



Patterns of post-fire invasion of semiarid shrub-steppe reveals a diversity of invasion niches within an exotic annual grass community

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Abstract Disturbances such as fire provide an opportunity for invasive plant species to exploit newly created niche space. Whether initial invaders facilitate, compete with, or do not affect later invaders is important to determine in communities affected by multiple invaders. This analysis focuses on the newer invaders *Taeniatherum caput-medusae* (medusahead) and *Ventenata dubia* (ventenata) in sagebrush-steppe communities previously invaded by *Bromus tectorum* (cheatgrass), during the first 5 years of recovery after wildfire. We combined probabilistic co-occurrence analysis and Getis-Ord spatial clustering analysis to assess relationships between different exotic annual grass species and native and introduced perennial bunchgrasses, then used Bayesian generalized linear models to determine if and how medusahead and ventenata differed in their environmental relationships and thus invasion niches. Medusahead presence was positively associated with both other exotic annual grasses, but ventenata presence was negatively associated with cheatgrass presence. Medusahead hotspots were more spatially similar to cheatgrass hotspots while ventenata hotspots were unique. Both invaders were negatively related to total perennial bunchgrass cover but disassociations between invaders and

different perennial bunchgrasses were species-specific. Medusahead and ventenata occupied different niches; medusahead in low elevation, low precipitation areas and ventenata in higher elevation, higher precipitation areas. Despite seemingly similar ecology and growth requirements among these annual grasses and a tendency to be considered uniformly in both research and management, the species appeared to have different invasion niches.

Keywords Cheatgrass · Medusahead · Ventenata · Sagebrush steppe · Invasion meltdown

Introduction

Disturbances can alter resource availability and disrupt landscape resistance to invasion by creating open niche space and resource fluctuations advantageous for an invader (Sher and Hyatt 1999; Davis et al. 2000, Britton-Simmons and Abbott 2008). Whether or not a change of state occurs from native to invaded system depends on the resistance of the landscape against invasion and the resilience of native vegetation to return after disturbance (Brooks and Chambers 2011, Chambers et al. 2014, D’Antonio et al. 2001). In some cases, positive feedback loops can develop where disturbance creates suitable conditions for invasion to occur and the invader increases the susceptibility of the ecosystem to disturbance

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(D'Antonio and Vitousek 1992; Buckley et al. 2007). Reduced ecosystem resistance must coincide with propagule availability in order for the invasion process to be realized (Davis et al. 2000).

Three different mechanisms can occur in the community succession following a disturbance. Early successional species facilitate later successional species, or both early and late successional species co-exist without facilitating or inhibiting each other, or early successional species inhibit establishment or growth of later successional species (Connell and Slatyer 1977). These mechanisms could explain interactions among invaders in disturbed systems, whereby early invaders can facilitate or inhibit establishment of other species. Priority advantages or advantages gained by the first arriving species, whether native or invasive, can have longer term effects on what mechanisms of succession occur on the landscape (Catford et al. 2012; Fraser et al. 2015). Initial invasion by priority invaders can in some cases cause an “invasional meltdown” where landscape resistance is lowered to secondary invaders via invader-invader facilitation (Green et al. 2011, O’Loughlin and Green 2017).

The mechanisms of post-disturbance plant invasion are particularly relevant to the ongoing invasion of the vast sagebrush steppe by multiple species. Sagebrush steppe once occupied nearly 45 million ha across the western United States, but to date nearly half of this has been lost, in large part due to positive fire-invasion feedback loops where invasion by exotic annual grasses increases fire size and frequency, which in turn increases invasion (Schroeder et al. 2004; Miller et al. 2011, Chambers et al. 2014). Conversion of sagebrush steppe landscapes to exotic annual grass monocultures increases soil erosion, alters soil eco-hydrological processes, reduces wildlife habitat, and changes time scales of nutrient cycling (Miller et al. 2011; Wilcox et al. 2012; Bansal et al. 2014b). Higher elevation, wetter sites dominated by perennial natives capable of regenerating after fire are thought to have more resistance to invasion than lower elevation, drier sites, especially those lacking perennial bunchgrasses that can regenerate after fire (Chambers et al. 2014, Roundy et al. 2018). Perennial bunchgrasses have been considered a key component to providing landscape resistance, although different species vary in how much competitive pressure they exert upon exotic annual grasses (Davies et al. 2015). Substantial

land management efforts have sought to increase native or introduced perennial bunchgrasses via seedling while temporarily removing invasive annual grasses via herbicide or grazing to confer additional landscape resistance to mass invasion, although results have been mixed (Knutson et al. 2014).

The primary exotic grass invader of sagebrush-steppe ecosystems is *Bromus tectorum* (cheatgrass), a Eurasian annual grass introduced in the 1890s; however, two other species *Taeniatherum caput-medusae* (medusahead) and *Ventenata dubia* (ventenata), display a similar capacity to establish, form monocultures, and potentially displace native vegetation (Young 1992, Chambers et al. 2014, Jones et al. 2020). The growth patterns of these invaders are somewhat similar in their short lifecycle and shallow-rooting patterns, which contrast the generally deeper-rooting perennial traits of the native plants, although differences exist (Klemmedson and Smith 1964; Young 1992; Pavek et al. 2011). Medusahead and ventenata mature later than cheatgrass and display a degree of seed dormancy (Young 1992; Pavek et al. 2011). With regards to competition, a preliminary greenhouse study suggested that, at the seedling stage, ventenata displayed more negative competitive effects on a native perennial bunchgrass (bluegrass wheatgrass, *Pseudoroegneria spicata*) than either cheatgrass or medusahead did (McKay et al. 2017). Additionally, there is some indication from the Pacific Northwest, where ventenata has a longer history of invasion, that it is positively associated with medusahead and cheatgrass and negatively correlated with perennial bunchgrass cover (Jones et al. 2020). The degree to which these three exotic annual grass species may facilitate or compete with each other and with different native and introduced perennial bunchgrass species in a post-disturbance sagebrush steppe landscape is unclear.

Temporary site conditions, as influenced by factors such as weather or management interventions, may transiently affect landscape resistance. Post-fire weather, particularly the timing of precipitation, can influence establishment of both exotic annual grasses, as well as native perennials in sagebrush steppe ecosystems (Bishop et al. 2020, Applestein et al. 2021). Bansal et al. (2014a) found that medusahead, but not cheatgrass or ventenata, biomass increased with larger infrequent water pulses, as opposed to smaller more frequent waterings. However, despite the

importance of both precipitation quantity and timing for establishment of both perennial and exotic annual species, it is not yet clear how variability in precipitation could affect the competitive balance between perennial and exotic grass species in post-fire systems (Bishop et al. 2020) or between exotic annual grass species. Herbicide treatments have shown at least temporary success in substantially reducing cheatgrass and medusahead cover, providing a window for re-establishment of perennial bunchgrass species, although results can be variable (Morris et al. 2009; Kyser et al. 2013; James et al. 2015; Applestein et al. 2018). Initial field trials indicate that the same herbicides that have been used for cheatgrass and medusahead control may also provide control of *ventenata* (Wallace et al. 2015, Davies and Hamerlynck 2019). Temporarily reducing the seed rain pressure of these exotic annual grasses with herbicide can give perennial native grasses and shrubs a chance to establish and subsequently provide resistance to invasion even if seeds from invaders continue to arrive at the site in future years (Applestein et al. 2018, Davies and Boyd 2018, Metier et al. 2018).

We sought to assess the relationships between dominant native bunchgrasses and invasive annual grasses, spatial patterning of invasive annual grasses, and characteristics of landscape resistance against medusahead and *ventenata* during the first 5 years post-fire on the ~ 113 ha Soda wildfire, where the dominant invasive grass was cheatgrass. We were particularly interested in the two invaders, medusahead and *ventenata*, and whether their spread across the landscape suggested facilitation or competition between invaders or separate niches. Our questions were as follows:

1. What is the relationship between the dominant invasive grass (cheatgrass), medusahead and *ventenata*, and dominant native bunchgrasses on the post-fire landscape?
2. How does the spatial patterning of invasion hotspots change over the first 5 years post-fire and do medusahead and *ventenata* patterns follow overall spatial trends?
3. In a post-fire system, which landscape variables confer resistance or susceptibility to initial invasion by invaders medusahead and *ventenata* in the first 5 years after fire? In areas that become

invaded, how does abundance increase in relation to these landscape characteristics?

Methods

Site description

The Soda wildfire was 113 ha fire that occurred along the border of southeastern Idaho and southwestern Oregon in 2015 in the Owyhee Mountains. The burned area spanned a large elevational gradient from 701 to 2054 m (U.S. Geological Survey Digital Elevation model 30-m pixel). Mean annual precipitation across the burned area ranges from 23.3 to 55 cm and mean annual temperature is between 6.8 and 10.8 °C. Several herbicide applications (imazapic, at a rate of 100 g ai ha⁻¹) were applied across several parts of the fire during the winters of 2015/2016 and 2016/2017 (see Applestein et al. 2018 for additional details). Drill seedings of perennial grass species (either native or introduced species) were applied either before or after herbicide treatments in the falls of 2015, 2016, and 2017.

Data collection

Permanent field plots were selected via a stratified-random method with approximately 1 plot per 54.5 ha but were moved if they overlapped roads, had more than 20% trail area within an 18 m radius, or fell within 400 m of a water source. We monitored plots every growing season between 2016 and 2020. There were variations in the number of plots monitored each year, due to budgetary restraints. For this analysis, we selected only plots monitored every year ($n = 1347$). At each plot, we captured a 2 × 3 m aerial photo from nadir at 2 m height from the north side of the plot. In 2017–2020, a second aerial photo was taken directly 5.5 m south from the first photo. All species in the photo areas were visually observed and recorded (in 2016, only species in the central 1 × 1 m quadrat were recorded). After the photo plot species occurrences were recorded, a larger 13 m radius circle plot was walked and presences of all species in the larger plot area were recorded. We, therefore, had two different sets of presence/absence species data based on plot size: “microsite” presence if a species was

recorded in the first photo plot area and “extended” plot presence if a species was recorded in the 13 m radius circle.

