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RESEARCH ARTICLE

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Expanding the invasion footprint: *Ventenata dubia* and relationships to wildfire, environment, and plant communities in the Blue Mountains of the Inland Northwest, USA

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Abstract

Questions: A recently introduced non-native annual grass, *Ventenata dubia*, is challenging previous conceptions of community resistance in forest mosaic communities in the Inland Northwest. However, little is known of the drivers and potential ecological impacts of this rapidly expanding species. Here we (1) identify abiotic and biotic habitat characteristics associated with the *V. dubia* invasion and examine how these differ between *V. dubia* and other problematic non-native annual grasses, *Bromus tectorum* and *Taeniatherum caput-medusae*; and (2) determine how burning influences relationships between *V. dubia* and plant community composition and structure to address potential impacts on Inland Northwest forest mosaic communities.

Location: Blue Mountains of the Inland Northwest, USA.

Methods: We measured environmental and plant community characteristics in 110 recently burned and nearby unburned plots. Plots were stratified to capture a range of *V. dubia* cover, elevations, biophysical classes, and fire severities. We investigated relationships between *V. dubia*, wildfire, environmental, and plant community characteristics using non-metric multidimensional scaling and linear regressions.

Results: *Ventenata dubia* was most abundant in sparsely vegetated, basalt-derived rocky scablands interspersed throughout the forested landscape. Plant communities most heavily invaded by *V. dubia* were largely uninvaded by other non-native annual grasses. *Ventenata dubia* was abundant in both unburned and burned areas, but negative relationships between *V. dubia* cover and community diversity were stronger in burned plots, where keystone sagebrush species were largely absent after fire.

Conclusions: *Ventenata dubia* is expanding the overall invasion footprint into previously uninvaded communities. Burning may exacerbate negative relationships between *V. dubia* and species richness, evenness, and functional diversity, including in communities that historically rarely burned. Understanding the drivers and impacts of the *V. dubia* invasion and recognizing how these differ from other annual grass invasions may provide insight into mechanisms of community invasibility, grass-fire feedbacks, and aid the development of species-specific management plans.

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KEYWORDS
annual grass, *Bromus tectorum*, forest, grass-fire cycle, Inland Northwest, invasive species, non-native plants, scabland

1 | INTRODUCTION

Over the past century, non-native annual grass invasions have transformed the American West. Throughout much of the Great Basin, southwestern deserts, and Californian Mediterranean regions, non-native annual grasses have initiated grass-fire cycles that have converted invaded shrublands to annual grasslands, altering community dynamics, hydrologic and nutrient cycling, reducing livestock forage, and increasing fire frequency and extent (Mack, 1981; D'Antonio and Vitousek, 1992; Brooks *et al*., 2004, 2016; Fusco *et al*., 2019). In contrast, many Inland Northwest shrublands and forests remain relatively unaffected by annual grass invasion (Chambers *et al*., 2007; Brooks *et al*., 2016; Fusco *et al*., 2019), despite having been exposed to propagule pressure from nearby invasions for decades (Johnson and Swanson, 2005). However, some historically resistant communities have shown susceptibility to the recently introduced non-native annual grass, *Ventenata dubia* (commonly known as ventenata), challenging previous conceptions of community resistance to annual grass invasion and potentially expanding the grass-fire cycle footprint into Inland Northwestern dry forest mosaic communities (Youngblood *et al*., 2006; Bansal *et al*., 2014; Jones *et al*., 2018; Downing *et al*., 2020).

Invasion success is heavily driven by the environmental and biotic characteristics of the recipient community, in concert with propagule pressure. Ecosystems with abundant available resources (e.g., soil moisture, nutrients, or sunlight) are often considered more susceptible to invasion than those with low resource availability (Elton, 1958; Davis *et al*., 2000). For example, nutrient-limited serpentine soils in California maintain low abundances of non-native species despite these same species thriving on adjacent non-serpentine soils (McNaughton, 1968; Harrison, 1999). Alternatively, in productive ecosystems, competition from established species may reduce net resource availability and increase community resistance to invasion (Davis *et al*., 2000).

Resistant communities can become susceptible to invasion if disturbance creates opportunities for invaders by reducing competition from resident species and increasing available resources (D'Antonio and Vitousek, 1992; Davis *et al*., 2000; Chambers *et al*., 2007; Chambers *et al*., 2014). Establishment of annual grasses can increase surface fuel loads and fire activity in their recipient communities, improving conditions for further invasion and generating a positive feedback between invasion and fire (Mack and D'Antonio, 1998; Brooks *et al*., 2004). A notable example of this exists in the Great Basin of western North America where the non-native annual grass *Bromus tectorum* (cheatgrass) increases fine fuel accumulation, continuity, and ignitability in invaded sage-steppe ecosystems. *Bromus tectorum* recovers quickly after fire, often generating grass-fire cycles that result in state shifts in invaded and burned communities previously dominated by species that evolved under pressure from low intensity and infrequent or patchy fires and recover more slowly than fast-growing non-native annuals (Young and Evans, 1970; Balch *et al*., 2013).

Since its introduction to eastern Washington state in 1952 (Barkworth *et al*., 1993), *V. dubia* has spread to 10 US states and four Canadian provinces (USDA plants 2020). *Ventenata dubia* is now widespread across Inland Northwest pastures and natural areas and is rapidly expanding into California's Mediterranean shrublands and throughout the Great Basin (Pavek *et al*., 2011; USDA-NRCS, 2019). *Ventenata dubia*, like *B. tectorum*, is a cool-season C3 grass that germinates in the fall, allowing it to take advantage of early spring moisture in the otherwise dry growing season (Wallace *et al*., 2015). Once established, *V. dubia* grows quickly and senesces in early summer after seed set when soil moisture is depleted. These characteristics, along with *V. dubia*'s high reproductive potential (Wallace *et al*., 2015), may provide *V. dubia* a competitive advantage over established native species, especially in historically sparsely vegetated communities that were previously resistant to fire and invasion. However, the extent to which *V. dubia* actively competes with native species, the influence of fire on *V. dubia*'s competitive potential, and the overall impacts of *V. dubia* invasion on community composition and structure remain relatively unexplored.

Invasive species management becomes increasingly challenging as the invasion progresses (Harvey and Mazzotti, 2014). It is imperative to develop an understanding of the drivers and impacts of new non-native species in early invasion stages to inform proactive management strategies, aid early detection and rapid response, and curb invasion spread. Although prevalent across many Inland Northwest communities, it is believed that *V. dubia* has not yet met its full invasion potential (Jones *et al*., 2018). Here, we use field collections of plant community and site characteristics across the Inland Northwest to: (1) identify abiotic and biotic habitat characteristics associated with the *V. dubia* invasion and examine how these drivers might differ between *V. dubia* and other problematic non-native annual grasses in the Inland Northwest, B. *tectorum* and *Taeniatherum caput-medusae*; and (2) determine how burning influences relationships between *V. dubia* and plant community composition and structure to address potential impacts of the invasion and altered disturbance regimes on Inland Northwest dry forest and shrubland communities.

2 | METHODS

2.1 | Study area

The study was located in the heart of the Inland Northwest, USA, within the Blue Mountains Ecoregion (Figure 1). The Blue Mountains Ecoregion lies in the rain shadow of the Cascade Range, resulting in

continental, semiarid climates more typical of the warmer and drier Great Basin. These areas receive on average between 27 and 57 cm (10.6–22.4 in) of precipitation per year (PRISM Climate Group, 2019). Precipitation primarily falls between November and June. Average high temperatures are in the mid to upper 20s (°C) and average low temperatures fall in the −10s (°C) (Western Regional Climate Center, 2019). However, temperature and precipitation exhibit high spatial variation with higher elevations typically receiving more precipitation and cooler temperatures than lower elevations.

