing arrow* indicates snowmelt, and separates winter from spring

$118^{\circ}22'W$; elevation 1,300 m) between November 2010 and June 2011. Vegetation at the site is a mixture of shrub and perennial bunchgrasses, typical of the Wyoming big sagebrush steppe in western North America. Soils are a clay loam, Xeric Haplargids. The sagebrush steppe is characterized by cold wet winters and hot dry summers, with most precipitation falling as rain and snow between November and April. Mean annual precipitation and temperature over the last 70 years are 283 ± 76 mm and 7.6 ± 1.05 °C, respectively. Snowfall in this area has been declining since the 1920s (Kunkel et al. 2009b).

Snow pack, disturbance, and fungicide manipulation

We evaluated the effects of snowpack (snow removal, snow addition, ambient snow), soil disturbance (disturbed, not disturbed), and fungicide (fungicide-coated seeds, untreated seeds) on the germination, emergence, and survival of *B. tectorum* and *P. spicata*. The 8-month field experiment was a fully factorial randomized block design with six replicates per treatment combination for treatments that included disturbance and 12 replicates per treatment combination for treatments that did not include disturbance. Experimental plots (2 m²) were randomly arranged in a 10 \times 20 grid separated by 2-m buffer strips on all sides of each experimental plot.

We created three snowpack treatments where snow was removed (–S), added (+S), or left in place (ambient). Snow was removed from the –S plots using a metal blade that rested on guides 5 cm above the soil surface outside the experimental plot. The snow was applied to the +S plots by collecting snow from the surrounding area with a shovel and redistributing this snow evenly across replicates. Snow manipulations were implemented after every major snow event (11 times in total, see Fig. 1). During the experiment, snowfall levels were typical of winters in eastern Oregon and adequate to achieve differences among

snowpack treatments. Specifically, the ambient treatment received 133 cm of snowfall (Fig. 1). We measured snowpack in five randomly selected replicates from each snow treatment once a week until all plots were free of snow.

To evaluate the effects of soil disturbance on seedling recruitment, we tilled half of the experimental plots to a depth of 10 cm and then raked the plot surface smooth prior to seeding. We evaluated the impacts of pathogenic soil fungi on seed germination by coating seeds with 0.5 and 0.047 % Thiram and Allegiance® (Bayer Crop Science, Research Triangle Park, NC, USA), two seed-borne and soil-borne fungicides, and adding fungicide and untreated seeds to all of our treatments. In general, the half-lives of these fungicides are less than 20 days, so we expected any potential positive effects of each fungicide to occur within 2 months after sowing seed.

Germination, emergence, and establishment probabilities

We estimated the germination, emergence, and establishment of *B. tectorum* and *P. spicata* with two different techniques to identify the effects of our treatments on key plant life stage transitions. First, germination probabilities were quantified using nylon mesh bags planted at a soil depth of 5 cm. In each plot, we planted two germination bags in fall 2010 prior to the first snowfall. Bags contained a mixture of seed-free field soil and 50 seeds of the target species. This approach allowed seeds to remain in contact with bulk soil and facilitated the complete recovery of all seed over two harvests (Abbott and Roundy 2003). Plots assigned to the fungicide treatment received seed coated in fungicide. We pulled the germination bags in February and March 2011. Bag contents were rinsed over a fine screen and all seeds were visually categorized into three groups: seeds with a radicle present at the time of harvest were scored as germinated; nongerminated seeds at harvest that produced a radicle following 4 weeks of incubation on moist filter paper at 20 °C were considered dormant; and nongerminated seeds at harvest that did not germinate when incubated or were visibly decomposed were scored as dead. Second, we quantified treatment effects on seedling emergence and establishment by seeding 600 seeds m⁻² into the center 1 × 1 m portion of each 2 × 2 m plot and covering the seeds with 1 cm of soil. Plots were sown with *B. tectorum* or *P. spicata* seed at the same time as the germination bags were planted. Following snowmelt in mid-March, plots were monitored weekly for 9 weeks to quantify emergence (probability of a germinated seed producing a coleoptile above the soil surface; Fenner and Thompson 2005). Emerged seedlings were marked with a toothpick and tracked monthly to quantify establishment (probability of an emerged seedling producing leaves and becoming independent of seed reserves;

Fenner and Thompson 2005) and survival through the first growing season.