For photos taken in 2017–2020, both photos were cropped to retain only the middle 50% in order to reduce parallax at the edges of the photos. We then assessed species cover as a percentage of total area via grid-point intercept (GPI) using the software SamplePoint, using 100 points for the single overhead photos taken in 2016 and 49 points each for the two cropped photos taken in 2017–2020. Total perennial bunchgrass cover was calculated as the sum of all individual species cover in the photo plots.

Cooccurrence analysis

To examine the relationships between different invasive annual grass components and perennial bunchgrasses, we ran a probabilistic co-occurrence analysis in R, using the package *cooccur* (Griffith et al. 2016) across all plot-year microsite combinations. This algorithm computes the probability of each pair of species occurring more or less frequently together in microsites than what would be expected if each were distributed randomly. Our species matrix was composed of cheatgrass, medusahead, ventenata, and the four most common perennial bunchgrasses; *Poa secunda* (Sandberg’s bluegrass), *Pseudoroegneria spicata* (bluebunch wheatgrass), *Agropyron cristatum* (crested wheatgrass), and *Elymus elymoides* (squirreltail). Occurrences were based only on microsite presence/absences, without taking cover into account. The co-occurrence algorithm calculates a probability of a co-occurrence being greater than or less than what would be expected at random, so *p*-values are directly relatable to probabilities (i.e. $p = 0.05$ means that the probability of co-occurrence greater than chance is 95%).

Hotspot analysis

In order to examine spatial patterning of annual grass invasion, we ran a Getis-Ord statistical analysis for each year for all annual grass cover, as well as for medusahead and ventenata cover individually, using the hotspot analysis in ArcGIS 10.0 (Getis and Ord 2010). The Getis-Ord statistic indicates areas where higher or lower values are significantly spatially

clustered as compared with a randomly spatial distribution with no clustering.

Landscape resistance regressions

In order to determine the effect of landscape resistance factors on the extended plot occupancy of exotic annual grass invaders medusahead and ventenata, we parameterized two models for each species; an occupancy-only model and an abundance (cover) model for locations where the species occurred during the 5 years of monitoring.

Data extraction

We used the extract multiple values tool in ArcMap 10.0 to extract the values of elevation (from the U.S. Geological Survey Digital Elevation Model 10 m), percent clay (NRCS Soil Survey STATSGO data), and daily precipitation values for October–March of each water year from PRISM 800 m data for each plot location. From the daily precipitation, we calculated total cumulative precipitation between October and March, number of precipitation events (each individual event is considered consecutive days with measurable precipitation), average amount of precipitation per event, and average number of days between precipitation. We were specifically interested in these precipitation variables because they address frequency and size of precipitation events associated with establishment of different exotic annual grasses (as in Bansal et al. 2014a). Cumulative precipitation was strongly correlated with average amount of precipitation per event and number of precipitation events was strongly correlated with average number of days between precipitation. As a result, we only selected cumulative precipitation and average number of days between precipitation as the two variables to represent frequency and amount of precipitation.

We assigned two binary indices to each plot for each year as either drilled or not drilled and as either sprayed or not sprayed (with herbicide) based on polygon layers on landscape treatments.

Scaling variables

Following the suggestions of Gelman et al. (2008) for scaling input variables for logistic regression, we scaled our variables as follows: for binary variables,

we scaled them to have a mean of 0 and a range of 1. For continuous variable, we scaled them to have a mean of 0 and a standard deviation of 0.5.

Occupancy-only model

We built a generalized linear mixed model that included landscape resistance variables (with no spatial processes) using the *brms* package in R. Probability of species occurrence was given as:

$$O_i \sim \text{Bernoulli}(\Omega_i)$$

$$\log \text{it}(\Omega_i) = \gamma_0 + \gamma_1 * \text{Elev}_i + \gamma_2 * \text{Clay}_i$$

$$+ \gamma_3 * \text{BRTE}_i + \gamma_4 * \text{PBG}_i + \gamma_5 * \text{Drill}_i$$

$$+ \gamma_6 * \text{Herb}_i + \gamma_7 * \text{DrillHerb}_i$$

$$+ \gamma_8 * \text{DysBtwPrecip}_i$$

$$+ \gamma_9 * \text{TotPrecip}_i + \gamma_{10} * \text{Year}_i + \omega_0$$

where O is a binary indicator of extended plot species occurrence (0 = not present, 1 = present), $Elev$ is plot elevation, $Clay$ is percent clay in the soil at the plot, $BRTE$ is percent cheatgrass cover, PBG is percent perennial bunchgrass, $Drill$ is a binary indicator for drilled or undrilled, $Herb$ is a binary indicator for sprayed with herbicide or unsprayed, $DrillHerb$ is the interaction of drill seeding and herbicide, $DysBtwPrecip$ is the average days between precipitation for the fall and winter between October and March, $TotPrecip$ is the total precipitation between October and March, $Year$ is the time since fire, and ω_0 is a random intercept term for each plot. Including the random intercept term allowed us to account for multiple visits over 5 years at each plot.

Abundance model

In order to assess how invader abundance related to landscape resistance, we selected only the subset of points for each species (medusahead and ventenata) where it was present during at least 1-year post-fire. We transformed the percent cover using the transformation suggested for beta-distributed variables by Smithson and Verkuilen (2006) to scale the data between 0 and 1. Transformed species cover ($Cover_i$) was given as:

$$Cover_i \sim \text{Beta}(\mu_i, \phi)$$

$$\log \text{it}(\mu_i) = \gamma_0 + \gamma_1 * \text{Elev}_i + \gamma_2 * \text{Clay}_i$$

$$+ \gamma_3 * \text{BRTE}_i + \gamma_4 * \text{PBG}_i + \gamma_5 * \text{Drill}_i$$

$$+ \gamma_6 * \text{Herb}_i + \gamma_7 * \text{DrillHerb}_i$$

$$+ \gamma_8 * \text{DysBtwPrecip}_i$$

$$+ \gamma_9 * \text{TotPrecip}_i + \gamma_{10} * \text{Year}_i + \omega_0$$

Prior selection

Priors for landscape variable effects were selected through a literature search. If we could determine a quantitative effect of a landscape, weather, or management variable from previous research on the response of medusahead or ventenata, we would conservatively translate this effect to a reasonable estimate for the means odds effect on the establishment component of the occupancy model (justifications given in Appendix 1, Tables 1 and 2). For variables lacking background information, we set weakly informative default priors for each variable as a normal distribution with a mean of 0 and a standard deviation of 4 to stabilize the prior distribution on the probability scale, as suggested by Lemoine (2019). The same priors were used for the abundance beta regression, with the assumption that the magnitude of an effect on occupancy would be similar to the effect on cover.

Model accuracy and parameter significance

We calculated Cohen's kappa for each logistic model and bayes R^2 for each beta regression model. We assessed parameter significance of each predictor variable with the probability of direction index in the *bayestestR* package (Makowski et al. 2019). Probability of direction (pd) has equivalence to frequentist p -values with pd values of 0.975 and 0.995 corresponding to p -values of 0.05 and 0.1, respectively. In this paper, $\text{pd} > 0.9999$ is rounded up and reported as $\text{pd} = 1$.

Results

What is the relationship between the dominant invasive grass (cheatgrass), medusahead and ventenata, and dominant native bunchgrasses on the post-fire landscape?

Cheatgrass was negatively associated with all perennial bunchgrass species, except for the low-statured short-lived Sandberg's bluegrass ($p < 0.002$ for all negative associations, $p = 0.0003$ for positive association, Fig. 1). This contrasted with the relationship of medusahead and ventenata to perennial bunchgrasses; both exotic annual grass species were negatively associated with Sandberg's bluegrass ($p < 0.0001$ and $p = 0.0004$, respectively), but had no relationship to other perennial bunchgrasses ($p > 0.22$ for all comparisons) except for a negative association of medusahead with crested wheatgrass ($p = 0.003$). Cheatgrass and ventenata were negatively related ($p = 0.0001$), but medusahead was positively associated with both cheatgrass ($p = 0.05$) and ventenata ($p < 0.0001$).

How does the spatial patterning of invasion hotspots change over the first 5 years post-fire and do medusahead and ventenata patterns follow overall spatial trends?

Hotspots of higher cheatgrass cover were located on both the southeast and northwest sides of the fire (as well as some smaller hotspots dispersed throughout) primarily in the lower elevation areas close to the fire boundary (Fig. 2). The largest cheatgrass cover hotspot in the northwest encompassed a larger spatial footprint in the first 2 years after fire and a smaller spatial footprint during the third and 4th year after fire (which were the 2nd and 3rd years after herbicide application) but expanded again in the last year of monitoring (2020). Medusahead cover hotspots were aggregated in geographically similar, albeit more localized areas (Fig. 3). There were no medusahead cover hotspots on the eastern edge of the fire, and areas with lower-than-expected cover (coldspots relative to rest of the landscape) were apparent in later years, perhaps indicating the presence of dispersal barriers. Ventenata cover hotspots were highly localized in all years and had minimal overlap with the other exotic grasses, and ventenata cover hotspots contracted in

Species Co-occurrence Matrix

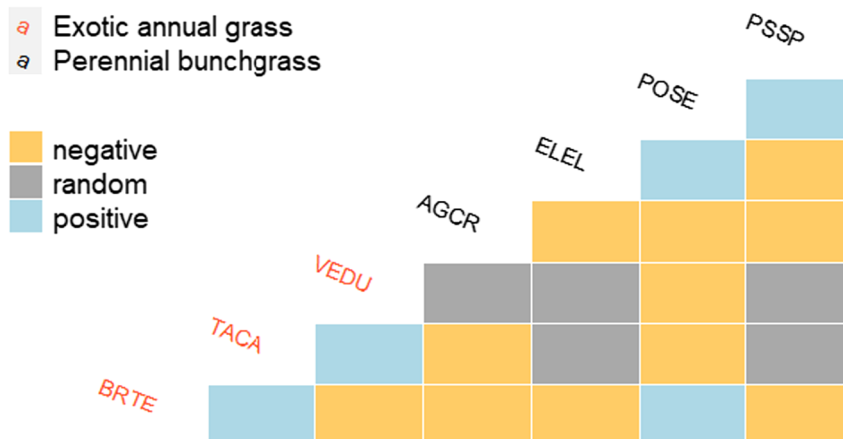


Fig. 1 Species co-occurrence matrix between perennial bunchgrasses specified with black text (AGCR: *Agropyron cristatum* (crested wheatgrass), ELEL: *Elymus elymoides* (squirreltail), PSSP: *Pseudoroegneria spicata* (bluebunch wheatgrass), and POSE: *Poa secunda* (Sandberg's bluegrass)) and exotic annual grasses specified in red text (BRTE: *Bromus tectorum* (cheatgrass), VEDU: *Ventenata dubia* (ventenata), and TACA: *Taenatherium caput-medusae* (medusahead)). Each box

represents the direction of the probabilistic co-occurrence between two species in the matrix; yellow represents that two species are negatively associated and occur less frequently together than if each were independent, grey represents no significant relationship between the two species, and blue represents that two species are positively associated and occur more frequently together than if each were independent

