Indicators of Ventenata (*Ventenata dubia*) Invasion in Sagebrush Steppe Rangelands

Lisa C. Jones[1], Nicholas Norton[2] and Timothy S. Prather[3]

[1]Research Specialist, Department of Plant Sciences, University of Idaho, Moscow, ID, USA, [2]Conservation Projects Manager, Palouse Land Trust, Moscow, ID, USA and [3]Professor, Department of Plant Sciences, University of Idaho, Moscow, ID, USA

Abstract

Ventenata [*Ventenata dubia* (Leers) Coss.], an invasive winter annual grass, significantly reduces forage production in grassland systems and displaces species within both perennial- and annual-dominated grasslands within the Inland Northwest. The range of *V. dubia* is expanding into sagebrush steppe communities, an expansive habitat critical for forage production, wildlife, and recreation. Currently, there is limited knowledge of *V. dubia*'s distribution and abundance within sagebrush steppe communities. We performed field surveys at 15 locations in sagebrush steppe rangelands in southern Idaho and eastern Oregon to assess where *V. dubia* occurs, with the aim of providing insight about its niche in this new habitat. Specifically, we evaluated biotic and abiotic factors of the plant community as indicators of *V. dubia* presence. We also correlated species diversity measures with no, low (<12.5%), and high (>12.5%) *V. dubia* cover. Though widely distributed throughout the study region, *V. dubia* only appeared in 45% of the 225 plots, and foliar cover was typically less than 50%. It was primarily found in ephemerally wet microhabitats. Species richness and the Shannon diversity index were lowest in plots with high *V. dubia* cover. Nonmetric multidimensional scaling analysis revealed that *V. dubia* and medusahead [*Taeniatherum caput-medusae* (L.) Nevski] were closely associated. Furthermore, chi-square indicator analysis showed that *T. caput-medusae* was more prevalent, while mountain big sagebrush [*Artemisia tridentata* Nutt. spp. *vaseyana* (Rydb.) Beetle] was less prevalent, in plots containing *V. dubia*. Abiotic factors that explained variation in *V. dubia* abundance included rock cover, soil depth, and a north/south aspect. Higher *V. dubia* cover also correlated with higher clay content and lower phosphorus and potassium concentrations in the soil. We suggest that at this point, detection survey efforts to locate incipient infestations of *V. dubia* in sagebrush steppe communities should focus on moist areas and sites susceptible to invasion by *T. caput-medusae*.

Introduction

Biological invasions are an unfortunate component of global environmental change. Major goals of many biological invasion studies are to understand the factors that affect the spread of invasive species and to determine their current and potential distributions (With 2002). Typically, the more advanced the invasion process is, the more difficult it is to mitigate (Hester and Cacho 2009). As such, early observation and action are critical to native communities. Proactive efforts can be undertaken to eliminate infestations when species first invade an area (Rejmanek and Pitcairn 2002). For example, several small infestations of small broomrape (*Orobanche minor* Sm.), tropical soda apple (*Solanum viarum* Dunal), wild red rice (*Oryza sativa* L.), and killer algae [*Caulerpa taxifolia* (Vahl) C. Ag.] were successfully eradicated in the United States in the 1990s and 2000s due to early recognition (Simberloff 2013). Even eradicating isolated populations can keep the invader out of a region for years (Mack et al. 2000; Simberloff 2013).

Site characteristics are a major component that determine invasion success (Radosevich et al. 2003; Thuiller et al. 2012). Knowledge of the biotic and abiotic features of the areas experiencing a new invasion is critical to limiting negative impacts (Vilà et al. 2007). Environmental data, that is, abiotic site features such as soil type and topographic position, help to improve our understanding of site characteristics that influence invasive species occurrence (Stohlgren et al. 2003). Additionally, recent studies indicated that abiotic and biotic features of recipient habitats play a prominent role in plant invasions (Chytrý et al. 2008a, 2008b; Pyšek et al. 2010). For example, among 32 habitats in the Czech Republic, disturbed human-made habitats with herbaceous vegetation (e.g., agricultural land) were the most invaded, whereas dry, wet, and saline grasslands, base-rich fens, and broad-leaved deciduous woodlands were most resistant to invasion (Chytrý et al. 2008a). The composition of the recipient community

Management Implications

Ventenata [*Ventenata dubia* (Leers) Coss.] is an invasive annual grass that has expanded south into sagebrush steppe communities from its original invaded range in the Inland Northwest. Where it is well established in the Inland Northwest, this weed has negatively affected forage production and could also negatively affect sagebrush steppe communities. We present a description of *V. dubia*'s invasion of sagebrush steppe plant communities to offer land managers site characteristics associated with *V. dubia* to inform management, including detection surveys to find new infestations of *V. dubia*.

Within the study region, *V. dubia* was present at a wide elevational range (916 m to 1,662 m) and across a variety of different plant community types from highly disturbed annual grasslands to intact *A. tridentata* communities. *Ventenata dubia* was found commonly in plant communities located in areas of higher precipitation and/or in topographic features that retain greater soil moisture (e.g., ephemeral streams). At this early stage of invasion, its presence was patchy and its abundance typically low.

High *V. dubia* cover (>12.5%) was associated with lower plant species richness and plant community evenness, but when *V. dubia* cover was low (<12.5%), both richness and evenness were similar to what was seen in areas without *V. dubia*. Plant species richness and evenness were affected more for native plant species than for nonindigenous plant species. When *V. dubia* cover increased, medusahead [*Taeniatherum caput-medusae* (L.) Nevski] abundance increased, but downy brome (*Bromus tectorum* L.) abundance decreased, suggesting that *V. dubia* currently shares a niche with *T. caput-medusae*. *Taeniatherum caput-medusae* often is associated with mesic uplands, while *B. tectorum* often is associated with xeric uplands. In addition, abiotic characteristics associated with *V. dubia* included rocky, shallow, clayey soils with low phosphorus and potassium and sites with a more southerly aspect and gentle slopes. If *V. dubia* continues to expand within sagebrush steppe communities, land managers should consider searching moist microhabitats and areas commonly associated with *T. caput-medusae* to limit *V. dubia* from continuing its invasion.