The Blue Mountains Ecoregion functions ecologically and floristically as a transverse bridge between the Cascade Mountains to the west and the Rocky Mountains to the east. Variable topography, wide elevation gradient, and a patchwork of soil types within the region support ecosystems ranging from dry grasslands and shrub-steppe to woodlands and mixed-conifer forests (Anderson *et al.*, 1998; Soulard, 2012). Dry conifer forests embedded with patches of sparsely vegetated, rocky dry meadows and dwarf shrublands ("forest scablands") are prevalent across the landscape. We sampled an elevation and soil moisture gradient spanning a variety of biophysical settings characterized by dominant woody vegetation and structure (Table 1).

2.2 | Data acquisition

Field sampling was conducted from May through August 2018 within and adjacent to seven recently burned fire perimeters (from 2014 to 2017) spanning the Blue Mountains Ecoregion (Figure 1; Table 2). Because *V. dubia* had not yet been mapped throughout the study region, our study was designed to maximize the likelihood of finding *V. dubia* according to local experts (USFS botanists). We stratified our sampling to capture a range of *V. dubia* abundance, environmental characteristics, burn severities, and biophysical settings within 1 km of the fire perimeters and limited to federally managed lands. We chose fire perimeters that burned within the last five years on accessible federally managed land, and covered a wide environmental gradient including at least one of our five defined biophysical settings, outlined in Table 1. All fire perimeters encompassed more than one biophysical setting, but the range of biophysical settings encompassed varied between fire perimeters and their corresponding elevational gradients. Fire perimeters at lower elevations were sampled in May and June and fire perimeters at higher elevations were sampled in July and August to capture the flora at similar phenological stages throughout the sampling period.

An equal number of "burned" plots (exhibiting visual burn evidence) and "unburned" plots were sampled (n = 110 plots). We attempted to sample burned and unburned plots with similar environmental and community characteristics when possible (Table 1). Plots of the same burn status (burned or unburned) were separated by at least 400 m to maintain independence between samples. Burned and unburned plots of similar environmental and community characteristics ranged in separation distance from 50 m to several kilometers. We surveyed a range of biophysical settings within the fire perimeters for *V. dubia* abundance prior to establishing plots and established fewer plots in fire perimeters and biophysical settings where we found little or no *V. dubia* to focus sampling efforts on fire perimeters and biophysical settings with a wide range of *V. dubia* abundances.

We used a modified version of the USDA nested three-spoke survey approach (Herrick *et al.*, 2017) for field sampling. Each plot consisted of three 30 m transect "spokes". On each transect, six 50 cm × 20 cm quadrats were placed, one every 5 m, totaling 330 transects and 1,980 quadrats. In each quadrat, we measured vascular plant foliar cover by species and soil surface cover to the nearest 1%, burn evidence (binary: visual char), evidence of grazing (binary), and litter depth (cm). Soil surface categories included cover of bare ground (loose mineral soil), biocrust, moss, rock, gravel, litter, woody litter, and scat. Quadrat level vegetation and soil surface cover and litter depth were averaged up to the plot level for analyses. Burn and grazing evidence were totaled at the plot level for analyses.

Vascular plants that we were unable to identify to species in the field were sampled and identified to the lowest taxonomic group possible using dichotomous keys. Poor quality specimens were recorded by lifeform (e.g., unknown shrub). Vascular plant identifications were

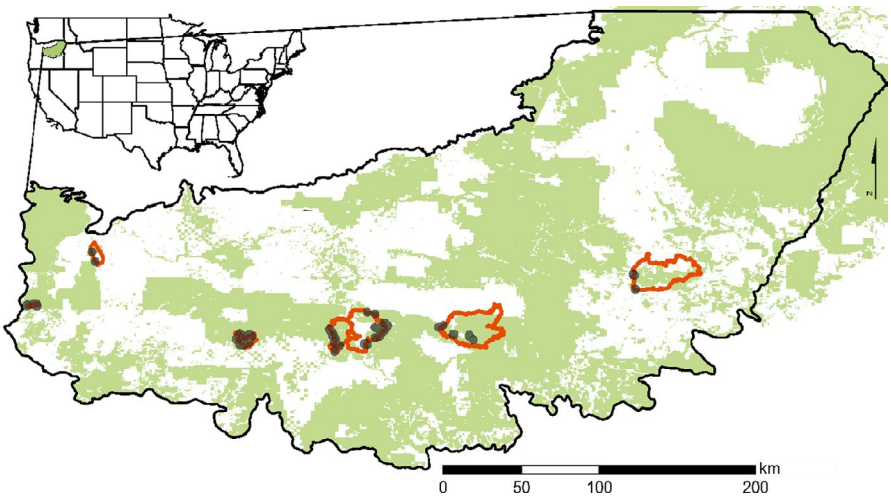

FIGURE 1 Location of sample plots within and just outside of seven fire perimeters (red polygons) in the Blue Mountains Ecoregion study area in northeastern Oregon, USA. In total, 110 plots (55 burned and 55 unburned) were sampled across seven fire perimeters within federally managed lands (green shaded areas).

TABLE 1 Biophysical settings across which vegetation sampling was conducted

Biophysical setting	Dominant woody species	Associated species	Elevation[a] (m)	Soil temperature regime	No. of plots
Dry shrubland	*Artemisia tridentata* subsp. *wyomingensis*	*Poa secunda/ Pseudoroegneria spicata*	750–1,200	mesic	3 unburned; 4 burned
Forest scabland	*Artemisia rigida/ Artemisia arbuscula*	*Poa secunda/ Danthonia unispicata*	850–1,660	mesic-frigid	23 unburned; 12 burned
Woodland	*Juniperus occidentalis/ Pinus ponderosa*	*Pseudoroegneria spicata/ Festuca idahoensis/ Poa secunda*	800–1,550	mesic-frigid	8 unburned; 15 burned
Dry forest	*Pinus ponderosa/ Pseudotsuga menziesii*	*Pseudoroegneria spicata/ Carex geyeri / Festuca idahoensis*	1,300–1,600	mesic-frigid	16 unburned; 23 burned
Moist shrubland	*Artemisia tridentata* subsp. *vaseyana*	*Ericameria nauseosa/ Festuca idahoensis*	1,800–2,050	frigid-cryic	5 unburned; 1 burned

[a]Elevation ranges represent the elevational range of sample plots within the study area.

TABLE 2 Ignition dates, acres burned, elevation range, and number of plots sampled within 1 km of each fire perimeter

Fire name	Ignition date	Hectares burned	Elevation range (m)	No. plots sampled
Fox	7/17/2014	3,780	1,311–1,601	26
South Fork Complex	7/31/2014	27,010	1,257–2,054	27
Corner Creek	6/29/2015	12,263	1,334–1,560	24
Cornet-Windy Ridge	8/10/2015	41,502	1,146–1,862	6
Canyon Creek Complex	8/12/2015	44,428	1,462–1,805	11
Emerson	7/25/2017	4,297	752–829	4
Whychus	8/10/2017	623	821–885	12

confirmed by Richard Halse at Oregon State University (OSU) and vouchers are housed with the Landscape and Conservation Science Research Group at OSU. Nomenclature was recorded following the USDA Plants Database (2019). A complete species list is prestented in Appendix S1.

We sampled soils from depths of 0–10 cm and 10–20 cm and estimated soil depth from small pits at 5 m along each transect. Samples within each plot were combined by depth for processing and analysis. All soil samples were hand-textured and analyzed for pH (Thomas, 1996) and organic matter via loss on ignition (LOI) (Nelson and Sommers, 1996). Textures were reported as mean sand, silt, and clay (%) for each texture class (Thien, 1979). A subset of 58 plots were analyzed for phosphorus (Olsen and Sommers, 1982) at the OSU Watershed Forest Soils and Central Analytical Laboratories.