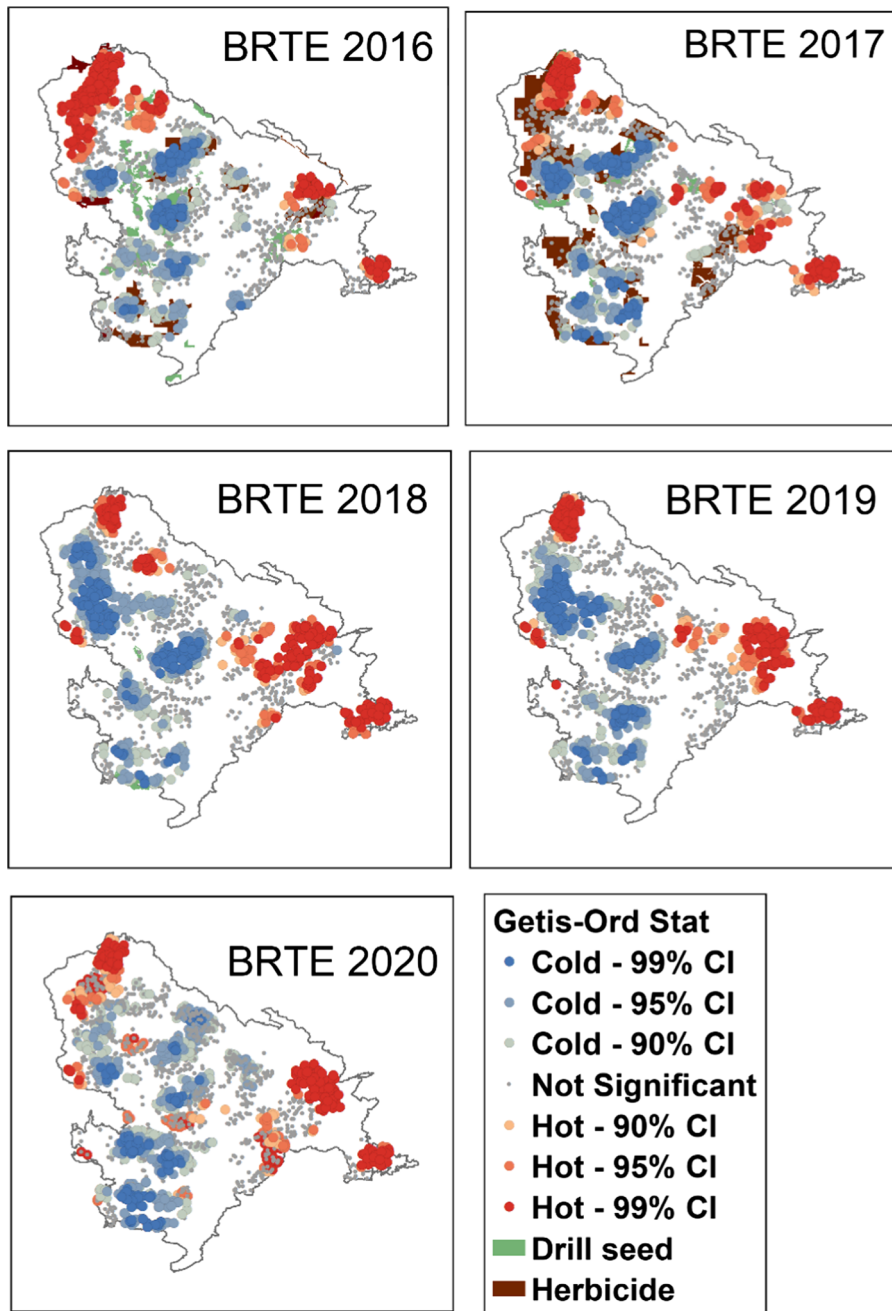


Fig. 2 Getis-Ord Gi hotspot analysis for cheatgrass (BRTE) cover for each year 2016–2020. Points in pink or red are plots where high cover values are clustered (with 90–99% confidence) and light blue to darker blue are areas where low cover values are clustered (with 90–99% confidence). Clustering is

based on values relative to those across the entire landscape for each year. Herbicide treatments are shown in brown and drill seedings in green for the fall/winter prior to the monitoring years shown 2016–2018

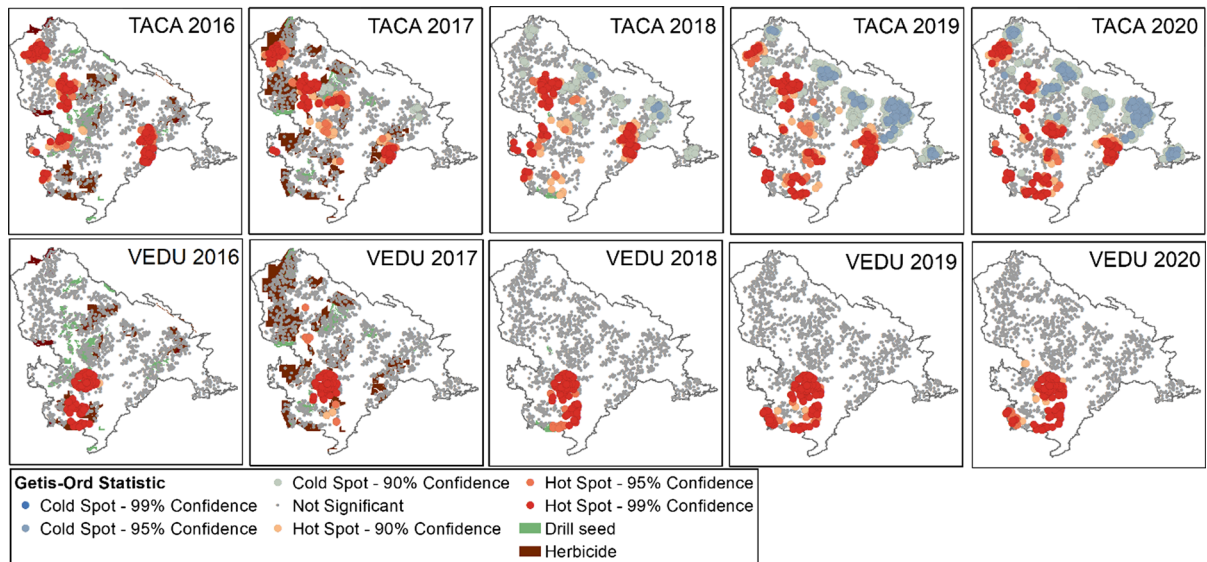


Fig. 3 Getis-Ord Gi hotspot analysis for medusahead (top, “TACA”) and ventenata (bottom, “VEDU”) cover for each year 2016–2020. Points in pink or red are plots where high cover values are clustered (with 90–99% confidence) and light blue to darker blue are areas where low cover values are clustered (with

90–99% confidence). Clustering is based on values relative to those across the entire landscape for each year. Herbicide treatments are shown in brown and drill seedings in green for the fall/winter prior to the monitoring years shown 2016–2018

2017 and then expanded again in the 3rd–5th post-fire years (Fig. 3).

In a post-fire system, which landscape variables confer resistance or susceptibility to initial invasion by invaders medusahead and ventenata in the first 5 years after fire? In areas that become invaded, how does abundance increase in relation to these landscape characteristics?

Presences of both invaders increased with time since fire ($pd = 1$ for both species, Fig. 4), with the probability of occurrence increasing by > 30% for both medusahead and ventenata by the 5th post-fire year (Figs. 5 and 6). Odds of medusahead occurring decreased by 13% per 100 m increase in elevation ($pd = 1$), whereas odds of ventenata occurring increased by 23% per 100 m increase in elevation ($pd = 0.9928$) (Figs. 4, 5, and 6). Odds of medusahead occurring decreased by 5% per 10 mm increase in cumulative winter precipitation ($pd = 1$, Fig. 5), whereas odds of ventenata occurring increased by 3% per 10 mm increase in cumulative winter precipitation (Fig. 6). Odds of both medusahead and ventenata decreased with greater perennial bunchgrass cover by 9% per 1% increase in perennial bunchgrass

cover ($pd = 1$, Fig. 5) and by 15% per 10% increase in perennial bunchgrass cover ($pd = 0.9955$, Fig. 6), respectively. Odds of both medusahead and ventenata occurring increased with greater percent soil clay by 24% ($pd = 1$, Fig. 5) and 23% ($pd = 1$, Fig. 6) per 1% increase in percent clay in the soil, respectively. Odds of medusahead occurring doubled in areas that were drill seeded ($pd = 1$, Fig. 5), but drill seeding did not affect ventenata occurrence (Fig. 4). Odds of ventenata occurring decreased by 18% per 10% increase in cheatgrass cover ($pd = 0.9988$), by 32% in sprayed compared with unsprayed plots ($pd = 1$), and by 59% per additional average day between precipitation ($pd = 1$, Fig. 6), whereas these variables had no significant effect on medusahead occurrence (Fig. 4).