Belgian forest. They concluded that since those three taxa characterize open habitats, forest-clearing activities are somewhat responsible for the spread of nonindigenous species. As such, land managers of this Belgian forest can work to limit, monitor, and/or revegetate areas of tree felling. In summation, knowing the abiotic and biotic features that increase the invasibility of a habitat allows managers to make educated predictions and develop integrated pest management strategies to prevent, control, or eliminate the spread of an invader. While foresight of the species' arrival is extremely difficult, knowledge of the features and availability of areas suitable for colonization and establishment in the new range may encourage focus on inhibiting the expansion of the invasion.

Ventenata [*Ventenata dubia* (Leers) Coss.] is a nonindigenous winter annual grass that has become increasingly invasive in grasslands and pasturelands in the Inland Northwest (Pavek et al. 2011) since its arrival to the region in 1952 (Barkworth et al. 1993). *Ventenata dubia* is capable of displacing perennial grasses as well as other invasive, nonindigenous annual grasses, including downy brome (*Bromus tectorum* L.) and medusahead [*Taeniatherum caput-medusae* (L.) Nevski] (Prather and Burke 2011). It has spread from its initial location in Spokane County, WA, to 10 other U.S. states and five Canadian provinces (CABI 2017). In 2001, *V. dubia* was spreading at a rate of 1.2 million ha yr^{-1} in the Pacific Northwest (Novak et al. 2015), and so it is likely that this range expansion will continue, increasing management challenges and ecological costs. As evidenced by herbaria specimen frequency and dates of collection, *V. dubia* is only just beginning its invasion into sagebrush steppe ecosystems. The oldest (ca. 1960s) and most abundant herbaria records are from grasslands in the Spokane, WA, and Coeur d'Alene, ID, areas, with fewer and newer (ca. 2010s) records in southern Idaho and eastern Oregon in sagebrush steppe habitat (Consortium of Pacific Northwest Herbaria 2018). Little is known about *V. dubia*'s distribution, abundance, and habitat niche in sagebrush steppe communities, a large region critical for forage production and wildlife habitat (Smith 1950). Documented impacts of *V. dubia* invasion include: (1) a significant decline in forage production in small pasture, grass–hay, and grassland systems of north-central Idaho due to displacement of perennial grasses and poor forage value of *V. dubia* (Prather and Burke 2011); and (2) a decline in nesting success of insectivorous birds due to a loss of biodiversity in conservation lands in northern Idaho (Mackey 2014).

Characterizing the new landscape where *V. dubia* is expanding is a valuable endeavor, because the spatial arrangement of different landscape elements affects the rate of spread of invasive species (Theoharides and Dukes 2007). In addition, quantifying if the plant community composition is different when this new invader is present as opposed to when it is absent provides insight into its competitive ability and the resistance ability of the resident community. To initiate investigation of *V. dubia*'s expansion into sagebrush rangelands, we asked: (1) What is the distribution and abundance of *V. dubia* in this new ecosystem? (2) How do plant diversity and abundance vary with increasing *V. dubia* cover? (3) What abiotic and biotic features are associated with *V. dubia* presence and abundance? Answers to these questions will help guide efforts to assess the kind of niche *V. dubia* may invade as it undergoes range expansion in sagebrush steppe communities. If preventing invasive plants from reaching new areas is the most cost-effective means of control (Davies and Sheley 2007), then proactive surveys for at-risk areas in rangelands are

of a new invader also plays a role in invasion success and severity of impacts (D'Antonio and Thomsen 2004). It is well documented that many invasions result in decreased biodiversity due to predation, competition for resources, habitat alteration, and other direct and indirect effects (Bertness 1984; Mack et al. 2000; Vitousek 1990). On the other hand, the invader may not necessarily precipitate a loss of biodiversity, but rather the existing community may be one where species are not resistant to invasion, either because of functional dissimilarity to the invader or a lack of structural complexity (Allen and Meyer 2014; Leffler et al. 2014). Thus, the invader's presence may correlate to a different species assemblage than when the invader is not present because of the traits of the previously established community. Furthermore, the presence of an indicator species in the recipient habitat may be used to evaluate a site's susceptibility to invasion (Godefroid and Koedam 2003). For example, Godefroid and Koedam (2003) identified three plant species that indicated areas at risk for colonization by nonindigenous species in a

worthwhile. We performed field surveys in sagebrush steppe communities in southern Idaho and eastern Oregon to answer these questions.

Materials and Methods

Study Location and Sampling

We conducted field surveys from June 2, 2015 to June 16, 2015 in six counties in southwestern Idaho and one county in eastern Oregon (Figure 1). We chose two ecoregions that support sagebrush steppe: the Blue Mountains in northeastern Oregon and the Snake River Plain in Idaho. In these regions, 15 locations were selected after consultation with local agency botanists who were knowledgeable concerning where *V. dubia* occurred. Because *V. dubia* is not common in these regions, conducting a random survey would have resulted in few or no inclusions of *V. dubia*. At each location, we established a site, defined as a circle with a 100-m diameter, based on ease of access (proximity to roads) and landscape conditions. Sites were selected to be representative of the dominant plant community at that location and they were classified based on types and abundance of important functional groups, including dominant woody species. All sites were disturbed by grazing, but disturbance severity was not recorded.