We used a continuation ratio model (Congdon 2001) to estimate how probabilities of transitioning between $K = 3$ growth stages (i.e., germinated seed, emerged seedling, established seedling) varied by species and with disturbance and snow treatments. The model for the $(K - 1) \times 1$ data vector for plot j (i.e., y_j) was

$$p(y_j|\eta) \propto \prod_{k=1}^{K-1} \left(\frac{e^{\eta_{j,k}}}{1 + e^{\eta_{j,k}}} \right)^{y_{j,k}} \left(\frac{1}{1 + e^{\eta_{j,k}}} \right)^{n_{j,k}}, \quad (1)$$

where $y_{j,k}$ is the number of individuals entering but failing to exit stage k , $n_{j,k}$ is the number of individuals living beyond stage k , and $\eta_{j,k} = \text{logit}(p_{j,k}) = \log\left(\frac{p_{j,k}}{1-p_{j,k}}\right)$, with $p_{j,k}$ being the probability of dying at stage k . We assumed that the η_j were multivariate and normally distributed, $\eta_j \sim N(X_j\beta, \Sigma)$. The linear model $X_j\beta$ has terms controlling for life stage transitions (i.e., germinated seed to emerged seedling, emerged seedling to established seedling) and plant species for plot j . An exploratory analysis led us to include seven additional terms in $X_j\beta$ controlling for particular interactions between life stage transitions, species, and snow and disturbance treatments. These terms model snow removal effects on (1) *B. tectorum* and (2) *P. spicata* emergence, snow addition effects on (3) *B. tectorum* and (4) *P. spicata* establishment, (5) the combined effect of snow removal and disturbance on *P. spicata* establishment, (6) the combined effect of ambient snow and disturbance on *P. spicata* establishment, and (7) the disturbance effect on *B. tectorum* emergence.

We used Bayesian methods to fit Eq. 1, which necessitated assigning prior distributions to β and Σ . To β , we assigned a uniform prior distribution and to Σ , an inverse-Wishart prior with K degrees of freedom and the $(K - 1) \times (K - 1)$ identity matrix as the scale parameter. We used a hybrid Gibbs sampler/Metropolis algorithm to sample the joint posterior distributions.

Because germination was not measured over entire plots, germination probabilities were analyzed separately with a model very similar to Eq. 1. Final estimates of germination probabilities were very similar regardless of whether or not species, disturbance, and snowfall covariates were included in the model, so these covariates were excluded.

Soil temperature, moisture, oxygen, and FTCs

To determine the effects of a snowpack on soil conditions, we measured soil temperature, moisture, and oxygen levels. Sensors were placed in the snow treatment plots in undisturbed (four replicates, for a total of twelve sensors) and disturbed replicates (two replicates, for a

total of six sensors) at a soil depth of 5 cm. We measured volumetric water content and temperature with ECH₂O-TM sensors (Decagon Devices, Pullman, WA, USA) and HOBO data loggers (Onset Computer Corp. Bourne, MA, USA). We averaged all values with a daily time-step to remove diel variability, which may mask the impact of our treatments on soil conditions (Carbone et al. 2008). In addition to measuring soil moisture and temperature, we used soil sensor data to quantify freeze–thaw cycles (FTC). We defined FTCs based on changes in soil moisture using the following criteria: first, moisture had to decline as free liquid water became ice (i.e., freeze); and second, moisture had to then increase (i.e., thaw) back to values similar to those prior to the freeze (Aanderud et al. 2013). We separated the environmental data into two time periods: winter (11 November–15 March) and spring (16 March–1 June), with these two periods separated by snowmelt. We tested for the effect of the snow treatments on our response variables (i.e., temperature and moisture) for each of these time periods with linear mixed-effects models (LMM) using the {nlme} package in the R Statistical Environment (R Development Core Team 2013).

Soil penetrability and N mineralization

We quantified the level of soil penetration resistance created by the snow and disturbance treatments. Specifically, we measured soil penetration and water content to predict the effects of our treatment on penetration resistance as a function of soil moisture (Tracy et al. 2011). We measured penetration resistance with a penetrometer and made 8–12 subsample readings per plot every 2 weeks. We also collected samples for gravimetric water content in the 0–2 cm soil layer each time we sampled penetration resistance and converted soil gravimetric water content to volumetric water content using soil bulk density. Regression models were used to estimate treatment effects on soil penetration resistance. Predictors of (log-transformed) soil penetration were disturbance, time of data collection, plot, volumetric water content, and the disturbance \times water content interaction. Week and plot were modeled as random effects, and all other factors were modeled as fixed.

To identify the impact of snowpack and disturbance on N availability, we evaluated net N mineralization rates in situ. Four times during the growing season we hammered two sets of 5 cm diameter plastic soil cores 7 cm into the soil, removed one core, and extracted inorganic N from the soils with KCl and analyzed for NH₄⁺, while the other core was capped and left in the soil for approximately 4 weeks and then collected and extracted. Ammonium concentrations were determined colorimetrically following Forster (1995).