Landscape variables that affected cover once invasion occurred differed somewhat from those most related to initial invader occurrences (Fig. 4). The full model bayes R^2 for medusahead cover was 0.50, but we had poor model fit ($R^2 = 0.003$) for ventenata cover because overall cover was low in all monitoring years. Both estimated medusahead and ventenata cover decreased as the average number of days between precipitation events increased from 2.5 to 6.2 by about 2.5% ($pd = 1$) and 1.5% ($pd = 0.9977$), respectively (Figs. 7 and 8). Both estimated

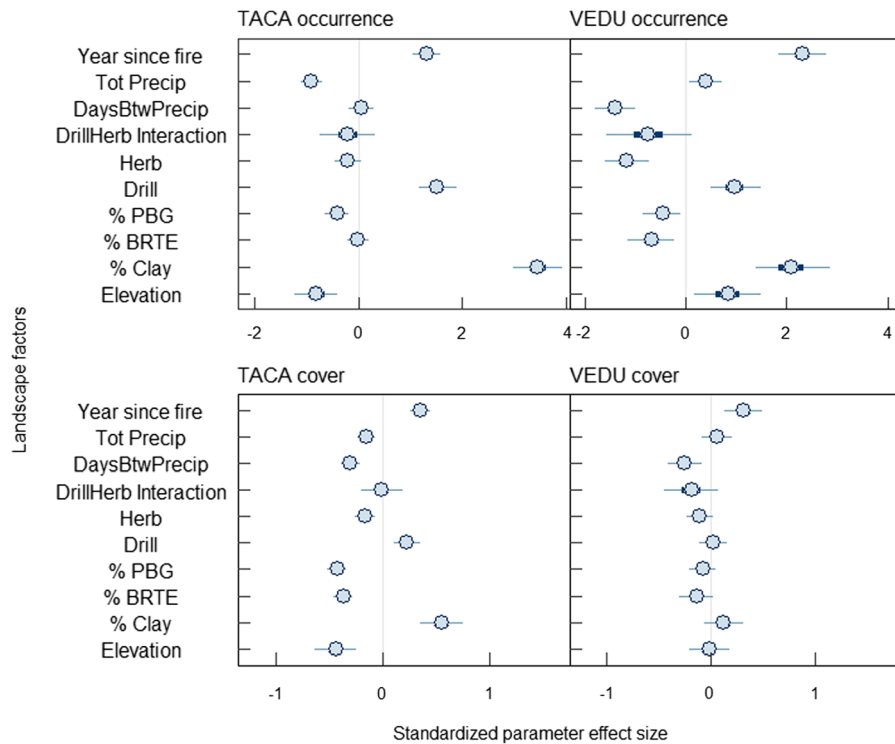


Fig. 4 Standardized parameter effect size of landscape resistance characteristics on occurrence (top) and cover (bottom) of medusahead (left, “TACA”) and ventenata (right, “VEDU”). Grey points display posterior predictive median

value, dark blue bars show the 50% posterior predictive intervals, and the thin blue lines show the 95% posterior predictive intervals

medusahead and ventenata cover also increased with year since fire by about 2% ($pd = 1$) and 1.2% ($pd = 0.9996$), respectively, between 2016 and 2020 (Figs. 7 and 8). Estimated medusahead cover varied as follows: decreased from 8.6 to 3.2% as elevation increased from 860 to 1782 m ($pd = 1$), increased from 1.6 to 5.9% as clay increased from 12 to 24% ($pd = 1$), decreased from 4.4 to 1.6% as cheatgrass cover increased from 0 to 95% ($pd = 1$), decreased from 5.3 to 1.6% as perennial grass cover increased from 0 to 76% ($pd = 1$), and decreased from 4.4 to 3.2% as cumulative winter precipitation increased from 124 to 402 mm ($pd = 0.9997$) (Fig. 7), whereas ventenata cover was not significantly affected by these variables (Fig. 4). Cover of medusahead was a mean 0.6% lower in plots sprayed with herbicide than unsprayed (4.3% vs. 3.7%) and 0.9% higher in drilled plots as compared with undrilled plots (4.7% to 3.8%) (Fig. 7).

Discussion

Interactions among invasive species can cause “invasional meltdown”, where a succession of different invaders increase ecosystem susceptibility to additional invasions (Green et al. 2011, O’Loughlin and Green 2017). We sought to assess whether two exotic annual grass invaders in post-fire sagebrush steppe are able to exploit a similar niche as the initial dominant annual-grass invader (cheatgrass), or if these species occupied different spaces on the landscape, and we asked if the patterns reflected positive, negative, or neutral interactions among the invaders. We found evidence of some potential facilitation or at least tolerance between the dominant exotic annual grass species (cheatgrass) and medusahead, whereas the third species (ventenata) appeared to occupy a different niche than the other two, possibly due to not having reached its full invasional niche in this system. Landscape characteristics generally considered to confer more resistance to invasion against cheatgrass

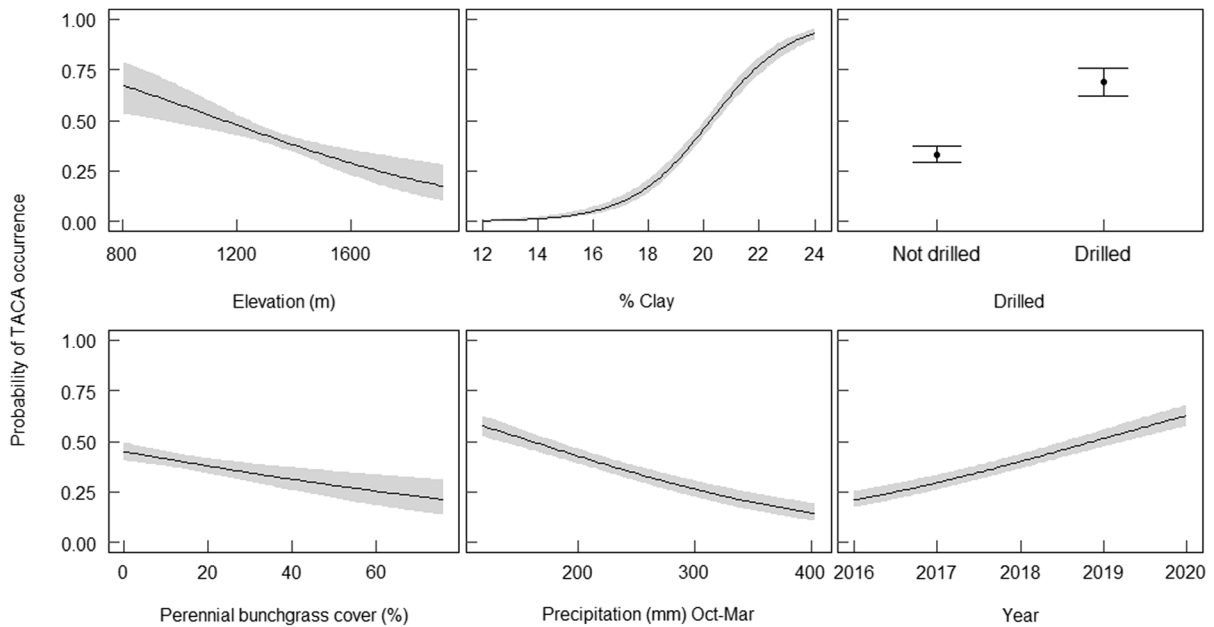


Fig. 5 Marginal effects of significant landscape predictors on probability of medusahead (TACA) occurrence. From top-left, left to right by row: elevation (meters), percent clay in the soil, drill-seeded or not, perennial bunchgrass cover, cumulative

precipitation between October and March (in millimeters), and year. The median effect is shown as the black line and the shaded ribbons are 95% credible intervals of the posterior

(higher elevation, more precipitation, more bunchgrass cover, less soil clay) were useful metrics for explaining medusahead presences and cover but did not necessarily confer the same resistance against *ventenata*. Our results indicate a more complex relationship between different exotic annual invaders (and perennial bunchgrasses) that cannot be simply explained via invasional meltdown or a continuous positive feedback loop, as we did not find strong signals of facilitation among all three species. Given the observational, correlational nature of this study, these results bring up questions that could be further explored in controlled experiments.

Species co-occurrence

One explanation for facilitation among the exotic annual grass species we evaluated could involve both displacement of native competitors, which are predominately perennial grasses in the landscapes we evaluated, and then alteration of nutrient availability, specifically nitrogen.

A controlled pot study revealed that (1) medusahead but not *ventenata* has a similar high-accumulation of foliar nitrogen at both low and high soil-

nitrogen levels as cheatgrass, and, moreover, (2) cheatgrass and medusahead but not *ventenata* had greater leaf nitrogen accumulation compared to natives (James 2008). While past studies do not consistently report that cheatgrass causes net increases or decreases in soil nitrogen, they do indicate that cheatgrass accelerates nitrogen cycling in ways that create mineral, bioavailable nitrogen pulses in soil that benefit it over native species (reviewed in Germino et al. 2016). By sharing nitrogen uptake traits, medusahead but not *ventenata* thereby could be facilitated by previous cheatgrass invasion in our hypothetical explanation. Another factor that could contribute to the disassociation of *ventenata* and cheatgrass could be *ventenata*'s tendency to occur in relatively cooler and wetter sites, ie niche separation (Jones et al. 2018).