Within each site, we arbitrarily located three transects where we recorded global positioning system coordinates, elevation, aspect, and slope. Transects were placed so they would characterize the site vegetation and remain within a single plant community type. Each transect was 20-m long, and along it we placed five quadrats (i.e., plots) sized 0.25 by 1 m at 5-m intervals beginning at 0 m. At the start of each transect, two soil depths were recorded on opposite sides of the 0-m plot. Each depth was determined by driving a 2.54-cm-diameter, pointed, iron rod into the ground in multiple locations and then calculating the average depth at which the rod could no longer penetrate. Soil core samples from these depth locations were collected and homogenized so that texture and nutrient analyses could be conducted later. Thus, at each site, there were 3 transects, 15 plots, 6 soil depth measurements, and 3 soil samples. In each plot, percent cover of all vascular plant species, biological soil crust, and abiotic variables (bare ground, rock, litter) were assessed via ocular estimation according to established cover classes: 0%, 1% to 5%, 5% to 12.5%, 12.5% to 25%, 25% to 50%,

50% to 75%, 75% to 95%, and 95% to 100%. For subsequent statistical analysis, the median percent from each cover class was used to represent estimates of cover.

A prior study indicated that there was less phosphorous in soil where *V. dubia* infestation was high compared with areas with low *V. dubia* infestation (Mackey 2014). Because of this possible link between soil fertility and infestation severity, of the 45 soil samples, a subset ($n = 21$) from 10 sites was analyzed for particle size distribution and available phosphorus and potassium concentrations. The subset was selected based on the *V. dubia* cover values at the 0-m plot (the plot in closest proximity to the soil sampling site) to provide the best comparison: five samples were from plots with no *V. dubia*, seven samples were from plots with low *V. dubia*, and nine samples were from plots with high *V. dubia*. Available phosphorus and potassium were determined via the Olsen sodium bicarbonate extraction method at the University of Idaho Analytical Science Laboratory.

Statistical Analysis

In general, within plots, *V. dubia* foliar cover was 0%, less than 12.5%, or greater than 12.5%, so three categories—none, low (<12.5%), and high (>12.5%)—were used for most analyses. At each site, we computed species richness for each of the three *V. dubia* cover categories using species presence/absence data at the plot level. Results were tested for statistical significance using one-way ANOVA with a Tukey honest significant difference (HSD) post hoc test to evaluate pairwise multiple comparisons. The response variable was square-root transformed when necessary to meet assumptions of normality and homogeneity of variance. In addition, at each site, the Shannon diversity index was calculated for each of the three *V. dubia* cover categories using the average percent foliar cover values at the plot level. The Shannon diversity index considers not only the number of species but their relative abundance within the plots and is better indicator of diversity when rare and abundant species are expected to be equally important (Morris et al. 2014). Results were tested for statistical significance using one-way ANOVA with a Tukey HSD post hoc test. However, when diversity values failed to meet ANOVA assumptions and data transformations did not remedy the problem, we used the nonparametric Kruskal-Wallis rank-sum test and the Dunn post hoc test to evaluate pairwise multiple comparisons. Because richness and diversity values between three levels of *V. dubia* cover were compared, *V. dubia*'s own presence and cover were not included in these analyses.

For further insight into species composition, rank abundance models were evaluated at the plot level with the best-fit model selected by the *radfit* function in the 'vegan' R software package (R v. 3.2.2, Vienna, Austria). To evaluate indicator species associated with *V. dubia*, a chi-square test with Pearson residuals was evaluated for species either positively or negatively associated with the three categories of *V. dubia* cover. A nonmetric multidimensional scaling (NMDS) analysis revealed biotic and abiotic features associated with *V. dubia* cover. Finally, the relationships between *V. dubia* cover and soil particle composition, phosphorus concentration, and potassium concentration were analyzed with a linear regression. To standardize the variance, one was added to *V. dubia* cover values, which were then natural log transformed. Outliers were adjusted by reweighting them by 1/studentized residual. All analyses were computed in R v. 3.2.2.
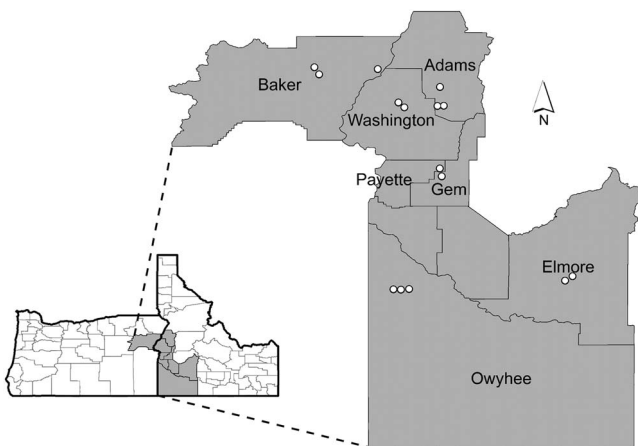

Figure 1. Sagebrush steppe survey locations in eastern Oregon and southwestern Idaho with county names indicated. See Table 1 for more information specific to each location.