Fungicide treatment and fungal abundance

We evaluated the effects of all of our treatments on the fungal colonization of seeds and seedlings by quantifying the abundance of fungi (i.e., rRNA gene copy number) with quantitative PCR (qPCR). Specifically, we extracted total genomic DNA from seeds and seedlings in snowpack and disturbance treatments (ambient, –S, +S, and disturbed ambient) at three times (once a month from February through April). Total genomic DNA was extracted from 10 *B. tectorum* and *P. spicata* seeds from buried bags at each replicate ($n = 3$) using a ZR Plant/Seed DNA Kit (Zymo Research Corporation, Orange, CA, USA), for a total of 144 samples. We used the fungal-specific (partial 18S rRNA gene) forward primer nu-SSU-0815-5' and reverse primer nu-SSU-1196-3' that target the internal transcribed spacer (ITS) region of fungal nuclear DNA (McGuire et al. 2010) for our qPCR analyses. We performed qPCR assays [25 μ L reaction, RealMasterMix SYBR ROX (5 Prime, Inc., Gaithersburg, MD, USA)] on a Mastercycler EP Realplex qPCR machine (Eppendorf, Hamburg, Germany) using SYBRGreen to detect the abundance of fungal DNA. We generated fungal qPCR standards from our site with a TOPO TA Cloning[®] Kit (Invitrogen, Aanderud et al. 2013). The coefficients of determination for our assays ranged from 0.93 to 0.99, and we found no evidence for primer dimers from our melting curve analyses.

To identify potential fungal pathogens, we extracted genomic DNA from single-spore isolates from germinated seeds grown on potato dextrose agar with the ZR Plant/Seed DNA Kit, PCR-amplified the ITS region using fungal specific primers ITS1 and ITS4 (Martin and Rygielwicz 2005), and identified the sequences (Sanger dideoxy sequencing, 3730xl DNA analyzer, Applied Biosystems, Foster City, CA, USA) with the Basic Local Alignment Search Tool in GenBank. We tested for the effects of the treatments on fungal biomass using two-way ANOVAs, separating differences with Tukey's range tests.

Results

Germination, emergence, and establishment probabilities

Germination probabilities were high for both species [0.80 ± 0.01 and 0.79 ± 0.02 (mean \pm SE), for *B. tectorum* and *P. spicata*, respectively] and were not significantly influenced by any experimental treatment. However, the –S treatment negatively affected emergence compared to ambient conditions ($P > 0.99$; Fig. 2), with the negative effects being greater for *P. spicata* than *B. tectorum* ($P = 0.99$, $P = 0.98$, respectively). For both species, the +S treatment had no effect on emergence relative to the

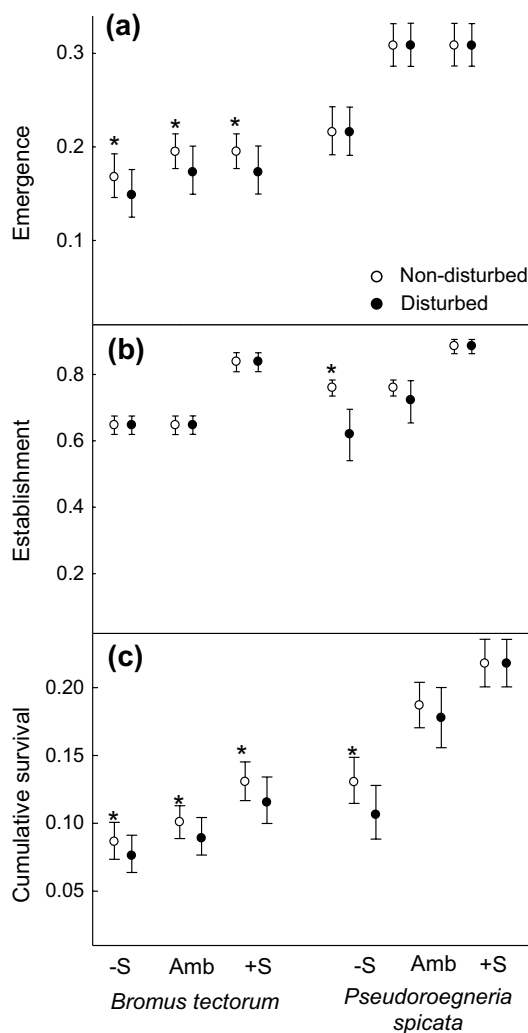


Fig. 2 Effects of snow addition on the probabilities of *Bromus tectorum* and *Psuedoroegneria spicata* **a** emergence, **b** establishment, and **c** cumulative survival in snowpack manipulation and disturbed soils. Emergence and cumulative survival were quantified starting in mid-March. Treatments included an ambient snowfall (Amb), snow removal (–S), snow addition (+S), and disturbed and undisturbed soils. Values are point estimates (circles) with 95 % CI; asterisks indicate significant effects ($p > 0.90$) of disturbance on survival probabilities within a snow treatment

ambient treatment. Soil disturbance had a negative effect on *B. tectorum* emergence across all snow treatments ($P > 0.99$), but did not affect *P. spicata* emergence in any of the snow treatments.