Established perennial bunchgrass species are considered the most important ecosystem component for increasing resistance to annual grass invasion in sagebrush-steppe and other habitats (Chambers et al. 2014, Davies and Johnson 2017). Some perennial bunchgrass species may confer more resistance against exotic annual grass invaders than others. Notably, we observed different disassociations

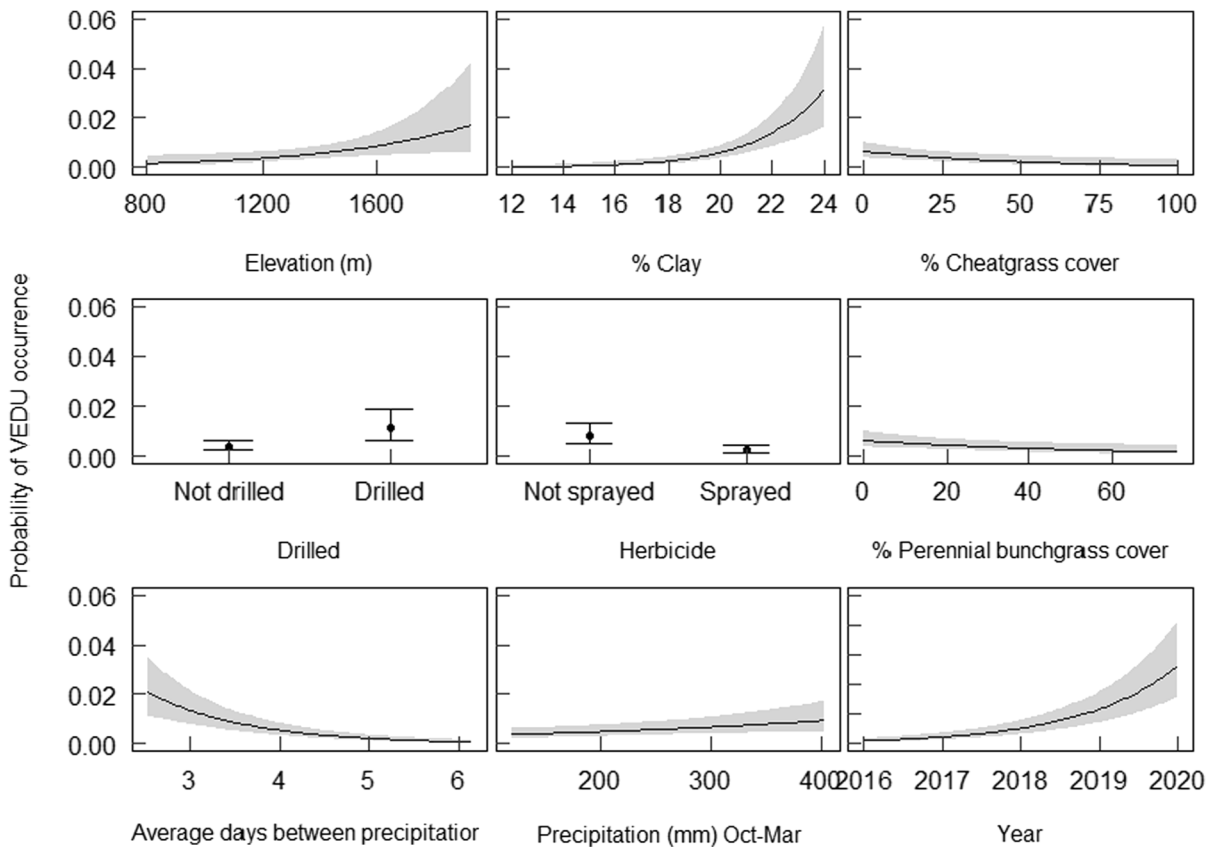


Fig. 6 Marginal effects of significant landscape predictors on probability of ventenata (VEDU) occurrence. From top-left, left to right by row: elevation (meters), percent clay in the soil, percent cheatgrass cover, drill seeding treatment, herbicide treatment, percent perennial bunchgrass cover, average days

between precipitation, cumulative between October and March (in millimeters), and year. The median effect is shown as the black line and the shaded ribbons are 95% credible intervals of the posterior

between various perennial bunchgrass species and each exotic annual grass invader. Of the common species we assessed, no single bunchgrass species was negatively associated with all three invaders. All three large-statured bunchgrasses (excluding Sandberg’s bluegrass) were negatively related with cheatgrass, while only the non-native crested wheatgrass was negatively associated with medusahead. Crested wheatgrass, which had a negative relationship to all the native perennial species we evaluated, is known to be a strong competitor and dominate areas where it is seeded to the exclusion of many other species, including medusahead (Davies et al. 2010, Nafus et al. 2015).

The variation in relationships between the low-statured widespread perennial grass Sandberg’s bluegrass and all three exotic annual species was

particularly noteworthy because Sandberg’s bluegrass is often not considered a strong competitor with annual grasses (Herget et al. 2015). While Sandberg’s bluegrass was positively associated with cheatgrass it was negatively related to both medusahead and ventenata. Our results indicate three possibilities; a successional gradient whereby Sandberg’s bluegrass facilitates or at least does not inhibit invasion by cheatgrass, which could then facilitate invasion by medusahead, Sandberg’s bluegrass inhibits invasion by medusahead or ventenata in a way that other native perennial grass species do not but yet it does not inhibit cheatgrass, or medusahead and ventenata exclude Sandberg’s bluegrass but do not compete as strongly with large statured perennial grasses. A prior study did indeed suggest that Sandberg’s bluegrass densities decrease when medusahead densities increase, but as this study

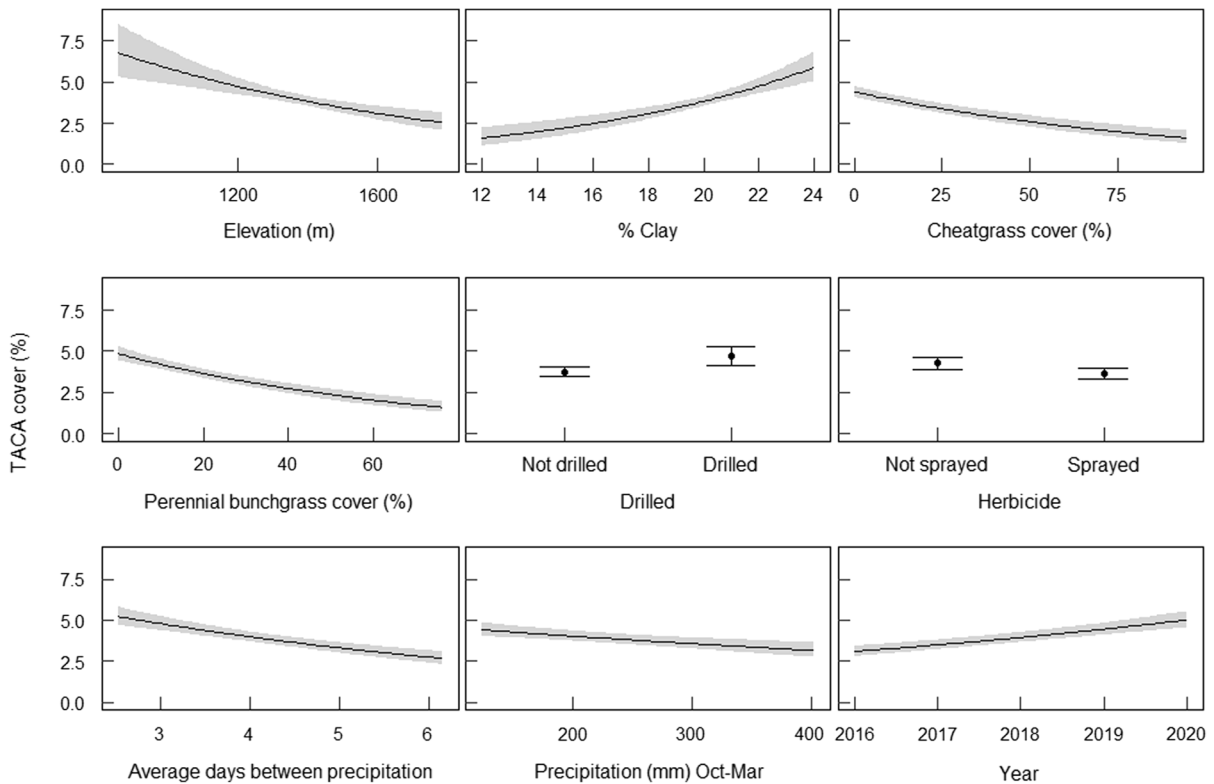


Fig. 7 Marginal effects of significant landscape predictors on medusahead (TACA) cover. From top-left, left to right by row: elevation (meters), percent clay in the soil, percent cheatgrass cover, perennial bunchgrass cover, drill-seeded or not, herbicide

treatment, average days between precipitation, cumulative precipitation between October and March (in millimeters), and year. The median effect is shown as the black line and the shaded ribbons are 95% credible intervals of the posterior

was also correlational in nature, directionality of competition is unclear (Davies 2011). These questions remain an opportunity for future experimental studies, given the limitations of a correlational analysis for determining causation.

Spatial patterning of invasion

Fire may present an opportunity for all exotic annual grass species to expand their populations from relatively rare to widespread and/or locally abundant (D'Antonio and Vitousek 1992). Buckley et al. (2007) showed that when exotic species promoted disturbance in surrounding unoccupied locations (as is the case with exotic annual grasses, which may promote fire burning into unoccupied native sagebrush-steppe communities), populations could expand from rarity to widespread. Invasion hotspots of medusahead and ventenata were more spatially constricted than trends in cheatgrass spatial patterning. This is unsurprising

based on past research on the distribution of different exotic annual grass species in sagebrush steppe. Cheatgrass is widespread across a variety of different landscapes and can be either locally abundant or locally sparse, while medusahead is more spatially constrained but usually locally abundant where it is present (Bradley 2013). As a more recent invader, ventenata likely has not yet realized the entirety of its potential niche (Jones et al. 2018); and we found it only in a very localized area. Although exotic annual grass hotspots fluctuated between years and showed contraction in certain years (most notably after herbicide application in the northwest section of the fire before 2017), hotspots for both entire exotic annual grass community and medusahead and ventenata began to appear in more new places throughout the 5 years post fire.