Table 1. List of locations surveyed, including county and state, global positioning system coordinates, elevation, and plant community type.

| Location | County, State | Coordinates[a] | | Elevation[a] | Community type[b] |
		Latitude in °N	Longitude in °W	m	
Gravel Pit	Adams, ID	44.559	116.480	916	Scabland sagebrush–big sagebrush
Schwenkfelder	Adams, ID	44.557	116.491	916	Big sagebrush–scabland sagebrush–annual grassland
Jackson Creek	Adams, ID	44.699	116.489	927	Scabland sagebrush–big sagebrush
Four Mile Road	Payette, ID	44.088	116.492	929	Annual grassland–big sagebrush–antelope bitterbrush
Bacher Creek	Baker, OR	44.836	117.424	952	Big sagebrush
Sparta	Baker, OR	44.840	117.426	952	Big sagebrush
Reeds Grove Lower	Washington, ID	44.571	116.785	962	Bitterbrush–big sagebrush–rock buckwheat
Pine Town Road	Baker, OR	44.834	116.956	970	Annual grassland–scabland sagebrush
Big Flat	Gem, ID	44.047	116.483	999	Annual grassland–big sagebrush–bitterbrush
Reeds Grove	Washington, ID	44.576	116.792	1,032	Bitterbrush–big sagebrush–rock buckwheat
Whiskey Hill	Owyhee, ID	43.185	116.778	1,318	Big sagebrush–bitterbrush–juniper
Ida Belle	Owyhee, ID	43.185	116.783	1,483	Big sagebrush–bitterbrush–juniper
Prairie Road	Elmore, ID	43.269	115.514	1,489	Big sagebrush–bitterbrush–rock buckwheat
Highway 20	Elmore, ID	43.255	115.542	1,514	Annual grassland–little sagebrush
Chipmunk Road	Owyhee, ID	43.184	116.821	1,662	Idaho fescue–little sagebrush

[a]Coordinates and elevation are average values from the starting points of the three transects placed at each site.
[b]Community types were defined according to important functional groups and listed from most prevalent to least prevalent within each 100-m-diameter site. Scabland sagebrush, *Artemisia rigida*; big sagebrush, *Artemisia tridentata*; antelope bitterbrush, *Purshia tridentata*; rock buckwheat, *Eriogonum sphaerocephalum*; juniper, *Juniperus occidentalis*; little sagebrush, *Artemisia arbuscula*; Idaho fescue, *Festuca idahoensis*.

Results and Discussion

Within the study area, we found *V. dubia* in a variety of plant communities at elevations ranging from 916 to 1,662 m (Table 1). At the study locations, *V. dubia* was primarily located in moist habitats; either in topographic features that retain water or in areas that receive more precipitation as inferred from the native vegetation present. Though widely distributed throughout the study region, *V. dubia* only appeared in 45% of the 225 plots across all sites, despite the site-selection method being positively biased for *V. dubia*. In addition, *V. dubia* only existed at greater than 50% cover in 2 of the 225 plots across all sites. The low percent cover of *V. dubia* and its presence in about half the plots indicate that its distribution is patchy and suggest that *V. dubia* may be in an early phase of invasion in sagebrush rangelands. In comparison, in the Inland Northwest where *V. dubia* has been present for many more decades, it frequently forms a near monoculture in areas up to hundreds of hectares (Novak et al. 2015). NMDS analysis of plot-level community data revealed that all of the categories of *V. dubia* cover were widely distributed in community space and overlapped extensively (Figure 2).

Three of the five locations where *V. dubia* was most abundant (Big Flat: 18% average *V. dubia* cover; Four Mile Road: 13% cover; Schwenkfelder: 10% cover) were located below 1,000-m elevation. These locations were characterized by extensive annual grass complexes largely composed of *T. caput-medusae*. *Taeniatherum caput-medusae* invades areas with relatively higher precipitation or, where precipitation is lower, it is associated with swales (Hironaka 1994). The association of *V. dubia* with *T. caput-medusae* in the Snake River Plain contrasts to observations in grasslands of

the Inland Northwest, where *V. dubia* is associated with *B. tectorum* (Northam and Callihan 1994). Within the native European range of *V. dubia*, it can be found in areas where *T. caput-medusae*, Japanese
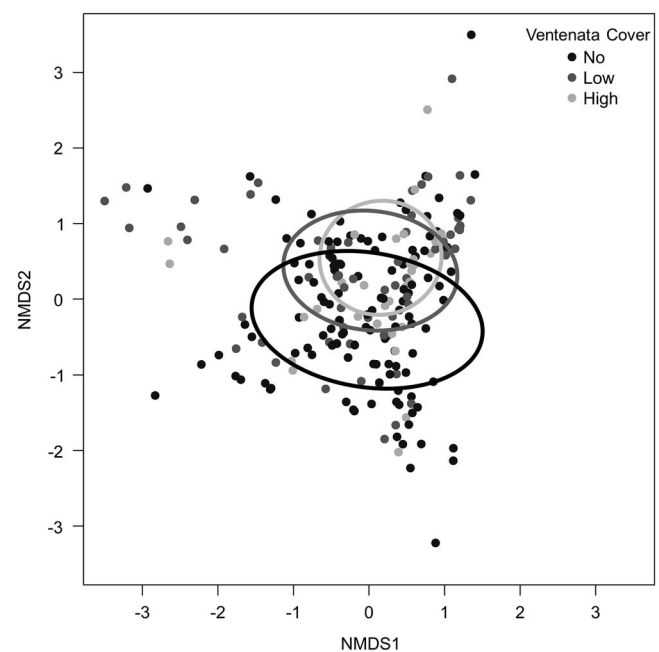