Once the seedlings emerged, establishment probabilities were high—exceeding 0.60 for all combinations of species and treatment, and were positively influenced by deeper snowpack levels. Averaged across all treatments, *P. spicata* had higher establishment than *B. tectorum*. Establishment of both species significantly increased under the +S treatment ($P > 0.99$), and there was a significant interaction between species and soil disturbance, with *P. spicata*

showing significantly lower establishment in disturbed plots under the –S treatment ($P > 0.99$).

Cumulative survival for both species did not surpass 25 % and was restricted almost entirely by low emergence. Averaged across all treatments, *P. spicata* had a greater cumulative survival than *B. tectorum* ($P > 0.99$), and cumulative seedling survival of both species decreased as winter snow depth declined. Disturbance decreased *B. tectorum* cumulative survival across all snowpack treatments but decreased *P. spicata* cumulative survival only in the –S treatment ($P > 0.90$).

Winter shifts in invasive phenology

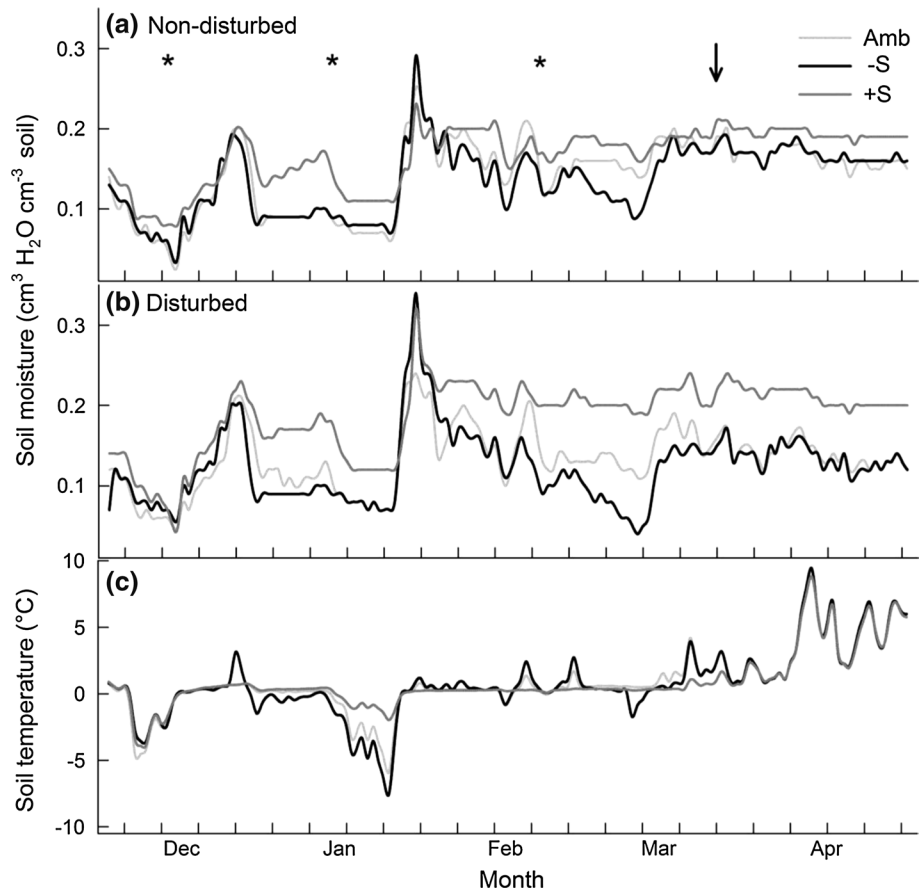
The phenology of *B. tectorum* but not *P. spicata* was accelerated by a shallower snowpack. In –S soils, *B. tectorum* emerged between mid-February and mid-April and established after April. In the ambient and +S soils, *B. tectorum* emerged between the end of March and beginning of May and began to establish at the beginning of April (Fig. 1). In all treatments, *P. spicata* emerged between the end of March and beginning of May and began to establish at the beginning of April. The disturbance treatment did not alter the phenology of either species.

Soil temperature, moisture, and FTCs

The snow manipulations created moderate levels of snowpack in the ambient ($7.8 \text{ cm} \pm 0.21$), a shallow snowpack in the –S ($3.2 \text{ cm} \pm 0.07$), and a deep snowpack in the +S ($18 \text{ cm} \pm 0.20$) treatments. The +S treatment received 315 cm of snowfall, or approximately double the snowpack present in the ambient treatment. Snowmelt started in mid-March; after this time, soil temperatures began to increase, and there was no new accumulation of snowfall in any of the treatments (Fig. 3a).