We recorded tree canopy cover and basal area, topography (slope, slope shape, aspect), vegetation and soil disturbance, and fire severity at the plot level. Canopy cover was measured at plot center by averaging spherical densiometer measurements facing each of the four cardinal directions. Basal area was estimated from plot center using a 20 basal area factor prism. Vegetation and soil disturbance were recorded as low (<10% soil and vegetation appeared to be physically disturbed by grazing, fire, rodent activity, or human activity), moderate (10–50%), or high (>50%; Seipel *et al.*, 2018). Plots were categorized by fire severity in the field as low severity or patchy (1–10% of woody vegetation appeared to be killed by fire), moderate severity (>10–50%), or high severity (>50%).

Coarse-scale burn severity was also calculated using differenced Normalized Burn Ratios (dNBR). We derived dNBR from 30-m Landsat TM$^+$ satellite imagery, measured immediately post-fire to improve estimates of burn severity by decreasing the detection of post-fire vegetation recovery. Calculations were made using Google Earth Engine (Gorelick *et al.*, 2017).

We characterized the antecedent climate conditions for the field season and the climatological norms for each plot. Precipitation from January through June 2018, 30-year mean yearly precipitation, mean temperature, and maximum temperature values were extracted from the Parameter-elevation Regressions on Independent Slopes Model database for each plot (PRISM Climate Group, 2019). Heat load and potential direct incident radiation were estimated using metrics from McCune (2007). Distance from the nearest road was calculated from plot center using Oregon Department of Transportation roads layer in ArcGIS (ESRI,). Estimates of parent material were extracted from the "Geology of Oregon" spatial layer in ArcGIS (Ludington *et al*., 2005; ESRI,). All recorded environmental variables are presented in Appendix S2.

2.3 | Analysis

2.3.1 | *Ventenata dubia* habitat characteristics

To address our first objective, we identified the environmental and community characteristics associated with the *V. dubia* invasion and compared how *V. dubia*'s realized niche differs from that of the non-native annual grasses *B. tectorum* and *T. caput-medusae* using non-metric multidimensional scaling (NMS) and indicator species analysis (ISA). Cover of each species was square-root-transformed and rare species that occurred in fewer than 5% of plots were removed from analysis to reduce noise and strengthen the relationship between community composition and environmental variables (n = 132 species; Appendix S1). We overlaid the ordination with biplots of environmental variables. Predictor variable vectors increase proportionally according to their linear correlation with the ordination axes (minimum R^2 = 0.2). Correlated predictor variables were identified and all but the variable with the highest R^2 values for each axis were removed to improve readability and interpretability of the ordinations (Appendix S2).

We superimposed nonlinear response surfaces on the ordination for *B. tectorum*, *T. caput-medusae*, and *V. dubia* using "hilltop" plots. The hilltop plots outline the contour representing the top 20% of each species' response surface in relation to the ordination axes by interpolating between the existing sample plots. These contours are accompanied by an R^2 measure of fit calculated using the sum of squared differences between observed and estimated values (McCune and Mefford, 2011). All NMS analyses were performed using the Bray–Curtis distance measure in the software package PCORD with sample plots ordinated in species space and rotated to load *V. dubia* on Axis 1 (McCune and Mefford, 2011).

We examined *V. dubia* relationships to total understorey cover (excluding *V. dubia* cover) and canopy cover in burned and unburned plots using linear mixed-effects models with an interaction term for plot level burn status (burned or unburned) and a random effect for fire perimeter. *Ventenata dubia* cover was log-transformed to improve model fit.

We used ISA to identify species that were strong indicators for plots with high *V. dubia* cover (Dufrêne and Legendre, 1997). We performed an ISA with our transformed and simplified study matrix for plots with over 15% *V. dubia* cover. This threshold was chosen to reflect plots that were clearly visibly invaded and would likely spread rapidly with favorable conditions. Non-native *Bromus* spp. (excluding *B. tectorum*), including *Bromus arvensis*, *Bromus briziformis*, *Bromus hordeaceus*, *Bromus racemosus*, and *Bromus squarrosus*, were lumped for ISA as field differentiation is difficult and they are known to hybridize (Knowles, 1944). Indicator values were tested for statistical significance using a randomization (Monte Carlo) test with 4,999 runs and performed in PCORD (McCune and Mefford, 2011).

2.3.2 | Plant communities, invasion intensity, and fire

To address objective 2, we examined the response of diversity and structure to *V. dubia* cover and burning in invaded communities by modeling Shannon diversity, native and non-native species richness, and foliar cover (%) for six functional groups in response to *V. dubia* cover. Plots where *V. dubia* was absent were removed from these analyses to focus the analyses on invaded aeras (n = 77 plots where *V. dubia* cover > 0). This was done to remove plots that may be susceptible to invasion but have potentially not yet been exposed to *V. dubia*. Rare species and *V. dubia* were not removed for Shannon diversity and species richness analyses to maintain the full species composition for each plot (n = 269 species). Shannon diversity and species richness response to *V. dubia* were modeled using linear mixed-effects models with an interaction term for plot level burned status and a random effect for fire perimeter. To evaluate how mean diversity and species richness differ in plots where *V. dubia* was absent (n = 33) and where *V. dubia* was present (n = 77), we modeled diversity and species richness response to *V. dubia* presence using linear mixed-effects models with an interaction term for *V. dubia* presence and burn status and a random effect for fire perimeter.

For each plot, foliar cover was lumped by functional group: native and non-native annual grasses (excluding *V. dubia*), perennial grasses, native and non-native annual forbs, perennial forbs, all non-native species (excluding *V. dubia*), and shrubs. Functional groups are often used to describe groups of morphologically similar species accessing similar resources (Grime, 1979). Species reported as both annual and biannual from the USDA Plants Database (2019), were classified as annuals, and species reported as only biannual, or perennial and biannual were classified as perennials. Cover values for functional groups were log-transformed to improve normality. We adjusted one zero value of annual grass cover by adding the square of the first quartile divided by the third quartile (Stahel, 2008). Cover of each functional group was modeled using mixed-effects models with an interaction term for burn status and a random effect for fire perimeter. Shrub cover was modeled using a Tweedie distribution with a log link to improve the fit of the data with a high proportion of

zeros (Tweedie, 1984; Jorgensen, 1987). We evaluated differences in mean shrub cover between burned and unburned plots with a linear mixed-effects model with a random effect for fire perimeter. All models were conducted in R using the lme4, nlme, and glmmTMB packages (R Core Team, 2018).

3 | RESULTS

3.1 | *Ventenata dubia* habitat characteristics

Ventenata dubia and *B. tectorum* hilltop response surfaces were separated in the three-dimensional NMS ordination (stress 14.68), indicating that plant communities differed between plots with high *V. dubia* cover and high *B. tectorum* cover (Figure 2). *Ventenata dubia* was most strongly associated with burned and unburned woodland, dry forest, and forest scabland plots (Figures 2 and 3), while *B. tectorum* was most strongly associated with burned woodland and dry forest plots (Figure 2). Environmental variables most strongly correlated with *V. dubia* along Axis 1 included basaltic parent material, total moss cover, low soil phosphorus (P) from 0 to 10 cm, and low mineral soil cover (bare ground). *B. tectorum* was negatively associated with rock cover (%) and basalt and positively correlated with plots with high cover of bare ground and high soil phosphorus along Axis 1 (Figure 2a). Both *V. dubia* and *B. tectorum* were weakly associated with Axis 2 and corresponding environmental variables including increasing tree canopy cover, soil organic carbon measured as LOI from 10 to 20 cm, elevation, and maximum temperature (T_{max}). However, the response surfaces separated along Axis 3, where, unlike *V. dubia* which was common in both burned and unburned plots, *B. tectorum* was primarily associated with burned plots and high fire severity (Figure 2b).

Ventenata dubia and *T. caput-medusae* displayed overlapping response surfaces. However, *T. caput-medusae* was more strongly correlated with lower-elevation forest scabland plots with high maximum temperatures along Axis 2 (Figure 2a) and severely burned forest plots along Axis 3 than *V. dubia* (Figure 2b). Unlike *V. dubia*, *T. caput-medusae* was weakly associated with basalt and sandstone along Axis 1. *Ventenata dubia* extended into higher elevation unburned forest scabland, woodland, and forest plots with higher canopy and litter cover compared to *T. caput-medusae*.