Figure 2. Nonmetric multidimensional scaling (NMDS) of plant communities from plots with no *Ventenata dubia* (black line), low (<12.5%) *V. dubia* cover (gray line), and high (>12.5%) *V. dubia* cover (light gray line). Ellipses represent standard deviations of the weighted average of different *V. dubia* categories at the 95% confidence level.
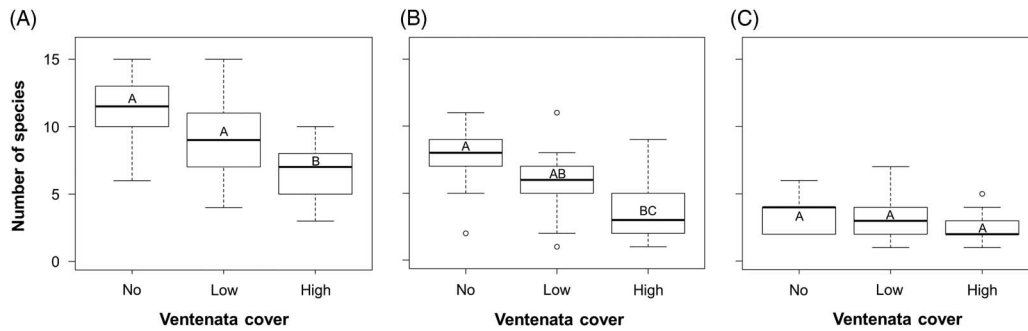
Figure 3. Box plots of species richness of (A) all plants, (B) only native plants, and (C) only nonindigenous plants within sample plots with no, low (<12.5%), and high (>12.5%) *V. dubia* cover. Groups with the same letter are not statistically different (α = 0.05).

brome (*Bromus japonicus* Houtt.), *B. tectorum*, and interrupted windgrass [*Apera interrupta* (L.) Beauv.] are found (CABI 2017; Contu 2013). Interestingly, the other two locations where *V. dubia* was most abundant (Ida Belle: 10% average *V. dubia* cover; Chipmunk Road: 8% cover) were located above 1,450-m elevation. These locations had significant stands of mountain big sagebrush [*Artemisia tridentata* Nutt. spp. *vaseyana* (Rydb.) Beetle] and little sagebrush (*Artemisia arbuscula* Nutt.). *Artemisia tridentata* spp. *vaseyana* inhabits a relatively higher precipitation zone and *A. arbuscula* inhabits poorly drained, shallow clay soils (Shultz 2012). Thus, elevation does not seem to be a good indicator of *V. dubia* presence. Instead, *V. dubia* appears to be associated with relatively wetter microhabitats, either because of the precipitation zone, topographic features, or edaphic qualities that maintain higher soil moisture.

Within sites, species richness between plots with no, low (<12.5%), and high (>12.5%) *V. dubia* cover was significantly different (ANOVA: $F = 13.54$, df = 2, P < 0.001), with the lowest species richness in plots with high *V. dubia* cover (Figure 3A). Comparatively, plots with no and low *V. dubia* cover had higher richness, but they were not significantly different from each other (Tukey HSD: no vs. low P = 0.088; Figure 3A). This finding supports evidence from other invasions showing a negative correlation between richness and the presence of an invasive species (Báez and Collins 2008; Porter and Savignano 1990).

When considering species richness of just the native plants, there was a significant difference between the three categories of *V. dubia* cover (ANOVA: $F = 8.20$, df = 2, P = 0.001; Figure 3B). Richness was lower in plots with high *V. dubia* cover compared with plots without *V. dubia* (Tukey HSD: P < 0.001; Figure 3B). Plots with low *V. dubia* cover had an intermediate species richness statistically equivalent to plots with no and high cover (Tukey HSD: low vs. no P = 0.092, low vs. high P = 0.168;

Figure 3B). It may be the case that there is a threshold in invader abundance that must be achieved to permit detection of a difference in native species diversity (Gooden et al. 2009; Grice 2004). Among nonindigenous species, there was a nearly significant difference in richness between the *V. dubia* cover categories (ANOVA: $F = 3.179$, df = 2, P = 0.053; Figure 3C). But when pairwise comparisons were evaluated, significance was not achieved, though it trended toward decreased richness in plots with high *V. dubia* compared with plots with no *V. dubia* (Tukey HSD: P = 0.070; Figure 3C). The effects of an invasive species on the diversity of other nonindigenous species is not well studied, though in a mesocosm of aquatic communities, invaders did not negatively influence each other (Preston et al. 2012). Overall, there was an association between high *V. dubia* cover and lower species richness, and the correlation was stronger among the resident native species than among the nonindigenous species.

The trends for Shannon's diversity values were weaker than those from species richness, as there was more variability in diversity values within the three *V. dubia* cover categories (Figure 4). Shannon's diversity considers not only the number of species but their relative abundances within plots. There was a significant correlation between diversity and *V. dubia* cover (Kruskal-Wallis rank sum: $\chi^2 = 6.386$, df = 2, P = 0.041; Figure 4A), in that diversity was lower in plots with high *V. dubia* compared with plots with no *V. dubia* (Dunn post hoc: no vs. high P = 0.042; Figure 4A). Thus, high *V. dubia* cover was correlated with a decreased richness and evenness of the plant community. Comparatively, plots with low *V. dubia* cover were not significantly different from plots with no or high cover (Dunn post hoc: no vs. low P = 0.964, low vs. high P = 0.084; Figure 4A).

When only native species were considered, there was no significant difference in diversity values between cover categories
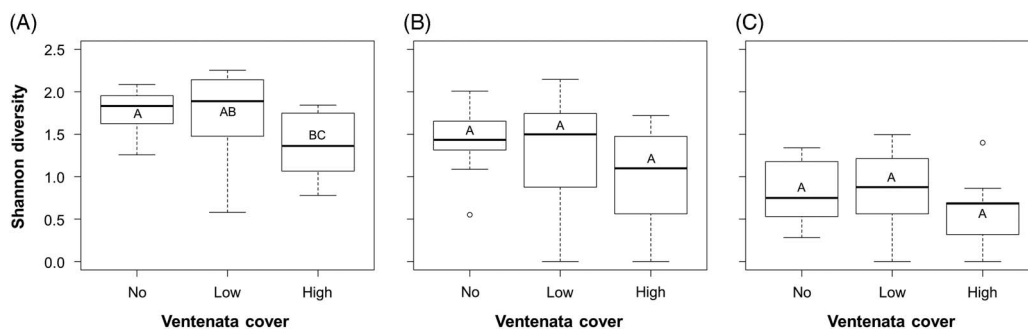