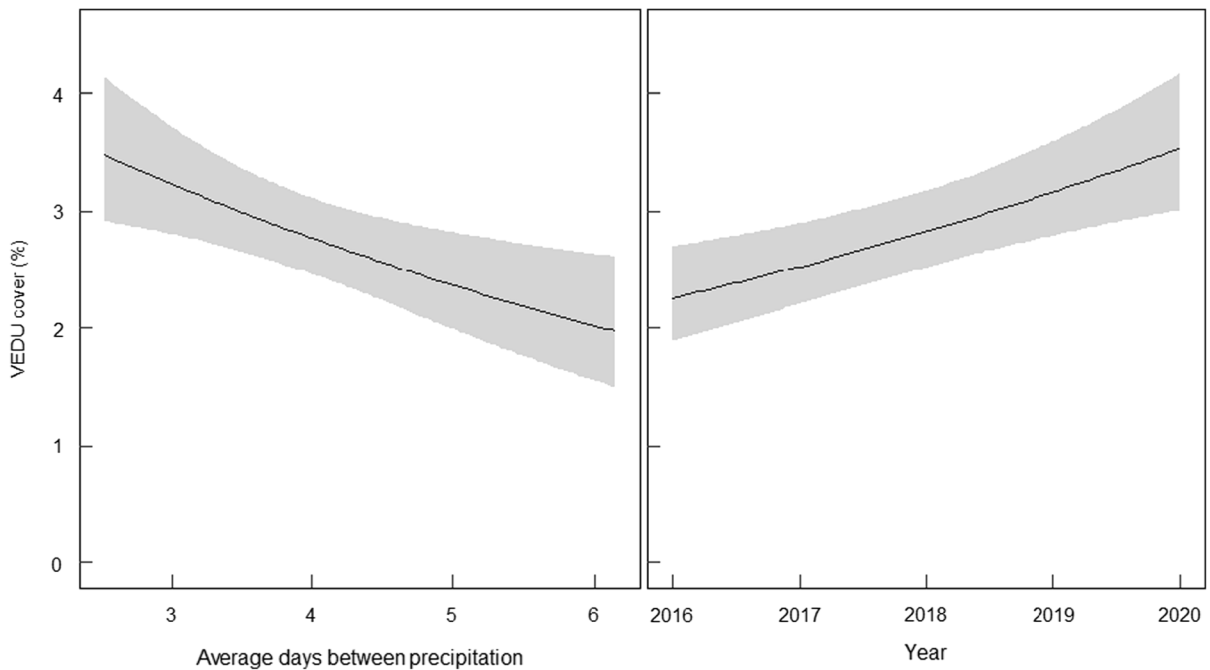


Fig. 8 Marginal effects of significant landscape predictors on ventenata (VEDU) cover; average days between precipitation (left) and year (right). The median effect is shown as the black line and the shaded ribbons are 95% credible intervals of the posterior

Landscape resistance

Our findings on factors limiting medusahead and ventenata occupancy and abundance largely agreed with previous studies and highlight niche differences between the two species. We found that medusahead shares a similar niche as that known for cheatgrass, occupying low elevation sites with low winter and spring precipitation (Chambers et al. 2014). Conversely, probability of ventenata occupancy increased with higher elevation and higher winter/spring precipitation. Cover of both species in occupied sites decreased with number of average days between precipitation, which was unexpected based on Bansal et al. (2014a) who found an increase in medusahead biomass with larger more infrequent water pulses. It may be that greater biomass does not necessarily correlate with greater cover or that growth = chamber results showing a competitive advantage around certain precipitation regimes do not transfer well to field conditions, where competition, chilling, and severe vapor deficits complicate plant water relations. Both ventenata and medusahead were found more frequently in areas with higher clay content, in agreement with Jones et al. (2018). Clay soils drain

slowly and maintain water near the surface, where it is easily accessible to the shallow roots of annual grasses. Combined with the relationship of ventenata to more frequent precipitation, this suggests that ventenata capitalizes upon wetter microsites in arid sagebrush-steppe habitat (also in agreement with Jones et al. 2018).

Cover and occupancy of both invaders increased as total perennial bunchgrass cover decreased, although results of our co-occurrence analysis indicate that specific species composition of the perennial bunchgrass community mattered. These results suggest both invaders have the ability to exploit disturbed space on the landscape and replace perennial bunchgrass, and also that generally higher perennial bunchgrass cover does provide increased resistance to both invaders, as expected. This aligns with previous research in sagebrush steppe regarding the importance of perennial bunchgrass cover for providing invasion resistance against cheatgrass and medusahead (Davies et al. 2010; Davies 2011, Chambers et al. 2014). Prior studies on ventenata in the Pacific Northwest have been less conclusive, suggesting that ventenata can co-exist in areas with moderate perennial bunchgrass cover (Tortorelli et al. 2020; Jones et al. 2020).

The relationship of each invader with cheatgrass cover was more nuanced. *Ventenata* was less likely to occur in areas with high cheatgrass cover, providing additional support for the idea that these two species do not facilitate one another and that one may inhibit the other or that the two species occupy different niches. Although *medusahead* and cheatgrass frequently occurred together (as shown in the co-occurrence analysis), *medusahead* cover in areas was inversely related to cheatgrass cover, indicating that one of these invaders may eventually win out as the local 'dominant' invader. Both species benefit from creating a litter layer, which moderates temperature and moisture and increases germination of seed, ultimately modifying the environment specifically to promote their own dominance. Studies suggest that *medusahead* benefits more than cheatgrass from this feedback effect (Young and Evans 1970).

Effects of landscape interventions on both invader occurrences and cover showed mixed effects. Many invasions rely on priority effects, i.e. advantages gained by early arriving individuals (Fraser et al. 2015). Indeed, in semi-arid systems, priority effects can have significant impacts on dominance of either native perennial grasses or exotic annual grasses (Vaughn and Young 2015; Young et al. 2015). The concept behind both herbicide application and drill seeding (especially in combination) is to temporarily remove invasive species to provide priority effects to native perennial bunchgrasses. As expected, herbicide application (which on our landscape was largely targeted at cheatgrass (the dominant invader) reduced occupancy of both exotic annual grasses and cover of *medusahead* (*ventenata* cover was generally too low to see an effect). However, probability of both *medusahead* and *ventenata* occurring and cover of *medusahead* increased with drill seeding. This could reflect either a response of each invader to soil disturbance and exploitation of new open space or it could reflect land manager's choices to drill seed in areas at higher risk of invasion. Interventions are frequently successful in slowing but not stopping reinvasion in burned sagebrush-steppe communities (e.g. Davies et al. 2015; Kyser et al. 2013, Davies et al. 2019 all showed exotic annual grasses were less abundant in treated areas than untreated areas but still increased with time after either drill seeding or herbicide use). Extent of invasion and density of invaders may be a key component of intervention success; restoration and rehabilitation efforts taken

before an invasion threshold has been crossed are generally most successful (Pyke et al. 2015). In our study area, both *medusahead* and *ventenata* were relatively rare. Thus, landscape interventions were targeted during a time period in which both species had an opportunity to exploit newly created niche space but were not yet widespread.

Conclusions

Our study revealed key differences in invasion patterns and successional mechanisms among exotic annual grasses, an otherwise narrowly defined functional guild. Agency management and even research often addresses the exotic annual grass community as a whole, and while we observed some uniformity in responses (e.g., to perennial grass cover), there were considerable differences in how each invader related to its environment. This has several implications for post-fire management. Firstly, when seeding perennial grasses, choosing seed mixes of species that best compete with a specific invader of concern or diversifying seed mixes to compete with different invaders may provide the best overall resistance to invasion. Secondly, treatment allocation on the landscape may depend on recognizing which invader was the greatest threat pre-fire or in the area surrounding a burned area. If *ventenata* is a concern, as opposed to cheatgrass or *medusahead*, treatments to increase landscape resistance may be allocated in wetter, higher elevation areas as opposed to lower land dry areas typically targeted to prevent cheatgrass or *medusahead* invasion.

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Author's contributions MJG led the conception of the study, procured funding, and directed the research. CA conducted the data analysis and led the writing. Both authors contributed critically to drafts and gave final approval for publication.

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Data availability All data will be available on U.S. Geological Survey ScienceBase Catalog.

Declarations

Conflict of interest The author's declared that they have no conflict of interest.

Appendix 1

See Tables 1 and 2.

Table 1 Priors for the parameters in the *T. caput-medusae* models

Parameter	Description	Prior	Scaled prior	Rationale
γ_0	Mean probability of occupancy	Normal (0,4)	Normal (0,4)	Default prior
γ_1	Elevation effect	Normal (0,4)	Normal (0,4)	Default prior
γ_2	Clay effect	Normal (0.095,4)	Normal (0.6931,4)	Medusahead is well known to be associated with clay soils (Nafus and Davies 2014), but we could not find any quantitative statistics relating percent clay to occupancy. We assume that this repeatedly observed effect is relatively strong. We set this prior at odds 1% increase in clay in the soils to relate to a 10% increase in odds of medusahead occurring. Odds ratio of 1.10 on log scale is 0.095
γ_3	Cheatgrass cover effect	Normal (0,4)	Normal (0,4)	Davies and Svejcar (2008) shows no difference in BRTE cover between areas invaded with TACA vs not invaded
γ_4	Perennial grass cover effect	Normal (-0.005,4)	Normal (-0.014, 4)	Davies (2011) suggests that increasing 1% in PBG reduces TACA cover by -0.04 to -0.03. This is a very small effect so we will give a prior assuming very small effect. 0.05% decrease in odds of TACA occurring per 1% increase in PBG cover. Odds ratio is 0.995. On a log scale = -0.0050
γ_5	Drill seeding effect	Normal (0,4)	Normal (0,4)	Default prior. All studies we could find combined herbicide with drill seeding so difficult to assess single term effect of drill seeding
γ_6	Herbicide effect	Normal (-0.5978, 4)	Normal (-0.5978,4)	Kyser et al. (2013) showed highly variable effects of imazapic on TACA, causing reductions in cover between 21 and 88%, with the average around 45% for the first year after application. If we assume cover reductions would be similar to frequency within small plot areas. The odds ratio of this would be 0.55, and on a log scale that is -0.5978
γ_7	Drill \times herbicide interaction	Normal (-2.3026, 4)	Normal (-2.3026,4)	James et al. (2015) in a meta-analysis showed that herbicide plus seeding resulted in a greater reduction than herbicide alone. Effect sizes were ranged from 1.5 to 3 = fold greater with combined treatments than herbicide alone. If we assume a twofold reduction in medusahead occurrence as a result of combined treatments, we might assume a 90% reduction (based on Kyser effects for herbicide). Odds ratio is 0.10 = log odds would be -2.3026
γ_8	Days between precipitation effect	Normal (0.049,4)	Normal (0.0750, 4)	Bansal et al. (2014a) suggests a 20% increase in biomass for TACA larger infrequent water pulses. Unclear how this might relate to occupancy, so we give a prior assuming a modest increase in medusahead with 1 extra average day between precipitation events relates to a 5% increase in odds ratio of TACA occurring. Odds ratio is 1.05 = 0.049
γ_9	Cumulative precipitation October–March	Normal (-0.051,4)	Normal (-9.2434, 4)	Turner et al. (1963) suggests medusahead is restricted to lower precipitation areas (annual precip under ~120 cm). We assume that a 1 cm increase in precipitation will result in a