Ventenata dubia heavily invaded plots with a wide range of understorey foliar cover and canopy cover (Figure 4). We observed plots with greater than 75% *V. dubia* cover in burned areas when understorey foliar cover was <50% (Figure 4a) and canopy cover was <20% (Figure 4b). *Ventenata dubia* was present in plots with up to 50% canopy cover, and heavily invaded burned and unburned plots (*V. dubia* > 30% cover) with up to 45% canopy cover (Figure 4b).

The strongest indicator species for plots with high cover of *V. dubia* were predominantly annual grasses and forbs. Non-native annual bromes (excluding *B. tectorum*) were the strongest indicator followed by three native annual forbs (*Agoseris heterophylla*, *Blepharipappus scaber*, and *Holosteum umbellatum*), a non-native annual forb (*Draba verna*), and a shallow-rooted perennial bunchgrass (*Danthonia unispicata*; Table 3).

3.2 | Plant communities, invasion intensity, and fire

Shannon diversity decreased when *V. dubia* cover increased in both burned and unburned plots (Figure 5a); however, Shannon diversity decreased more strongly with increasing *V. dubia* cover in burned plots than in unburned plots (Table 4). Native species richness decreased when *V. dubia* cover increased in burned plots and was variable in response to *V. dubia* cover in unburned plots (Figure 5b;

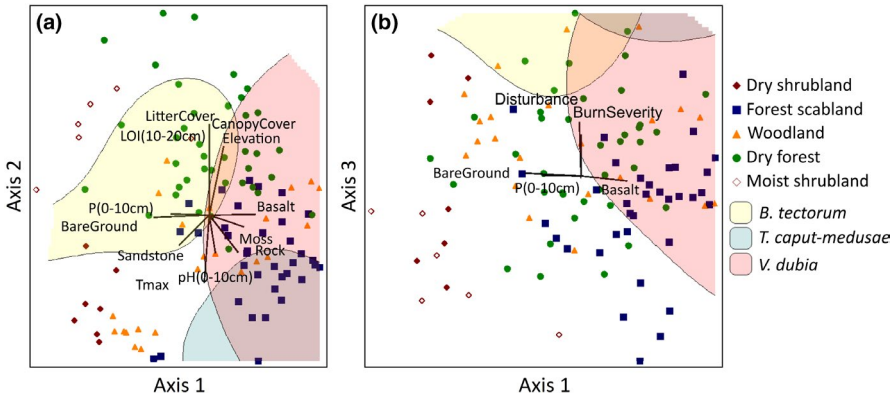

FIGURE 2 Species composition and environmental characteristics differed in sample plots with high *Ventenata dubia* cover compared to sites with high cover of *Bromus tectorum* and *Taeniatherum caput-medusae*. Nonparametric multidimensional scaling ordinations display sample plots in species space with Axis 1 rotated to load *V. dubia* cover. Sample plots are represented by their corresponding biophysical setting (Table 1). Shaded polygons represent the top 20% of *V. dubia*, *B. tectorum*, and *T. caput-medusae* response surfaces in relation to the ordination axes (R^2 = 0.60, 0.24, 0.10 respectively). Environmental variables linearly correlated with the ordination axes with R^2 > 0.2 are displayed by vectors proportional to the direction and strength of the linear relationship. *Ventenata dubia* and *B. tectorum* response surfaces separate along Axis 1 (panel a) and 3 (panel b). *Ventenata dubia* and *T. caput-medusae* response surfaces separate along Axis 2 (panel a) and Axis 3 (panel b)

FIGURE 3 *Ventenata dubia* heavily invaded burned and unburned historically sparsely vegetated and pyro-resistant "forest scablands" interspersed throughout the forested landscape. Panel a depicts an uninvaded, unburned forest scabland surrounded by mixed conifer forest. Panel b depicts a forest scabland heavily invaded with *V. dubia*. Panel c depicts a burned and invaded forest scabland

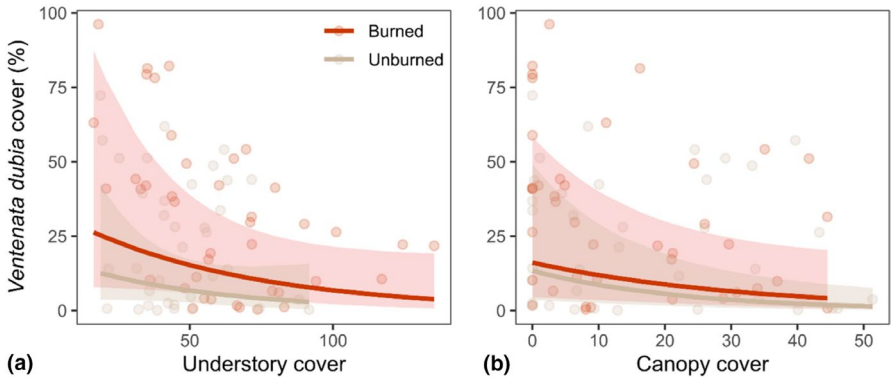

FIGURE 4 *Ventenata dubia* response to understorey foliar cover (excluding *V. dubia*; panel a) and canopy cover (panel b) in burned and unburned plots with 95% confidence intervals. *Ventenata dubia* heavily invaded plots in a wide range of understorey and canopy cover, although the most heavily invaded plots (*V. dubia* cover >75%) were burned with <50% understorey cover and <20% canopy cover. Understory cover was recorded for each species at all strata allowing total understorey cover to exceed 100%

TABLE 3 Indicator species for plots with greater than 15% *Ventenata dubia* cover

Species	IV	Mean	*SD*	*p*-value
Bromus spp. (annuals)	46.6	28.5	3.29	0.0002
Agoseris heterophylla	37.9	27.6	3.14	0.0062
Draba verna	37.3	30.5	2.63	0.0164
Danthonia unispicata	36.5	19.5	3.47	0.0002
Blepharipappus scaber	35.7	20.6	3.53	0.0008
Holosteum umbellatum	34.0	20.9	3.33	0.0036

Table 4). Non-native species richness had little relationship to *V. dubia* cover in both burned and unburned plots (Figure 5b; Table 4). Mean native species richness was greater than non-native species richness regardless of *V. dubia* cover or burn status (Figure 5b). Mean Shannon diversity and native species richness and variances did not strongly differ between plots where *V. dubia* was absent and where *V. dubia* was present (Appendix S3). Mean non-native species richness was higher in both burned and unburned plots where *V. dubia* was present than in plots where *V. dubia* was absent (estimates for this difference in richness = 3.1 and 3.2 more species respectively, CIs = 1.5–4.7 and 1.7–4.7 more species respectively; Appendix S3).

Annual forbs, annual grasses, non-native species, perennial forbs, and shrubs were negatively associated with *V. dubia* cover in burned plots (Figure 6). Perennial forbs were the only functional group to be negatively correlated with *V. dubia* in unburned plots (Figure 6). Burning had the greatest effect on functional group cover response to *V. dubia* cover for annual forbs, annual grasses, and non-native species (excluding *V. dubia*; Table 5). Shrubs were nearly absent from burned plots (mean shrub cover <2%). Mean shrub cover in burned plots was less than one third of mean shrub cover in unburned plots (Figure 7).