Figure 4. Box plots of average Shannon diversity indices of (A) all plants, (B) only native plants, and (C) only nonindigenous plants within sample plots with no, low (<12.5%), and high (>12.5%) *Ventenata dubia* cover. Groups with the same letter are not statistically different (α = 0.05). Higher diversity values indicate greater richness and evenness.
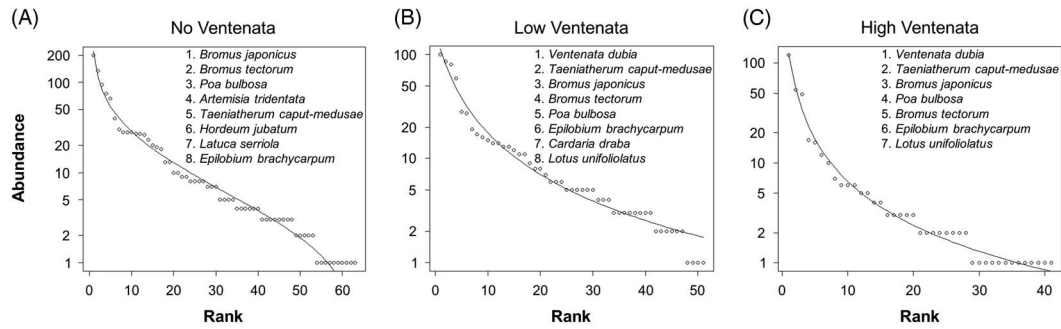
Figure 5. Rank abundance models of plots with (A) no, (B) low (<12.5%), and (C) high (>12.5%) *V. dubia* cover across all sites. The solid line represents the best-fit model for each data set, and a selection of the most abundant species have been listed in order starting with the highest rank to better reveal differences in community structure.

(ANOVA: $F = 2.742$, df = 2, $P = 0.078$; Figure 4B). The same was true when just the nonindigenous species were evaluated (ANOVA: $F = 1.965$, df = 2, $P = 0.155$; Figure 4C). In general, there was more variability in diversity values than in simple richness values, indicating that species' abundances covered a large range. In fact, within sites, the average cover values within the *V. dubia* cover categories ranged from 0% to 69%. Thus, at this snapshot in time, high *V. dubia* cover was weakly associated with decreased diversity, but high variability in the data prevented detection of whether this correlation existed for native and nonindigenous species when evaluated separately.

Next, rank abundance models elucidate the dominant species present within plots stratified by the three *V. dubia* cover categories. The models show that invasive annual grass species such as *B. tectorum*, *T. caput-medusae*, and *B. japonicus*, as well as bulbous bluegrass (*Poa bulbosa* L.), a nonindigenous perennial grass, were consistently the most abundant across all plots but their relative abundance rankings changed depending on the amount of *V. dubia* cover (Figure 5). With no *V. dubia*, *A. tridentata* was the fourth most dominant species. But when *V. dubia* was present, this important shrub moved down in rank. Also, as *V. dubia* cover increased, *T. caput-medusae* moved up in rank, and *B. tectorum* moved down. Unsurprisingly, the most abundant native species present when *V. dubia* was present were annual forbs (foxtail barley (*Hordeum jubatum* L.), panicle willowherb (*Epilobium brachycarpum* C. Presl), and deervetch [*Lotus unifoliolatus* (Hook.) Benth.] that inhabit disturbed, moist habitats (Jepson Flora Project 2017).

Chi-square indicator analysis revealed the presence of several species positively correlated with the different categories of *V. dubia* cover and other species that negatively correlated with the cover categories (Figure 6). Species positively associated with *V. dubia* included *T. caput-medusae*, needleleaf navarretia [*Navarretia intertexta* (Benth.) Hook.], and *E. brachycarpum*. These species were less frequent in plots that did not contain *V. dubia*. Conversely, species negatively associated with *V. dubia* included *A. tridentata*, threetip sagebrush (*Artemisia tripartita* Rydb.), antelope bitterbrush [*Purshia tridentata* (Pursh) DC.], rock buckwheat [*Eriogonum sphaerocephalum* Douglas ex Benth.], and *B. tectorum*. These species were less common in plots containing *V. dubia*. These data indicate that in sagebrush steppe, *V. dubia* is associated with *T. caput-medusae* and is less prevalent in dry, intact shrub communities. These indicator species also provide insight into *V. dubia*'s niche: the species positively associated with *V. dubia* were annuals that inhabit moist areas, while the species negatively associated with *V. dubia* were primarily perennials (*B. tectorum* being the exception) that inhabit dry areas (Jepson Flora Project 2017). In arid and semiarid ecosystems, soil moisture strongly influences plant composition (Ehleringer et al. 1999). More abiotically benign environments (e.g., wet areas) typically support increased invasive plant growth and reproduction (Pfeifer-Meister et al. 2008). For example, in an oak savanna ecosystem, MacDougall et al. (2006) reported that the abundance of invasive plants increased in habitats with deeper soils that retain more soil moisture, and in an eastern deciduous forest. Warren et al. (2012) reported that an invasive annual grass
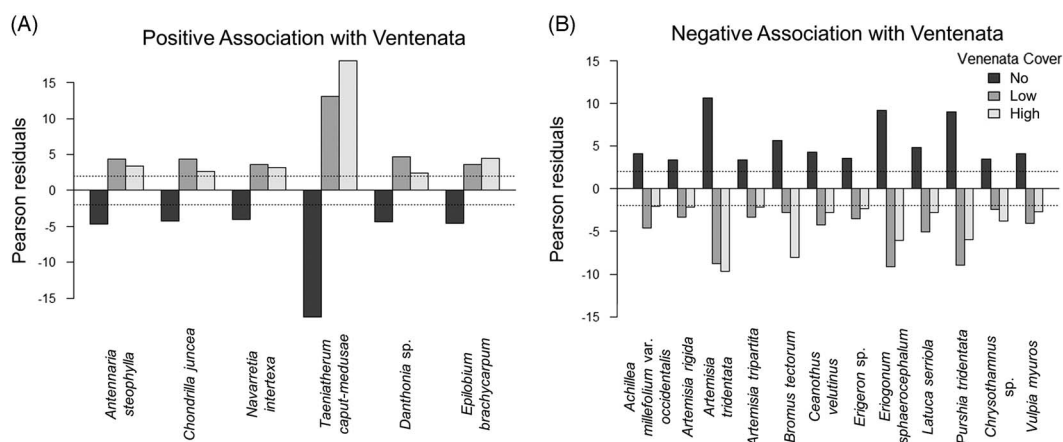