The snowpack manipulations affected soil moisture and created FTCs, with soil disturbance accentuating differences in the soil conditions. Disturbance altered the effects of snowpack variability on soil moisture during the winter (snow \times disturbance, $F = 13.8$, $P < 0.0001$, $df = 2$) and into the spring (snow \times disturbance, $F = 69.7$, $P < 0.0001$, $df = 2$; Fig. 3a, b). During the winter, ambient and –S treatments were relatively similar, except for a series of FTCs in undisturbed and disturbed soils occurring from late January to snowmelt. During this time period, –S soils were on average $0.02 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil} \pm 0.002$ lower in undisturbed and $0.03 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil} \pm 0.003$ lower in disturbed than ambient soils. Thus, freezing conditions were more extreme under the shallow snowpack, and disturbance accentuated these treatment differences. Soils under the +S treatment only experienced two FTCs, one of which occurred in all treatments before the snow

Fig. 3 Effects of snow manipulations on soil moisture in **a** undisturbed soil, **b** disturbed soil, and **c** soil temperature in both treatments. The snow treatments included an ambient snowfall (*ambient*), snow removal (*-S*), and snow addition (*+S*). Moisture values (undisturbed $n = 5$; disturbed $n = 2$) are from sensor data ($n = 7$), but because neither the snow treatment nor disturbance had a significant effect on temperature, data from undisturbed and disturbed treatments are combined. Asterisks in **a** indicate a freeze–thaw cycle (FTCs) or a series of FTCs occurring in the snow treatments; the downward pointing arrow in **a** indicates snowmelt and separates winter from spring



accumulated in November. In general, winter moisture levels in *+S* treatments compared to ambient were $0.02 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil} \pm 0.003$ wetter in undisturbed and $0.05 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil} \pm 0.002$ wetter in disturbed soils, and this trend continued into spring. Following snowmelt, soil moisture in the *+S* treatment was on average $20 \% \pm 0.60$ higher in undisturbed and $62 \% \pm 1.0$ higher in disturbed soils. Soil moisture gradually declined through spring since there was no large rainfall event through May.

Soil temperatures were influenced by snowpack and disturbance but only during the winter. Temperature was affected by snowpack treatment ($F = 3.46, P = 0.03, df = 2$) and disturbance ($F = 5.43, P = 0.02, df = 1$; Fig. 3c). From early December to snowmelt, average soil temperatures in the ambient treatment ($-0.19 \text{ }^\circ\text{C} \pm 0.14$) were intermediate with respect to those measured in the *-S* ($-0.35 \text{ }^\circ\text{C} \pm 0.17$) and *+S* ($-0.02 \text{ }^\circ\text{C} \pm 0.09$) treatments. Soil temperatures in all treatments fluctuated around $0 \text{ }^\circ\text{C}$ for most of the winter, with the most notable exception occurring as soils reached subzero conditions during FTCs. Lastly, disturbance caused soils to be slightly warmer on average in disturbed ($0.22 \text{ }^\circ\text{C} \pm 0.12$) than in undisturbed ($0.09 \text{ }^\circ\text{C} \pm 0.13$) soils from the winter to snowmelt.

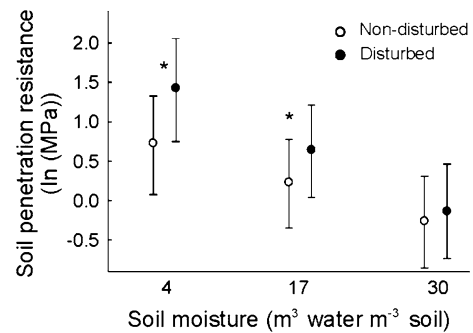


Fig. 4 Soil penetration resistance in disturbed and undisturbed treatments in relation to three levels of volumetric soil moisture content that span the range of soil moisture observed during the winter and spring. Values are mean \pm 95 % CI ($n = 6\text{--}12$)

Soil penetrability and nitrogen mineralization

Soil penetration resistance, which is a function of soil water content, was likely affected by FTCs occurring across the disturbance plots. For dry soils, soil penetration resistance increased up to 50 % in disturbed compared to undisturbed plots (Fig. 4). Thus, freezing conditions were more extreme under the shallow snowpack, and disturbance

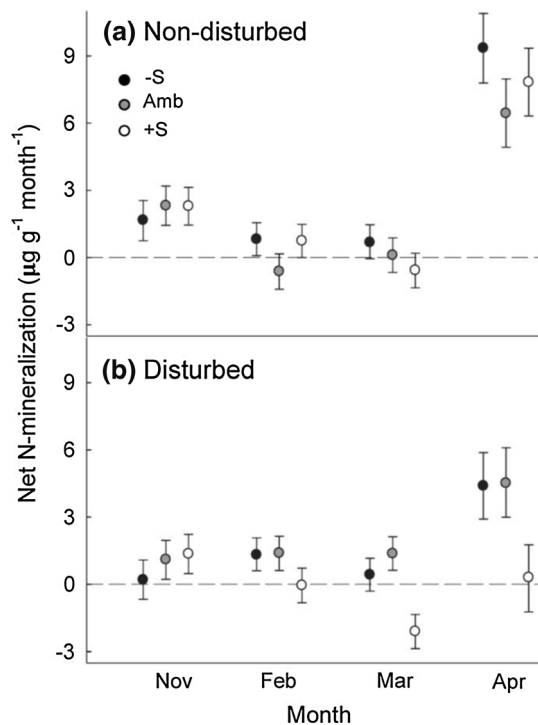


Fig. 5 N mineralization rate across snow treatments in **a** undisturbed and **b** disturbed soils. Values are mean \pm 95 % CI ($n = 6$)

accentuated these treatment differences. In wet soils, however, as soils reached 30 % volumetric water content (close to field capacity), there was little difference in soil penetration resistance due to soil disturbance. Moreover, in the