4 | DISCUSSION

Our study characterizes the unique niche invaded by *V. dubia* compared to other non-native annual grasses (*B. tectorum* and *T. caput-medusae*) and demonstrates that *V. dubia* is expanding the grass invasion footprint into previously resistant Inland Northwest forest mosaic communities. Our results suggest that *V. dubia* heavily invades unburned and burned areas and burning may exacerbate

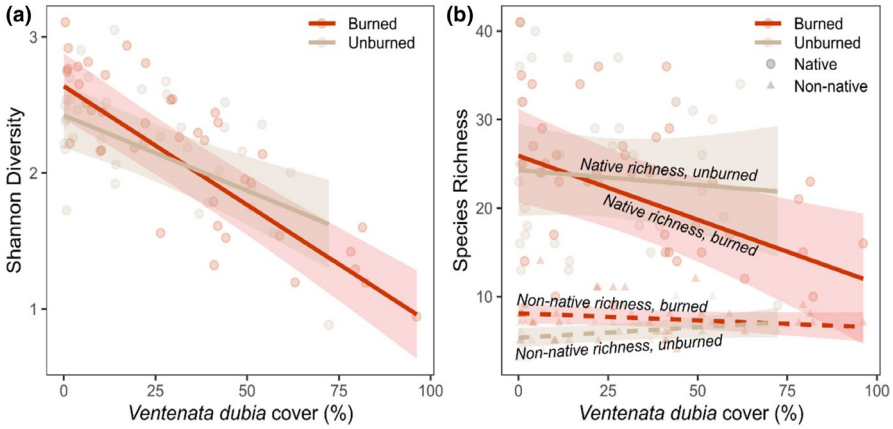

FIGURE 5 Species richness and Shannon diversity response to *Ventenata dubia* cover with 95% confidence intervals. Shannon diversity decreased with increasing *V. dubia* cover in burned and unburned plots (estimates −0.02 and −0.01, 95% CIs −0.02 to −0.01 and −0.02 to −0.01 respectively). Native species richness decreased with increasing *V. dubia* cover in burned plots, but was not strongly related to *V. dubia* cover in unburned plots (estimates −0.14 and −0.03, 95% CIs −0.24 to −0.05 and −0.15 to 0.09 respectively), whereas non-native species richness was not strongly related to *V. dubia* cover in burned or unburned plots (estimates −0.01 and 0.03, 95% CIs −0.03 to 0.01 and 0.00 to 0.06 respectively)

TABLE 4 Shannon diversity and species richness response to *Ventenata dubia* cover: Interactions between *V. dubia* cover and plot level burn status for plots where *V. dubia* is present (n = 77)

Response variable	*F*-statistic	Numerator *df*	Denominator *df*	*p*-value
Shannon diversity	4.23	1	71.1	0.043
Native species richness	2.29	1	71.2	0.135
Non-native species richness	5.56	1	71.3	0.022

Reported values are from an *F*-test with Kenward–Roger approximation.

negative relationships between *V. dubia* and diversity, species richness, and community structure, potentially contributing to state shifts from shrub-dominated communities to non-native annual grasslands.

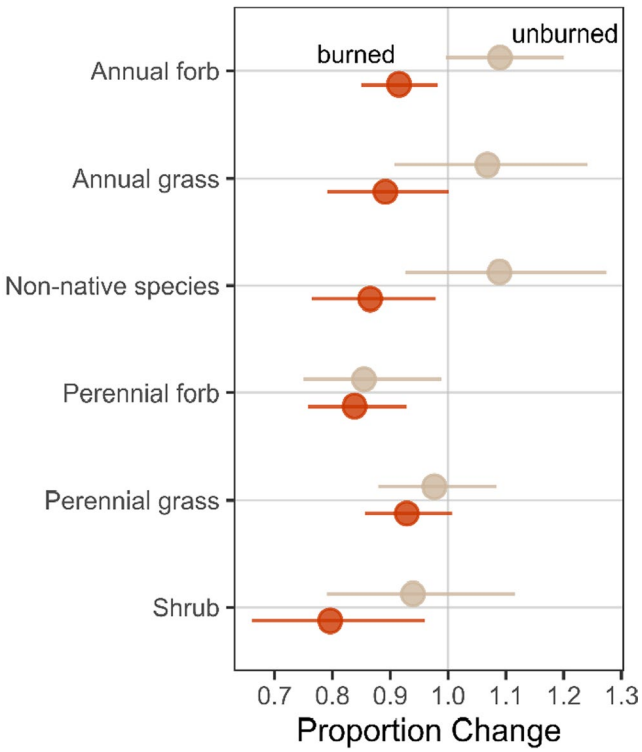

FIGURE 6 Estimates of the change in functional group cover for a 10% increase in *Ventenata dubia* cover in burned and unburned plots with 95% confidence intervals. Values above 1.0 indicate an increase and below 1.0 indicate a decrease

4.1 | *Ventenata dubia* expands invasion footprint

Ventenata dubia differed from *B. tectorum* and *T. caput-medusae* by heavily invading both burned and unburned dry forest, woodland, and forest scablands ranging from 1,250 to 1,665 m throughout the Blue Mountains Ecoregion. *Ventenata dubia*'s tolerance for the frigid basalt-derived lithosols characteristic of forest scablands further separated its realized niche from *B. tectorum* and *T. caput-medusae*, increasing the overall invasion footprint. Prior to the *V. dubia* invasion, forest scablands were relatively resistant to invasion impacts despite being exposed to non-native annual grasses for decades (Johnson and Swanson, 2005). Although *B. tectorum* often germinates in relatively cold temperatures, it experiences limited growth and reproduction under frigid soil temperature regimes (Chambers *et al.*, 2007; Roundy *et al.*, 2007). *Ventenata dubia*'s extremely shallow root system (between 1 and 5 cm) may allow it to take advantage of early spring moisture near the soil surface to thrive in these otherwise moisture-limited systems (Wallace *et al.*, 2015). *Ventenata dubia* was also positively associated with rock cover, which can partially

TABLE 5 Functional group cover response to *Ventenata dubia* cover: Interactions between *V. dubia* cover and burn status in plots where *V. dubia* is present (n = 77).

Functional group response variable	*F*-statistic	Numerator *df*	Denominator *df*	*p*-value
Annual forb cover (%)[a]	8.83	1	71.1	0.004
Annual grass cover (%)[a]	3.46	1	70.6	0.067
Non-native species cover (%)[a]	5.10	1	71.3	0.027
Perennial forb cover (%)[a]	0.05	1	70.2	0.819
Perennial grass cover (%)[a]	0.53	1	71.9	0.471
	Chi-sq			**Pr (>Chisq)**
Shrub cover (%)[b]	1.62	1		0.20312

[a]Reported values are from an *F*-test with Kenward–Roger approximation.
[b]Shrub cover response to *V. dubia* was modeled with a Tweedie distribution to account for a high proportion of zeros and reported values are from an Analysis of Deviance with Wald chi-square tests.

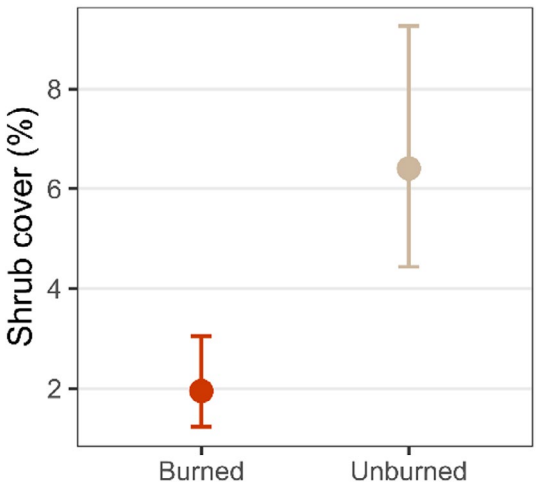

FIGURE 7 Mean shrub cover in burned plots was less than one third of mean shrub cover in unburned plots (estimated ratio = 0.3; 95% CI 0.2–0.5) in plots where *Ventenata dubia* was present (n = 77)

mediate the harsh seasonal swings in moisture availability by lowering the evaporation rate (Poesen and Lavee, 1994).