Figure 6. Indicator species in relation to *Ventenata dubia* cover across all survey plots. (A) Positive indicator species are defined as those with significantly negative Pearson residuals (<−2) in plots without *V. dubia* and significantly positive Pearson residuals (>2) in plots with low (<12.5%) and high (>12.5%) *V. dubia* cover. (B) Conversely, negative indicator species are defined as those with significantly positive Pearson residuals (>2) in plots without *V. dubia* and significantly negative Pearson residuals (<−2) in plots with low and high *V. dubia* cover.
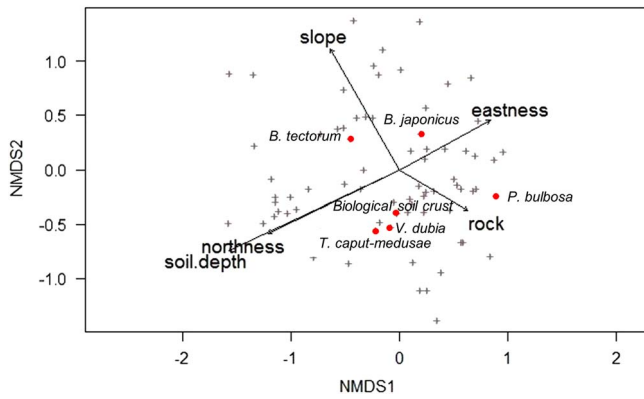
Figure 7. Nonmetric multidimensional scaling (NMDS) of species scores in relation to collected environmental variables across all surveyed plots. Plus signs indicate all species, and for clarity, red circles indicate a selection of plant species or functional groups of interest, which are labeled. Only significant ($\alpha = 0.05$) environmental predictors were included, and arrows show the direction of increasing gradient.

had higher germination and survival when soil moisture was higher. In our study, while we did not measure soil moisture, the results of the indicator species analysis suggest that *V. dubia* occurs with other species that inhabit a moist niche.

NMDS analysis revealed that *V. dubia*, *T. caput-medusae*, and biological soil crust were closely associated (Figure 7). Although biological soil crust is often linked to undisturbed areas, some crust components, such as lichens, can colonize disturbed sites more rapidly than other species (U.S. Department of the Interior [USDI] 2001). In addition, surveys show that communities invaded by annual plants can still maintain annual mosses and cyanobacteria on the soil surface (Kaltenecker 1997). In this study, because all sites were disturbed by grazing, the close association between *V. dubia*, *T. caput-medusae*, and soil crust is likely more indicative of a wetter microhabitat than of the level of disturbance. Biological crusts can produce a rough surface microtopography that acts as detention structures for water, which can increase water infiltration (USDI 2001). The NMDS analysis revealed that much of the variation in abundance of *V. dubia*, *T. caput-medusae*, and biological soil crust was explained by variation in rock, soil depth, and a north/south gradient (Figure 7). By contrast, *P. bulbosa* abundance was largely influenced by rock; *B. japonicus* was largely influenced by an east/west gradient; and *B. tectorum* was largely influenced by a combination of slope, soil depth, and a north/south gradient.

Linear regressions using natural log–transformed *V. dubia* cover values were calculated to test for a relationship between *V. dubia* cover and clay, sand, and silt content from 21 soil

samples. There was a significant positive relationship between *V. dubia* and clay [$F(1, 19) = 5.925$, $P = 0.025$, adj. $R^2 = 0.198$; Figure 8A]. Clay composed up to 41% of the soil particle distribution. There was no significant relationship between *V. dubia* and sand or silt ($P > 0.1$). These data provide further support that *V. dubia* occupies wetter areas, because clay particles retain more soil moisture compared with other soil particles (Marshall and Holmes 1988).

In agricultural systems, Mackey (2014) found an association between high *V. dubia* cover (>50%) and soils comparatively low in phosphorous and potassium concentration. In our study, linear regressions of natural log–transformed *V. dubia* cover values showed lower phosphorous [$F(1, 19) = 22.44$, $P < 0.001$, adj. $R^2 = 0.517$] and potassium [$F(1, 19) = 5.598$, $P = 0.029$, adj. $R^2 = 0.187$] concentrations with higher *V. dubia* cover (Figure 8B and C). For all samples, measured phosphorus values ranged from 5 to 31 ppm, and potassium values ranged from 200 to 520 ppm. In addition to providing more information about *V. dubia*'s abiotic niche, these results offer insight into *V. dubia*'s competitive ability to access these macronutrients when they are in limited supply. Evidence from meta-analyses suggests that invasive plants have higher nutrient resorption efficiencies than native plants when in nutrient-poor environments (González et al. 2010; Sardans et al. 2017).