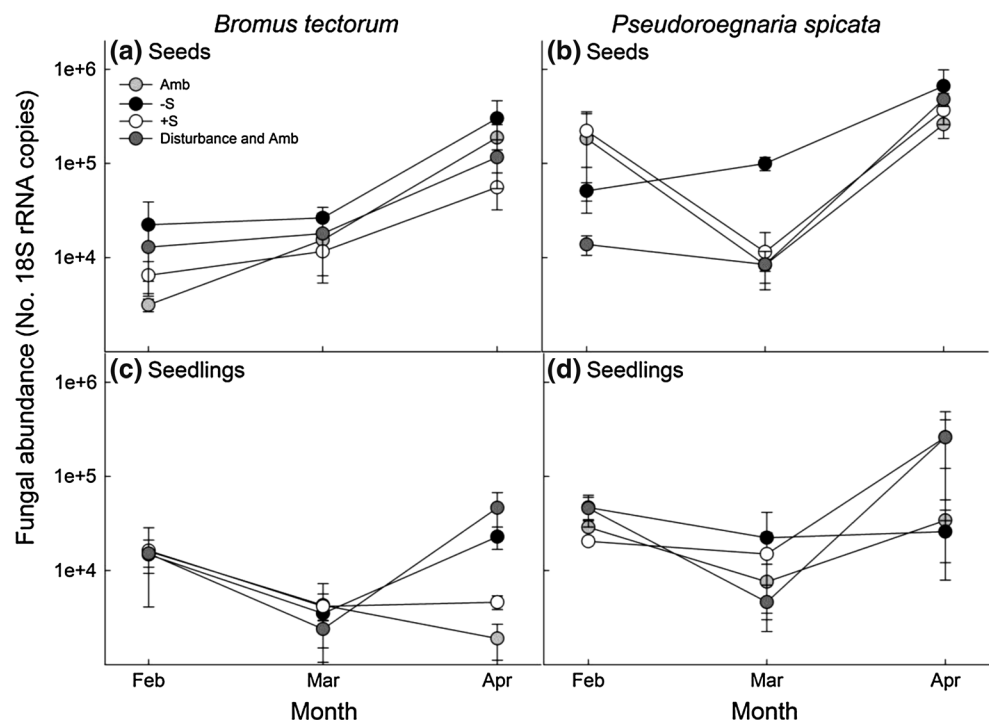
disturbed and undisturbed treatments, soil nitrogen mineralization was significantly higher ($P < 0.05$) in April, prior to establishment (Fig. 5). In the +S treatment, in the presence of disturbance, soil nitrogen mineralization was lower than in the ambient and -S plots ($P < 0.05$).

Fungicide treatment and fungal abundance

The fungicide treatment did little to reduce the fungal abundance in seeds of *B. tectorum*, but it did reduce fungal abundance in nongerminated seeds of *P. spicata*. Approximately a month after sowing fungicide-coated seeds in soils, fungal abundance in *P. spicata* seeds was 53 % lower in fungicide than in untreated seeds (two-way ANOVA, fungicide versus untreated \times species $F = 3.95$, $P = 0.05$, $df = 1$, Fig. S1 in the Electronic supplementary material, ESM). There was no significant difference in fungal abundance among the snowpack treatments.

Snow removal stimulated the fungal colonization of *B. tectorum* seeds and emerging seedlings and *P. spicata* seeds. For seeds of *B. tectorum* that germinated, fungal abundance was consistently higher in the -S treatment during the winter and into the spring (two-way ANOVA, treatment, $F = 2.90$, $P = 0.05$, $df = 3$; Fig. 6a). Alternatively, fungal abundance in *P. spicata* germinated seeds was at least 8.7 \times higher in -S than the other two treatments, but only in March (two-way ANOVA, treatment \times time, $F = 3.26$, $P = 0.02$, $df = 6$, Fig. 6b). In the spring, the -S and ambient disturbance treatments stimulated the fungal colonization of *B. tectorum* seedlings (two-way

Fig. 6 Snowpack effects on fungal abundance on **a** *Bromus tectorum* seeds and **c** emerging seedlings, and **b** *Pseudoroegneria spicata* seeds and **d** seedlings were quantified using quantitative PCR to measure the number of fungal 18S rRNA gene copies present. Values are means \pm SE



ANOVA, treatment \times time, $F = 23.0$, $P = 0.0007$, $df = 6$, Fig. 6c). For example, seedlings from all snow treatments had similar fungal abundance levels during the winter and into spring thaw, but abundance was $5.0\times$ higher in $-S$ and disturbed ambient soils (two-way ANOVA time \times treatment $F = 23.0$, $P = 0.0007$, $df = 6$). Based on culturing efforts in the lab, most of the fungi colonizing the seeds were known pathogens. For example, among hundreds of randomly selected seeds, we found only nine fungal species, and six of these were graminoid pathogens or general plant pathogens (Table S1 of the ESM).