Both dry and moist shrublands showed resistance to *V. dubia* invasion, despite lower-elevation sagebrush-steppe communities within the Inland Northwest and the nearby Great Basin demonstrating high susceptibility to invasion by *B. tectorum* (Chambers *et al*., 2007). Additionally, neither *B. tectorum* nor *T. caput-medusae* where found to be strong indicators for plots with >15% cover of *V. dubia*. In concordance with our findings, Jones *et al*. (2018) reported a negative relationship between *V. dubia* and *B. tectorum* abundances in Inland Northwest sagebrush communities, suggesting that this trend may extend outside of our immediate study area. However, as *V. dubia* is still in a relatively early stage of invasion (Jones *et al*., 2018), it is unknown whether the biotic and abiotic characteristics of these dry and moist shrublands confer an inherent resistance to *V. dubia* invasion, or if increased propagule pressure and residence time will find these areas susceptible.

Although we found *V. dubia* to be associated with a distinct realized niche, it may invade areas currently dominated by other non-native annual grasses under different environmental conditions. We note that our sampling was focused along a gradient of *V. dubia* cover and an unbalanced sample of biophysical classes during one sampling season within the Blue Mountains Ecoregion. We did not aim to characterize the entire environmental range of all annual grasses, nor did we perform a balanced random sample across biophysical settings over multiple years, potentially affecting the representativity of the gradient and limiting our findings to climatic conditions similar to those in summer 2018. For example, Jones *et al*. (2018) found *T. caput-medusae* to be a strong indicator for *V. dubia* in lower-elevation sagebrush-steppe (916–1,662 m) where soils are generally warmer and *T. caput-medusae* is more abundant. Additionally, *V. dubia* was reported replacing non-native annual grasses including *T. caput-medusa* and *B. tectorum* in more productive grassland communities within the Inland Northwest (Prather and Burke, 2011).

4.2 | Burning intensified negative *Ventenata dubia*-community diversity relationships

Ventenata dubia may be in-filling gaps rather than outcompeting resident species in unburned areas. Our findings of Shannon diversity decreasing with increasing *V. dubia* cover indicate that *V. dubia* is shifting the proportional contribution of species to composition. Species richness and cover of annual grasses and forbs did not decrease with *V. dubia* in unburned plots, indicating that *V. dubia* may be in-filling unoccupied gaps and vacant niches surrounding existing species in unburned communities, impacting species evenness rather than competitively excluding species. These results contrast findings of *B. tectorum* preventing establishment of native species and reducing diversity by depleting spring moisture in unburned communities (Cline *et al*., 1977; Harris, 1977) and studies finding non-native annuals to competitively exclude native annuals from unburned Californian desert communities (Brooks, 2000; DeFalco *et al*., 2003).

Communities with high cover are often more resistant to invasion, in part because the communities are more highly saturated and host fewer available resources (Elton, 1958; MacArthur, 1970). Our findings show a negative relationship between *V. dubia* and perennial forbs in both burned and unburned plots, suggesting that *V. dubia* may preferentially invade areas with lower cover of established perennial forbs. Compared to findings from the Great Basin, where perennial grasses have been shown to increase community resistance to *B. tectorum* invasion (Booth *et al*., 2003; Beckstead and Augspurger, 2004), we found limited evidence to suggest that perennial grasses confer community resistance to *V. dubia* in the Blue Mountains Ecoregion.

Burning intensified negative relationships between *V. dubia* cover and native species richness, annual forb cover, annual grass cover, and non-native species cover. This finding may suggest that, while not heavily competing with species in unburned areas, *V. dubia* may more efficiently allocate post-fire resources, potentially excluding species from burned areas. This could provide an example of increased priority effects of *V. dubia* in burned areas. In the Great Basin sagebrush-steppe, *B. tectorum* establishes quickly after fires and is known to suppress the recovery of native species by more efficiently allocating and depleting soil resources (Melgoza and Nowak, 1991; Monaco *et al*., 2003). This is especially impactful for the establishment of seedlings that depend on water availability near the soil surface where competition with annual grasses is greatest (Harris, 1977; Melgoza *et al*., 1990). For example, post-fire establishment of an obligate-seeding conifer in Australia was found to be heavily impacted by the invasion of the non-native perennial grass *Andropogon gayanus* (gamba grass) in a tropical savanna (Bowman *et al*., 2014). Our findings complement studies from invaded California grasslands and ponderosa pine forests that have found disturbance to be a stronger driver of non-native annual grass dominance than competitive ability or community composition alone (Corbin and D'Antonio, 2004; Kerns and Day, 2017), and support general invasion frameworks that suggest community invasibility increases following disturbances such as fire (Davis *et al*., 2000; Chambers *et al*., 2007).

Alternatively, negative relationships between *V. dubia* and community diversity in burned plots could indicate that increasing species richness and cover of functionally similar annuals may limit *V. dubia* establishment and growth post-fire. Functional similarity between invaders and resident communities has been shown to increase community resistance to invasion, although often more successfully limiting the establishment of invading forbs than grasses (Price and Pärtel, 2013).

Shrubs were largely absent from burned plots with high *V. dubia* cover. This observation was strongly driven by the loss of non-sprouting sagebrush species *Artemisia rigida* and *Artemisia arbuscula* from burned forest scabland plots. Despite our short observation window, 2–4 years post fire, we saw no evidence of sagebrush individuals re-establishing to indicate recovery of this important structural component of forest scabland communities. Although *Artemisia tridentata* seeds have been found to survive in the seedbank for up to five years post fire, few seeds germinate after the first year (Meyer, 2008). Re-establishment after fire is thought to occur very slowly for *Artemisia rigida* and is likely maintained by short-distance dispersal from nearby unburned sagebrush islands acting as fire refugia (Agee, 1994; Steenvoorden, Meddens, Martinez, Foster, & Kissling, 2019). The loss of *Artemisia rigida* and *Artemisia arbuscula* could have broad ecosystem effects. These relatively deep-rooted shrubs improve moisture infiltration into the soil, help prevent erosion, and concentrate soil nutrients creating fertile "islands" in otherwise nutrient-limited systems (Stubbs and Pyke, 2005; Allen *et al*., 2011). *Artemisia rigida* provides important habitat for endangered sage grouse and provides winter forage for elk (Daubenmire, 1970; Tirhi, 1995). Grass-fire cycles in arid and semi-arid shrub-steppe ecosystems have reduced soil fertility and overall ecosystem productivity by removing shrub components (Allen *et al*., 2011). Burning as a result of the rapid post-fire accumulation of fine fuels could shift historically pyro-resistant forest scablands to annual grasslands, consequently altering hydrologic cycling, soil stability, and habitat quality in these ecosystems.

4.3 | Management implications

Mitigating large-scale ecological impacts of an invasion is contingent on predicting areas at high risk for invasion, on early detection, mitigating spread, and prioritizing treatments (Harvey and Mazzotti, 2014). We identified the environmental and community characters associated with *V. dubia* (including high rock cover and basalt parent material) and indicator species (annual bromes, annual forbs, and *Danthonia unispicata*), which can be used to detect areas at high risk for *V. dubia* invasion across the Blue Mountains Ecoregion and prioritize treatments at early stages in the invasion process when eradication is most likely (Harvey and Mazzotti, 2014). Additionally, we characterize how *V. dubia*'s realized niche differs from that of other annual grasses, aiding the design of effective *V. dubia*-specific management plans.

Unlike *B. tectorum* and *T. caput-medusae*, the invasion by *V. dubia* is impacting forest scablands interspersed throughout the larger forested landscape rather than within dominantly shrub-steppe ecosystems. Rapid accumulation of *V. dubia* cover post-fire could initiate a positive feedback cycle between *V. dubia* and fire, similar to *B. tectorum*-induced grass-fire cycles in the Great Basin (D'Antonio and Vitousek, 1992). Prior to invasion, fuel-limited forest scablands served as natural fire breaks, increasing burn heterogeneity throughout the larger forested landscape. Increased fine fuel cover in these historically fuel-limited communities could allow fire to spread into and between adjacent forests more easily, potentially increasing forest fire activity (Kerns *et al*., 2020). The increasing loss of forest canopy from stand-replacing fire in these dry forest ecosystems (Odion *et al*., 2010; Reilly *et al*., 2020), and reduced competition from understorey species may promote the further expansion of *V. dubia* into recently burned dry mixed-conifer forests, further exacerbating the invasion. Such shifts have the potential to alter landscape-scale disturbance regimes and ecological processes in open and forested ecosystems across the Intermountain West (Kerns *et al*., 2020).