Table 1 continued

Parameter	Description	Prior	Scaled prior	Rationale
γ_{10}	Year effect	Normal (0.4055, 4)	Normal (0.8796, 4)	5% decrease in the odds of TACA occupancy. Odds ratio is $0.95 = -0.051$ on log scale In Davies et al. (2015), in a medusahead dominated grassland, exotic annual grass cover increased by ~ 1.5 fold per year after a prescribed fire. We assume this would translate closely to the probability of finding medusahead in a small plot area so we assume a 50% increase per year after fire the odds ratio as $1.50 = 0.4055$ on a logscale
ω_0	Plot specific intercept	Student_t (3, 0, 2.5)	Student_t (3, 0, 2.5)	Default prior
γ_{11}	Time since drill seeding	Normal (0.3365, 4)	Normal (0.7280, 4)	While the effects of drilling seeding and herbicide application are somewhat confounded in the study, Davies et al. (2015) suggests that exotic annual grass cover increases with time since drill seeding by 1.5-fold per year. If we assume frequency in 1×1 m plots are similar to cover and that TACA is only one component of exotic annual grasses, we might estimate an increase of 40% highly probability of TACA occupancy with each year after drilling. Odds ratio of 1.40, on a log scale is 0.3365
γ_{12}	Time since herbicide	Normal (1.099, 4)	Normal (2.0108, 4)	We would expect the effect of herbicide to decrease over time (so increase in TACA with more time since treatment). With regards to imazapic application in the first 3years, Kyser et al. 2013 found \sim threefold increase per year in medusahead cover relative in herbicide plots as compared to control plots. Odds ratio is 3.00 = log odds would be 1.099

Scaled priors were adjusted to match scaled variables transformed by dividing by two standard deviations of the variable. Species acronyms follow the USDA Plants database <http://plants.usda.gov>

Table 2 Priors for the parameters in the *V. dubia* models

Parameter	Description	Prior	Scaled prior	Rationale
γ_0	Mean probability of occupancy	Normal (0, 4)	Normal (0, 4)	Default prior
γ_1	Elevation effect	Normal (0, 4)	Normal (0, 4)	Thomas et al. (2020) suggests that Ventenata occurs across an elevation range and may not be associated with elevation
γ_2	Clay effect	Normal (0.131, 4)	Normal (2.6323, 4)	Jones et al. (2018) regression indicates that the difference in clay percentage between 0 and 1% VEDU cover is $\sim 7\%$ clay. Assuming that odds ratio increases on a similar scale between 0 and 1%, we might assume that 1% increase in clay relates to a 14% increase in the chance of VEDU occurring. So we assume a mean odds ratio of 1.14, which gives $\ln(1.14) = 0.131$ on the log scale
γ_3	Cheatgrass cover effect	Normal (- 0.010, 4)	Normal (- 0.4105, 4)	Tortorelli et al. (2020) suggest negative effect with annual grass in burned areas. Approximately 10% change in annual grass cover (relative) with 10% change in Venenata. We will estimate the prior at a 1-1 relationship. 1% increase in annual grass cover relates to a 1% lesser odds ratio of Venenata. Odds ratio of 0.99 = - 0.010
γ_4	Perennial grass cover effect	Normal (0, 4)	Normal (0, 4)	Tortorelli et al. (2020) suggest possible slight negative effect in burned areas but 95% confidence intervals include no change so setting average at 0
γ_5	Drill seeding effect	Normal (0, 4)	Normal (0, 4)	Default prior

Table 2 continued

Parameter	Description	Prior	Scaled prior	Rationale
γ_6	Herbicide effect	Normal (- 0.4155, 4)	Normal (- 0.4155, 4)	Davies et al. (2019) suggests 105 g ae*ha ⁻¹ imazapic results in reductions of approximately 34% exotic annual grass cover (mostly <i>Ventenata</i>) one year after application. If we assume that cover is similar to frequency, the odds ratio is 0.66, on a log scale that is - 0.4155
γ_7	Drill \times herbicide interaction	Normal (0,4)	Normal (0,4)	Default prior
γ_8	Days between precipitation effect	Normal (0,4)	Normal (0,4)	Bansal et al. (2014a) suggests no effect
γ_9	Cumulative precipitation October–March	Normal (0.0050,4)	Normal (0.4765, 4)	Thomas et al. (2020) suggests <i>Venenata</i> occurs with wetter winters but their variable (winter water deficit) is not directly translatable to cumulative winter precipitation. We will set a conservative prior estimate of a slight positive effect of cumulative winter weather on <i>Ventenata</i> 0.5% increase in odds ratio associated with 1 additional mm in precip (which relates to a 5% increase with 10 mm increase in precip). Odds ratio is 1.005. On a log scale = 0.0050
γ_{10}	Year effect	Normal (0.2546,4)	Normal (0.5984,4)	Both Tortorelli et al. (2020) and Ridder et al. (2021) suggest that <i>Venenata</i> is not more abundant and does not increase more in burned versus unburned plots. However, the general trajectory of the species is increasing in frequency and abundance across the region. We would expect frequency to still increase over time on our plots. Ridder et al. (2021) showed a twofold increase in frequency over 7 years, which equates to ~ 29% increase per year. We set the odds ratio to 1.29 = 0.2546422 on log scale
ω_0	Plot specific intercept	Student_t (3, 0, 2.5)	Student_t (3, 0, 2.5)	Default prior
γ_{11}	Time since drill seeding	Normal (0,4)	Normal (0,4)	Default prior
γ_{12}	Time since herbicide	Normal (0.0953,4)	Normal (0.0966, 4)	Davies et al. (2019) suggests the difference between control and herbicide applied areas decreases by about 10% in exotic annual grass cover (ie <i>Ventenata</i>) per year after herbicide. Odds ratio 1.10, o the log scale is 0.0953

Scaled priors were adjusted to match scaled variables transformed by dividing by two standard deviations of the variable

References

- Applestein C, Caughlin TT, Germino MJ (2021) Weather affects post-fire recovery of sagebrush-steppe communities and model transferability among sites. *Ecosphere* 12(4):e03446. <https://doi.org/10.1002/ecs2.3446>
- Applestein C, Germino MJ, Fisk MR (2018) Vegetative community response to landscape-scale post-fire herbicide (imazapic) application. *Invasive Plant Sci Manag* 11(3):127–135. <https://doi.org/10.1017/inp.2018.18>
- Bansal S, James JJ, Sheley RL (2014a) The effects of precipitation and soil type on three invasive annual grasses in the western United States. *J Arid Environ* 104:38–42. <https://doi.org/10.1016/j.jaridenv.2014.01.010>
- Bansal S, Sheley RL, Blank B, Vasquez EA (2014b) Plant litter effects on soil nutrient availability and vegetation dynamics: changes that occur when annual grasses invade shrub-steppe communities. *Plant Ecol* 215(3):367–378. <https://doi.org/10.1007/s11258-014-0307-1>
- Bishop TB, Nusink BC, Lee Molinari R, Taylor JB, St. Clair SB, (2020) Earlier fall precipitation and low severity fire impacts on cheatgrass and sagebrush establishment. *Ecosphere* 11(1):e03019. <https://doi.org/10.1002/ecs2.3019>
- Bradley BA (2013) Distribution models of invasive plants overestimate potential impact. *Biol Invasions* 15(7):1417–1429. <https://doi.org/10.1007/s10530-012-0380-0>
- Britton-Simmons KH, Abbott KC (2008) Short-and long-term effects of disturbance and propagule pressure on a biological invasion. *J Ecol* 96(1):68–77. <https://doi.org/10.1111/j.1365-2745.2007.01319.x>