Discussion

Mid-latitude ecosystems experience tremendous variation in the timing and amount of snowfall received. Despite this, our understanding of how snow influences plant population dynamics is almost exclusively derived from high-latitude and alpine ecosystems (e.g., Kreyling 2010). This constraint is particularly apparent for water-limited steppe ecosystems that experience immense intra-annual snowfall variability. We found that in a sagebrush steppe system, snow-induced changes in the intensity of FTCs, fungal pathogen infection, and frozen surface soils most likely reduced the emergence of both experimental species under shallower snowpack, while higher soil moisture availability in spring following the melting of deeper snowpack increased the establishment of both species. Our results suggest that snowpack variation and legacy effects of snowpack on environmental factors may have consequences in water limited, mid-latitude ecosystems, and may have a larger negative effect on invader grass populations than natives.

Comparing the effects of snowpack variation and disturbance on early life stage transitions of *B. tectorum* and *P. spicata* provided insight into how environmental change may ultimately influence invasive and native plant abundance. *B. tectorum* is the most prolific invader across the western United States, and has rapidly expanded across tens of millions of hectares over the last several decades (Novak and Mack 2001). Contrary to most of the invasion literature (e.g., Mack et al. 2000), disturbance did not facilitate establishment of the invasive *B. tectorum*, but instead inhibited *B. tectorum* survival across the three snowpack treatments. Overall, a key finding was that per capita recruitment of the native *P. spicata* was greater than that for the invasive *B. tectorum*, regardless of snowpack or disturbance treatment. Denser coleoptile and radical tissue may have allowed the slower-growing native to better tolerate abiotic and biotic stresses experienced in both the $+S$ and $-S$ treatments (Ryser 1996). Alternatively, a delayed phenology may have allowed *P. spicata* seedlings to avoid early periods of biotic

and abiotic stress (Bilbrough and Caldwell 1997). This finding is important because few studies to date have examined the influence of snowpack on co-occurring native and invasive species. Previous work has shown that warmer, moister winters increased cheatgrass abundance (Compagnoni and Adler 2014), but this work did not evaluate the simultaneous response of co-occurring native grasses. Our work here shows that, relative to the native grass, *B. tectorum* may experience only modest decreases in survival under climate change scenarios that involve warmer and drier winters, but that *P. spicata* per capita recruitment likely will exceed per capita recruitment of *B. tectorum* in multiple snowpack change scenarios. However, future work should consider the possibility of nonlinear responses of these two species to changes in gradients of temperature and snow.

Between germination and emergence, our snowpack manipulations resulted in large variations in abiotic and biotic seedbed conditions. However, these different micro-environmental shifts produced a 10 % change in emergence probability at most. While our snowpack-induced variation in emergence probabilities is ecologically meaningful because it occurred during the transition that commonly exerts the strongest selective pressure on the number of individuals entering a population, we possibly missed one or more key universal factors or events that created the observed emergence bottleneck. For example, single or several key FTCs and winter dry periods experienced periodically in all treatments may have been sufficient to cause rapid and abrupt change in seedling survival probability. Likewise, relatively high fungal pathogen loads, as described below, may have been sufficient to cause large mortality events in all treatments, and all three of these factors could have interacted to cause significant mortality during emergence across all treatments. Finally, high seed output by both species could compensate for emergence limitation. For example, *B. tectorum* can produce over 150 seeds per panicle (Ball et al. 2004), depending on habitat type.