Ventenata dubia invaded readily after wildfires that burned during the summer (between June 29 and August 12) in dry forests and forest scablands, suggesting that summer-season-prescribed fires alone may not be an effective control strategy for reducing invasion levels. Fire, coupled with *V. dubia* invasion was associated with lower diversity, species richness, and functional group cover, indicating that prescribed fire during the summer season could reduce biodiversity and have negative ecological impacts to invaded communities. This may be especially true in forest scablands where burning coupled with invasion may initiate a state shift from shrub-steppe to annual grasslands. However, the areas that we sampled burned in wildfires with specific weather conditions and may not be representative of plant community or *V. dubia* response to summer prescribed burning under different conditions or burning in other seasons. Further observations and experimentation are necessary to fully understand the ecological impacts of the *V. dubia* invasion. However, our findings may aid managers in developing species-specific, early response management plans to mitigate potential impacts, while adding evidence to further develop community invasibility and grass-fire cycle frameworks.

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AUTHOR CONTRIBUTIONS

All authors developed the research idea and study design. CT collected data, performed statistical analyses, and, with contributions from BK and MK, wrote the paper. All authors discussed the results and made comments on the manuscript.

DATA AVAILABILITY STATEMENT

Data are archived online at the Open Science Framework (osf.io/4qc3x/) (Tortorelli, 2020) https://doi.org/10.17605/osf.io/4qc3x.

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REFERENCES

Agee, J.K. (1994) *Fire and Weather Disturbances in Terrestrial Ecosystems of the Eastern Cascades*. Portland, OR: USDA Forest Service.

Allen, E.B., Steers, R.J. and Dickens, S.J. (2011) Impacts of fire and invasive species on desert soil ecology. *Rangeland Ecology and Management*, *64*, 450–462.

Anderson, E.W., Borman, M.M. and Krueger, W.C. (1998) *The ecological provinces of Oregon: A treatise on the basic ecological geography of the state*, Corvallis, OR: Oregon State University. Agricultural Experiment Station. https://ir.library.oregonstate.edu/concern/administrative_report_or_publications/0r967464v

Balch, J.K., Bradley, B.A., D'Antonio, C.M. and Gómez-Dans, J. (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, *19*, 173–183. https://doi.org/10.1111/gcb.12046

Bansal, S., James, J.J. and Sheley, R.L. (2014) The effects of precipitation and soil type on three invasive annual grasses in the western United States. *Journal of Arid Environments*, *104*, 38–42. https://doi.org/10.1016/j.jaridenv.2014.01.010

Barkworth, M.E., Capels, K.M. and Long, S. (1993) *Ventenata*. In: Flora of North America Editorial Committee (Eds.) *Flora of North America North of Mexico*. Volume *24*, Magnoliophyta: Commelinidae (in part): Poaceae, part 1. New York, NY: Oxford University Press, pp. 683–684.

Beckstead, J. and Augspurger, C.K. (2004) An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions*, *6*, 417–432. https://doi.org/10.1023/B:BINV.0000041557.92285.43

Booth, M.S., Caldwell, M.M. and Stark, J.M. (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology*, *91*, 36–48. https://doi.org/10.1046/j.1365-2745.2003.00739.x

Bowman, D.M.J.S., MacDermott, H.J., Nichols, S.C. and Murphy, B.P. (2014) A grass-fire cycle eliminates an obligate-seeding tree in a tropical Savanna. *Ecology and Evolution*, *4*, 4185–4194. https://doi.org/10.1002/ece3.1285

Brooks, M.L., Brown, C.S., Chambers, J.C., D'Antonio, C.M., Keeley, J.E. and Belnap, J. (2016) Exotic annual *Bromus* invasions: Comparisons among species and ecoregions in the Western United States. In: Germino, M.J., Chambers, J.C. and Brown, C.S. (Eds.) *Exotic brome-grasses in arid and semiarid ecosystems of the western US: Causes, consequences, and management implications*, Series on Environmental Management. Switzerland: Springer International Publishing, pp. 11–60. https://doi.org/10.1007/978-3-319-24930-8

Brooks, M.L. (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. *The American Midland Naturalist*, *144*, 92–108 https://doi.org/10.2193/0091-7648(2006)34[177:FAROSE]2.0.CO;2.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Ditomaso, J.M. *et al.* (2004) Effects of invasive alien plants on fire regimes. *BioScience*, *54*, 677–688 https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B. *et al.* (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, *17*, 360–375. https://doi.org/10.1007/s10021-013-9725-5

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E. and Whittaker, A. (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, *77*, 117–145. https://doi.org/10.1890/05-1991

Cline, J.F., Uresk, D.W. and Rickard, W.H. (1977) Comparison of soil water used by a sage-brush-bunchgrass and a cheatgrass community. *Journal of Range Management*, *30*, 199–201.

Corbin, J.D. and D'Antonio, C.M. (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology*, *85*, 1273–1283.

D'Antonio, C.M. and Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*, 63–87. https://doi.org/10.1109/HIS.2008.71

Daubenmire, R. (1970) *Steppe Vegetation of Washington*, Technical bulletin 62 , Pullman, WA: Washington Agricultural Experiment Station.

Davis, M.A., Grime, J.P. and Thompson, K. (2000) Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

DeFalco, L.A., Bryla, D.R., Smith-Longozo, V. and Nowak, R.S. (2003) Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (Poaceae) and two native species. *American Journal of Botany*, *90*, 1045–1053. https://doi.org/10.3732/ajb.90.7.1045

Downing, W.M., Krawchuk, M.A., Coop, J.D., Meigs, G.W., Haire, S.L., Walker, R.B. *et al*. (2020) How do plant communities differ between fire refugia and fire-generated early-seral vegetation? *Journal of Vegetation Science*, *31*, 26–39.

Dufrêne, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, *67*(3), 345–366. https://doi.org/10.2307/2963459

Elton, C. (1958) *The Ecology of Invasions by Animals and Plants*, Chicago, IL: University of Chicago Press.

Fusco, E.J., Finn, J.T., Balch, J.K., Nagy, R.C. and Bradley, B.A. (2019) Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences*, *116*, 23594–23599.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. and Moore, R. (2017) Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Chichester: Wiley.

Harris, G.A. (1977) Root phenology as a factor of competition among grass seedlings root phenology as a factor of competition among grass seedlings. *Journal of Range Management*, *30*, 172–177.

Harrison, S. (1999) Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia*, *121*, 99–106. https://doi.org/10.1007/s004420050910

Harvey, R.G. and Mazzotti, F.J. (2014) *The Invasion Curve: A Tool for Understanding Invasive Species Management in South Florida*. Gainesville, FL: IFAS Publication Number WEC347. Available at: http://edis.ifas.ufl.edu/uw392. Accessed January 2019.

Herrick, J.E., Van Zee, J.W., Havstad, K.M., Burkett, L.M., Whitford, W.G., Pyke, D.A. *et al*. (2017) *Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems*, Volume *1*, Las Cruces, New Mexico: USDA-ARS Jornada Experimental Range.

Johnson, C.G., & Swanson, D.K. (2005 &) *Bunchgrass Plant Communities of the Blue and Ochoco Mountains: A Guide for Managers*. General Technical Report PNW-GTR-641. Portland, OR:U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Jones, L.C., Norton, N. and Prather, T.S. (2018) Indicators of ventenata (*Ventenata dubia*) invasion in sagebrush steppe rangelands. *Invasive Plant Science and Management*, *11*, 1–9. https://doi.org/10.1017/inp.2018.7

Jorgensen, B. (1987) Exponential dispersion models. *Journal of the Royal Statistical Society*, *B*, *49*, 127–162.