- Brooks ML, Chambers JC (2011) Resistance to invasion and resilience to fire in desert shrublands of North America. *Range Ecol Manag* 64(5):431–438. <https://doi.org/10.2111/REM-D-09-00165.1>
- Buckley YM, Bolker BM, Rees M (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecol Lett* 10(9):809–817. <https://doi.org/10.1111/j.1461-0248.2007.01067.x>
- Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC, Hulme PE (2012) The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspect Plant Ecol Evol Syst* 14(3):231–241. <https://doi.org/10.1016/j.ppees.2011.12.002>
- Chambers JC, Miller RF, Board DI, Pyke DA, Roundy BA, Grace JB, Schupp EW, Tausch RJ (2014) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Range Ecol Manag* 67(5):440–454. <https://doi.org/10.2111/REM-D-13-00074.1>
- Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
- D'Antonio C, Levine J, Thomsen M (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J Mediterr Ecol* 2:233–246
- D'Antonio CM, Vitousek PM (1992) Biological Invasions by exotic grasses, the grass/fire cycle, and global change. *Ann Rev Ecol Evol S* 23(1):63–87
- Davies KW, Nafus AM, Sheley RL (2010) Non-native competitive perennial grass impedes the spread of an invasive annual grass. *Biol Invasion* 12(9):3187–3194. <https://doi.org/10.1007/s10530-010-9710-2>
- Davies KW (2011) Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecol* 167(2):481–491. <https://doi.org/10.1007/s00442-011-1992-2>
- Davies KW, Boyd CS, Johnson DD, Nafus AM, Madsen MD (2015) Success of seeding native compared with introduced perennial vegetation for revegetating medusahead-invaded sagebrush rangeland. *Rangel Ecol Manag* 68(3):224–230. <https://doi.org/10.1016/j.rama.2015.03.004>
- Davies KW, Boyd CS (2018) Longer-term evaluation of revegetation of medusahead-invaded sagebrush steppe. *Rangel Ecol Manag* 71(3):292–297. <https://doi.org/10.1016/j.rama.2018.02.001>
- Davies KW, Hamerlynck E (2019) Ventenata and other coexisting exotic annual grass control and plant community response to increasing imazapic application rates. *Rangel Ecol Manag* 72(4):700–705. <https://doi.org/10.1016/j.rama.2019.02.010>
- Davies KW, Johnson DD (2017) Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. *Range Ecol Manag* 70(6):748–754. <https://doi.org/10.1016/j.rama.2017.06.001>
- Davies KW, Svejcar TJ (2008) Comparison of medusahead-invaded and noninvaded Wyoming big sagebrush steppe in southeastern Oregon. *Range Ecol Manag* 61(6):623–629. <https://doi.org/10.2111/08-005.1>
- Davis MA, Grime JP, Thomson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534. <https://doi.org/10.1046/j.1365-2745.2000.00473.x>
- Fraser CI, Banks SC, Waters JM (2015) Priority effects can lead to underestimation of dispersal and invasion potential. *Biol Invasions* 17:1–8. <https://doi.org/10.1007/s10530-014-0714-1>
- Gelman A, Jakulin A, Pittau MG, Su YS (2008) A weakly informative default prior distribution for logistic and other regression models. *Ann Appl Stat* 2(4):1360–1383. <https://doi.org/10.1214/08-AOAS191>
- Germino MJ, Belnap J, Stark JM, Allen EB, Rau BM (2016) Ecosystem impacts of exotic annual invaders in the genus *Bromus*. In: Germino MJ, Chambers JC, Brown CS (eds) *Exotic brome-grasses in arid and semiarid ecosystems of the Western US*. Springer, Cham Switzerland, pp 61–69
- Getis A, Ord JK (2010) The analysis of spatial association by use of distance statistics. In: Anselin L, Rey SJ (eds) *Perspectives on spatial data analysis*. Springer, Berlin Heidelberg, pp 127–145
- Green PT, O'Dowd DJ, Abbott KL, Jeffery M, Retallick K, Mac Nally R (2011) Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecol* 92(9):1758–1768. <https://doi.org/10.1890/11-0050.1>
- Griffith DM, Veech JA, Marsh CJ (2016) Cooccur: probabilistic species co-occurrence analysis in R. *J Stat Soft* 69(2):1–7. <https://doi.org/10.18637/jss.v069.c02>
- Herget ME, Hufford KM, Mummey DL, Meador BA, Shreading LN (2015) Effects of competition with *Bromus tectorum* on early establishment of *Poa secunda* accessions: can seed source impact restoration success? *Rest Ecol* 23(3):277–283. <https://doi.org/10.1111/rec.12177>
- James JJ (2008) Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *J Arid Environ* 72(10):1775–1784. <https://doi.org/10.1016/j.jaridenv.2008.05.001>
- James JJ, Gornish ES, DiTomaso JM, Davy J, Doran MP, Becchetti T, Lile D, Brownsey P, Laca EA (2015) Managing medusahead (*Taeniatherum caput-medusae*) on rangeland: a meta-analysis of control effects and assessment of stakeholder needs. *Rangel Ecol Manag* 68(3):215–223. <https://doi.org/10.1016/j.rama.2015.03.006>
- Jones LC, Davis C, Prather TS (2020) Consequences of *Ventenata dubia* 30 years post-invasion to bunchgrass communities in the Pacific Northwest. *Invas Plant Sci Mana* 13(4):226–238. <https://doi.org/10.1017/inp.2020.29>
- Jones LC, Norton N, Prather TS (2018) Indicators of ventenata (*Ventenata dubia*) invasion in sagebrush steppe rangelands. *Invasive Plant Sci Manag* 11(1):1–9. <https://doi.org/10.1017/inp.2018.7>
- Klemmedson JO, Smith JG (1964) Cheatgrass (*Bromus tectorum* L.). *Bot Rev* 30(2):226–62. <https://doi.org/10.1007/BF02858603>
- Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, Brooks ML, Chambers JC, Grace JB (2014) Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *J Appl Ecol* 51(5):1414–1424. <https://doi.org/10.1111/1365-2664.12309>

- Kyser GB, Wilson RG, Zhang J, DiTomaso JM (2013) Herbicide-assisted restoration of great Basin sagebrush steppe infested with medusahead and downy brome. *Rangel Ecol Manag* 66(5):588–596. <https://doi.org/10.2111/REM-D-12-00184.1>
- Lemoine NP (2019) Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128(7):912–928. <https://doi.org/10.1111/oik.05985>
- Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D (2019) Indices of effect existence and significance in the Bayesian framework. *Front Psychol* 10:2767. <https://doi.org/10.3389/fpsyg.2019.02767>
- McKay S, Morris LR, Morris CE, Leger EA (2017) Examining the potential competitive effects of *Ventenata dubia* on annual and perennial grasses. *Prairie Nat* 49:19–22
- Metier EP, Rew LJ, Rinella MJ (2018) Establishing Wyoming big sagebrush in annual brome-invaded landscapes with seeding and herbicides. *Rangel Ecol Manag* 71(6):705–713
- Miller RF, Knick ST, Pyke DA, Meinke CW, Hanser SE, Wisdom MJ, Hild AL (2011) Characteristics of sagebrush habitats and limitations to long-term conservation. In Knick S, Connelly JW (eds) *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*, pp 145–184. *Stud in Avian Biol* (38), University of California Press, Berkeley, California
- Morris C, Monaco TA, Rigby CW (2009) Variable impacts of imazapic rate on downy brome (*Bromus tectorum*) and seeded species in two rangeland communities. *Invasive Plant Sci Manag* 2(2):110–119. <https://doi.org/10.1614/IPSM-08-104.1>
- Nafus AM, Davies KW (2014) Medusahead ecology and management: California annual grasslands to the Intermountain West. *Invasive Plant Sci Manag* 7(2):210–221. <https://doi.org/10.1614/IPSM-D-13-00077.1>
- Nafus AM, Svejcar TJ, Ganskopp DC, Davies KW (2015) Abundances of coplanted native bunchgrasses and crested wheatgrass after 13 years. *Rangel Ecol Manag* 68(2):211–214. <https://doi.org/10.1016/j.rama.2015.01.011>
- O’Loughlin LS, Green PT (2017) Secondary invasion: when invasion success is contingent on other invaders altering the properties of recipient ecosystems. *Ecol Evol* 7(19):7628–7637. <https://doi.org/10.1002/ece3.3315>
- Pavek P, Wallace J, Prather T (2011) *Ventenata* biology and distribution in the Pacific Northwest. *Proc Western Soc Weed Sci* 64:107
- Pyke DA, Chambers JC, Pellant M, Knick ST, Miller RF, Beck JL, Doescher PS, Schupp EW, Roundy BA, Brunson M, McIver JD (2015) Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat: part 1. Circular 1416. Washington, DC: U.S. Department of the Interior; Reston, VA: U.S. Geological Survey. p. 43
- Ridder LW, Perren JM, Morris LR, Endress BA, Taylor RV, Naylor BJ (2021) Historical fire and *Ventenata dubia* invasion in a temperate grassland. *Rangel Ecol Manag* 75:35–40. <https://doi.org/10.1016/j.rama.2020.11.006>
- Roundy BA, Chambers JC, Pyke DA, Miller RF, Tausch RJ, Schupp EW, Rau B, Gruell T (2018) Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* 9(9):e02417. <https://doi.org/10.1002/ecs2.2417>
- Schroeder MA, Aldridge CL, Apa AD, Bohne JR, Braun CE, Bunnell SD, Connelly JW, Deibert PA, Gardner SC, Hilliard MA, Kobriger GD (2004) Distribution of sage-grouse in North America. *Condor* 106(2):363–376. <https://doi.org/10.1093/condor/106.2.363>
- Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biol Invasions* 1(2):107–114. <https://doi.org/10.1023/A:1010050420466>
- Smithson M, Verkuilen J (2006) A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychol Methods* 11(1):54. <https://doi.org/10.1037/1082-989x.11.1.54>
- Thomas NM, Rodhouse J, Stucki DS, Shinderman M (2020) Rapid invasion by the annual grass *ventenata dubia* into protected-area, low-elevation sagebrush steppe. *West N Am Nat* 80(2):243–252. <https://doi.org/10.3398/064.080.0212>
- Tortorelli CM, Krawchuk MA, Kerns BK (2020) Expanding the invasion footprint: *Ventenata dubia* and relationships to wildfire, environment, and plant communities in the Blue Mountains of the Inland Northwest, USA. *Appl Veg Sci* 23(4):562–574. <https://doi.org/10.1111/avsc.12511>
- Turner RB, Poulton CE, Gould WL (1963) *Medusahead: a threat to Oregon rangeland*. Oregon State University, Agricultural Experiment Station, Special report 149
- Vaughn KJ, Young TP (2015) Short-term priority over exotic annuals increases the initial density and longer-term cover of native perennial grasses. *Ecol Appl* 25(3):791–799. <https://doi.org/10.1890/14-0922.1>
- Wallace JM, Pavek PL, Prather TS (2015) Ecological characteristics of *Ventenata dubia* in the Intermountain Pacific Northwest. *Invasive Plant Sci Manag* 8(1):57–71. <https://doi.org/10.1614/IPSM-D-14-00034.1>
- Wilcox BP, Turnbull L, Young MH, Williams CJ, Ravi S, Seyfried MS, Bowling DR, Scott RL, Germino MJ, Caldwell TG, Wainwright J (2012) Invasion of shrublands by exotic grasses: ecophysiological consequences in cold versus warm deserts. *Ecohydrol* 5(2):160–173. <https://doi.org/10.1002/eco.247>
- Young JA (1992) Ecology and management of medusahead (*Taeniatherum caput-medusae* ss.p *asperum* [Simk.] Melderis). *Great Basin Nat* 52(3):245–52
- Young JA, Evans RA (1970) Invasion of medusahead into the Great Basin. *Weed Sci* 18(1):89–97. <https://doi.org/10.1017/S0043174500077419>
- Young TP, Zefferman EP, Vaughn KJ, Fick S (2015) Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. *AoB Plants* 7:plu081. <https://doi.org/10.1093/aobpla/plu081>

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