Snow-induced changes in FTCs and fungal pathogen infection potentially contributed to our measured decline in seedling emergence under a shallower snowpack. Based on our sensor and soil penetrability data, more intense FTCs under the $-S$ treatment created drier and colder winter soil conditions for germinated seeds to contend with and harder soil surfaces for emerging seedlings to break through. Early life history dynamics are strongly influenced by frost damage (Waters et al. 2005) and desiccation (Johnson and Aguirre 1991), both of which were intensified by more severe FTCs. For example, Laude (1957) found that, following uniform freezing, emergence of *B. tectorum* and the bunchgrass *Agropyron cristatum* was reduced by 90 and 70 %, respectively. As free liquid water became ice, soil surfaces

were harder to break through for emerging seeds, especially under a shallower snowpack where surfaces were not insulated by snow cover. Besides this factor, pathogenic fungi possibly infected and killed seeds, further limiting emergence. Fungi often respond strongly to changes in moisture availability (Brooks et al. 1996), and they can disproportionately affect seeds and seedlings compared to adult plants (Kirkpatrick and Bazzaz 1979; Ride 1983). Further, fungal pathogens influence seedling emergence more than seed germination (Munkvold and O'Mara 2002), and can be one of the most important causes of seedling mortality (Moles and Westoby 2004). We found that snowpack removal resulted in consistently higher fungal abundance in seeds of both species during the winter and into the spring. Although fungi colonized seeds and germinated seeds, we suspect that the more stressful abiotic conditions in this treatment may have exacerbated the potentially negative effects of pathogenic fungi on germinated seeds, causing them to be more susceptible to attack. Four of the six fungal species we cultured from germinated seeds were graminoid pathogens, while none of the taxa were snow molds that attack predominantly established dormant plants at low temperature under snow cover (Hoshino et al. 2009). Thus, our fungi were potentially psychrophilic (cold-loving) or psychrotrophic (cold-tolerant) species that are adapted to winter soil conditions. Finally, the fungicide treatment did little to promote the emergence of either species, but this does not necessarily support an absence of the role of fungi in the death of emerged seeds. More likely, the ability of the fungicide to protect seeds was transient, as suggested by data on fungicide half-life.

Deeper snowpack and its effects on soil moisture likely promoted the establishment of both experimental species. In arid ecosystems, soil moisture is paramount for seedling establishment, with higher levels of moisture alleviating competitive pressures on seedlings from existing vegetation with more developed root systems (Davis et al. 1998). Rainfall inputs and soil moisture dynamics often drive seedling survival (Reichenberger and Pyke 1990), with relatively small changes in the timing or the amount of rainfall often having large consequences for plant population dynamics and species coexistence (Chesson et al. 2004). The majority of these findings are based on spring rainfall variations or pulses of summer rainfall; however, we found that snowpack amount also increased the survival of emerged seedlings. Based on our sensor results, deeper snowpack led to higher and more constant soil moisture availability, which buffered against dramatic swings of availability in spring. This increase in moisture coincided with more than 80 % of emerged seedlings establishing and surviving, similar to rates found in comparable studies (e.g., Newingham et al. 2007; Griffith 2010). Thus, early life stage transitions may also be very

sensitive to soil moisture availability due to legacy effects of snowpack.

Unexpectedly, disturbance exacerbated the negative effects of the snow treatment on *B. tectorum*, possibly as a result of the exotic species indirectly responding to modified soil moisture and FTCs. For example, soil moisture was further reduced on already dry snow removal plots in the presence of disturbance. This enhanced drying was likely responsible for the increased penetration resistance of the soil, inhibiting the emergence of fragile seedlings (Vleeshouwers 1997; Reisner et al. 2013). Our results support the evidence that the development of physical soil crusts may act as a barrier for emerging seedlings. This reduction in soil moisture likely also contributed to a reduction in establishment probability and cumulative survival for *P. spicata* in the disturbed and -S treatment plots. *P. spicata* cover responds strongly to disturbance (Reisner et al. 2013), and a lack of adequate soil moisture is an important factor regulating young bunchgrass mortality (Dyer and Rice 1999). Alternatively, in relatively moist +S soils, disturbance appeared to further increase soil moisture, which may have stimulated an increase in fungal infection measured in *B. tectorum* seedlings in spring. Elevated soil N did not stimulate the establishment of invasive seedlings. Disturbance often directly affects resource availability and seed and seedling dynamics (Auestad et al. 2013; Kempe et al. 2013). Soil N mineralization (and thus inorganic N availability) was higher in spring under shallower and ambient snowpack, but this increase did not relate to an increase in *B. tectorum* establishment or survival.

We found that, during periods when soil seed banks have generally been considered dormant or quiescent, fluctuating winter snowpack can drive significant changes in both native and invasive plant recruitment probability. A shallower snowpack had a larger negative effect on the recruitment of the native grass than the invasive grass. The timing of annual snowpack build-up and loss also corresponds to when the bulk of plant population mortality occurred. While we could not separate effects of drier soils from the effects of colder soils due to the nature of FTCs, our results suggest that, as snowpack-free winters become more frequent in these systems, native plant recruitment will become increasingly constrained, even if total precipitation remains unchanged. Furthermore, we observed that a deeper snowpack promoted the establishment of both species, possibly due to the legacy effects of more snow creating higher levels of soil moisture availability in spring. Importantly, our manipulations only explained about 15 % of the mortality associated with emergence, strongly suggesting that a more refined understanding of the mechanisms driving this mortality is needed if we are to adequately forecast and effectively manage recruitment dynamics in these and similar ecosystems.

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