Kerns, B.K. and Day, M.A. (2017) The importance of disturbance by fire and other abiotic and biotic factors in driving cheatgrass invasion varies based on invasion stage. *Biological Invasions*, *19*, 1853–1862. https://doi.org/10.1007/s10530-017-1395-3

Kerns, B.K., Tortorelli, C., Day, M.A., Nietupski, T., Barros, A.M.G., Kim, J.B. *et al*. (2020) Invasive grasses: a new perfect storm for forested ecosystems? *Forest Ecology and Management*, *463*, 117985. https://doi.org/10.1016/j.foreco.2020.117985

Knowles, P.F. (1944) Interspecific hybridizations of Bromus. *Genetics*, *29*(2), 128–140.

Ludington, S., Moring, B.C., Miller, R.J., Flynn, K.S., Evans, J.G. and Ston, P.A. (2005). *Geology of Oregon, USA*. http://pubs.usgs.gov/of/2005/1305/.

MacArthur, R. (1970) Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, *1*, 1–11. https://doi.org/10.1016/0040-5809(70)90039-0

Mack, M.C. and D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, *13*, 195–198. https://doi.org/10.1016/S0169-5347(97)01286-X

Mack, R.N. (1981) Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agro-Ecosystems*, *7*, 145–165. https://doi.org/10.1016/0304-3746(81)90027-5

McCune, B. (2007) Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. *Journal of Vegetation Science*, *18*, 751–754.

McNaughton, S.J. (1968) Structure and function in California grasslands. *Ecology*, *49*, 962–972. https://doi.org/10.2307/1936547

Melgoza, G. and Nowak, R.S. (1991) Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. *Journal of Range Management*, *44*, 27–33.

Melgoza, G., Nowak, R.S. and Tausch, R.J. (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia*, *83*, 7–13.

Meyer, S.E. (2008) *Artemisia* L., *sagebrush*. In: Bonner, F.T. and Karrfalt, R.P. (Eds.) *Woody Plant Seed Manual*. Washington, DC: Department of Agriculture, Forest Service, pp. 274–282.

Monaco, T.A., Johnson, D.A., Norton, J.M., Jones, T.A., Connors, K.J., Norton, J.B. *et al*. (2003) Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management*, *56*, 282–290.

Nelson, D.W. and Sommers, L.E. (1996) Total carbon, organic carbon, and organic matter. In: D. L. Sparks A. L. Page P. A. Helmke R. H. Loeppert P. N. Soltanpour M. A. Tabatabai C. T. Johnston & M. E. Sumner (Eds.). *Methods of Soil Analysis. Part. 3*, Madison, WI: SSSA Book Series, pp. 961–1010.

Odion, D.C., Moritz, M.A. and DellaSala, D.A. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, *98*, 96–105.

Olsen, S.R. and Sommers, L.E. (1982) Phosphorus. In: *Methods of Soil Analysis: Part 2. Chemical and Microbiological Properties*, 2nd edition. Madison, WI: ASA and SSSA, pp. 403–430.

Pavek, P., Wallace, J.M. and Prather, T.S. (2011) Ventenata biology and distribution in the Pacific Northwest. In: *Proceedings of Western Society of Weed Science*. Spokane, WA.

Poesen, J. and Lavee, H. (1994) Rock fragments in top soils: significance and processes. *Catena*, *23*, 1–28. https://doi.org/10.1016/0341-8162(94)90050-7

Prather, T.S. and Burke, I.C. (2011) *Ventenata dubia* - an emerging threat to agriculture and wildlands? In: *Proceedings of Western Society of Weed Science*. Spokane, WA, pp. 107–111.

Price, J.N. and Pärtel, M. (2013) Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos*, *122*, 649–656.

PRISM Climate Group (2019). Oregon State University. Available at http://prism.oregonstate.edu. Accessed November 2018.

Reilly, M.J., McCord, M.G., Brandt, S.M., Linowksi, K.P., Butz, R.J. and Jules, E.S. (2020) Repeated, high-severity wildfire catalyzes invasion of non-native plant species in forests of the Klamath Mountains, northern California, USA. *Biological Invasions*, *22*(6), 1821–1828.

Roundy, B.A., Hardegree, S.P., Chambers, J.C. and Whittaker, A. (2007) Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecology and Management*, *60*, 613–623. https://doi.org/10.2111/05-206R3.1

Seipel, T., Rew, L.J., Taylor, K.T., Maxwell, B.D. and Lehnhoff, E.A. (2018) Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. *Applied Vegetation Science*, *21*, 385–394. https://doi.org/10.1111/avsc.12370

Soulard, B.C.E. (2012). Blue Mountains Ecoregion. In: B. M. Sleeter, T. S. Wilson, & W. Acevedo (Eds.). *Status and Trends of Land Change in the Western United States—1973 to 2000*, Menlo Park, CA: U.S. Geological Survey Professional Paper 1794–A. https://pubs.usgs.gov/pp/1794/a/

Stahel, W.A. (2008) *Statistische Datenanalyse: Eine Einführung für Naturwissenschaftler*, 5. Auflage. Wiesbaden: Vieweg.

Steenvoorden, J., Meddens, A. J., Martinez, A. J., Foster, L. J., & Kissling, W. D. (2019) The potential importance of unburned islands as refugia for the persistence of wildlife species in fire-prone ecosystems. *Ecology and Evolution*, *9*(15), 8800–8812.

Stubbs, M.M. and Pyke, D.A. (2005) Available nitrogen: A time-based study of manipulated resource islands. *Plant and Soil*, *270*, 123–133. https://doi.org/10.1007/s11104-004-1306-0

Thien, S.J. (1979) A flow diagram for teaching texture by feel analysis. *Journal of Agronomic Education*, *8*, 54–55.

Thomas, G.W. (1996) Soil pH and soil acidity. In: Sparks, D.L. (Ed.) *Methods of Soil Analysis: Part 3-Chemical Methods*. Madison, WI: SSSA Book Series, pp. 475–490.

Tirhi, M.J. (1995) *Washington state management plan for sharp-tailed grouse*, Olympia, WA: Washington Department of Fish and Wildlife, Wildlife Management Program.

Tortorelli, C. (2020) Data and script files in support of the manuscript: Expanding the invasion footprint: *Ventenata dubia* and relationships to wildfire, environment, and plant communities in the Blue Mountains of the Inland Northwest, USA. *Open Science Framework*., http://osf.io/4qc3x/

Tweedie, M.C.K. (1984) An index which distinguishes between some important exponential families. In *Proceedings of the Indian Statistical Institute Golden Jubilee International Conference*.

USDA NRCS (2019) *The PLANTS Database*. Greensboro, NC: National Plant Data Team. Available at: http://plants.usda.gov. Accessed January 2019.

Wallace, J.M., Pavek, P.L.S. and Prather, T.S. (2015) Ecological Characteristics of *Ventenata dubia* in the Intermountain Pacific Northwest. *Invasive Plant Science and Management*, *8*, 57–71. https://doi.org/10.1614/IPSM-D-14-00034.1

Western Regional Climate Center (2019) *Oregon*. Available at: https://wrcc.dri.edu/summary/Climsmor.html. Accessed January 2019.

Young, J.A. and Evans, R.A. (1970) Invasion of medusahead into the Great Basin. *Weed Science*, *18*, 89–97.

Youngblood, A., Metlen, K.L. and Coe, K. (2006) Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. *Forest Ecology and Management*, *234*, 143–163. https://doi.org/10.1016/j.foreco.2006.06.033

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Complete species list

Appendix S2. Description of environmental variables and associations with NMS axes

Appendix S3. Shannon diversity and species richness response to *Ventenata dubia* presence and burn status

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