These data, coupled with herbaria records, suggest that *V. dubia* is still in the early stages of invasion in sagebrush steppe communities. Its presence was patchy across a range of elevations, and its abundance was low. Currently, areas with high *V. dubia* cover were associated with decreased plant plant species richness and diversity, particularly native plant species richness. While soil moisture was not directly measured, *V. dubia* was observed in ephemerally wet areas, and results from the indicator species and NMDS analyses show associations between *V. dubia* and plants that occupy moist habitats, suggesting that *V. dubia* initially occupies wet microhabitats. In addition, there were strong positive associations between *V. dubia* and the abundance of *T. caput-medusae* and the amount of clay in the soil. There were negative correlations between *V. dubia* cover and phosphorus and potassium concentrations in the soil.

In grasslands of the Inland Northwest, before the 1990s, *V. dubia* was initially observed in seasonally wet areas (Miller et al. 1998). Now, however, *V. dubia* dominates dry, south-facing slopes originally populated by xeric perennial bunchgrasses, such as bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve] and Sandberg bluegrass (*Poa secunda* J. Presl) (Wallace and Prather 2013b). In this region, *V. dubia* in moist areas initially acted as source populations, with it later expanding its
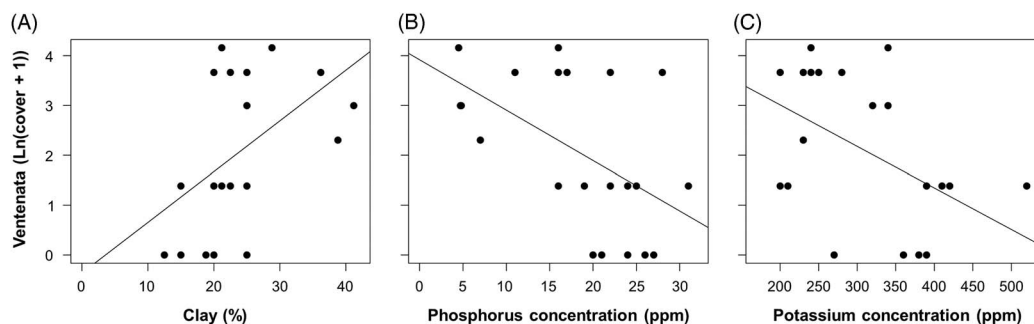

Figure 8. Relationships between percent *Ventenata dubia* cover and (A) percent clay content [$\ln(y+1) = -0.363 + 0.102x$], (B) phosphorous concentration [$\ln(y+1) = 3.917 - 0.101x$], and (C) potassium concentration [$\ln(y+1) = 4.676 - 0.008x$] in the soil. Fitted lines are significant ($\alpha = 0.05$) regressions.

habitat niche to also include dry areas. We hypothesize a similar phenomenon may occur where *V. dubia* has expanded its range to sagebrush steppe ecosystems. Source-sink dynamics explain patch demography of metapopulations for animals, plants, and microbes (Eriksson 1996; Hall et al. 2016; Horvath et al. 1996). For example, Wallace and Prather (2013a) concluded that high shrub communities, compared with three other habitat types, were more suitable for a nonindigenous annual forb, which may then act as source populations for invasive spread at a landscape scale. Our experience of *V. dubia*'s spread in the Inland Northwest leads us to conclude that *V. dubia*'s current distribution in sagebrush rangelands may not always be limited to seasonally wet areas. Instead, its presence in moist microhabitats may initially serve as source populations that will permit its spread to other, drier habitat types. Moreover, *B. tectorum* and *T. caput-medusae*, with life-history traits similar to those of *V. dubia*, are problem weeds in both the grasslands of the Inland Northwest (Northam and Callihan 1994) and sagebrush rangelands of the Inter-mountain West (Miller et al. 1999). Thus, in sagebrush steppe ecosystems, *V. dubia* management efforts should: (1) seek to use *T. caput-medusae* as an indicator species, such that initial monitoring efforts are focused around areas where *T. caput-medusae* has previously established or has the potential to be a problem; and (2) focus control and restoration efforts on moist habitats, as these may act as source populations where *V. dubia* is initially most competitive.

Locating areas where the risk of invasion is high by using knowledge of existing flora and site characteristics offers a preventive control policy of invasive taxa in place of a curative control policy (Godefroid and Koedam 2003). Knowledge of the distribution of *T. caput-medusae* in sagebrush steppe rangelands would elucidate the potential area of future *V. dubia* invasion. Preventive action is more efficient than a reactive one (Macdonald 1994), and the importance of detecting invasions early and initiating appropriate levels of control immediately must continue to be emphasized (Dickson 1998; Usher 1989).

References

Allen PS, Meyer SE (2014) Community structure affects annual grass weed invasion during restoration of a shrub-steppe ecosystem. Invasive Plant Sci Manag 7:1–13

Báez S, Collins SL (2008) Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. PLoS ONE 3:e2332

Barkworth ME, Capels KM, Long S (1993) *Ventenata*. Pages 683–684 *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: Oxford University Press

Bertness M (1984) Habitat and community modification by an introduced herbivorous snail. Ecology 65:370–381

CABI (2017) *Ventenata dubia* [original text by Timothy Prather]. *In* Invasive Species Compendium. Wallingford, UK: CAB International. https://www.cabi.org/isc/datasheet/117772. Accessed: October 31, 2017

Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008b) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458

Consortium of Pacific Northwest Herbaria (2018) Specimen Database, University of Washington. http://www.pnwherbaria.org/data/search.php. Accessed: January 23, 2018

Contu S (2013) *Ventenata dubia*. The IUCN Red List of Threatened Species 2013: e.T44392189A44414263. http://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T44392189A44414263.en. Accessed: October 31, 2017

D'Antonio CM, Thomsen M (2004) Ecological resistance in theory and practice. Weed Technol 18:1572–1577

Davies KW, Sheley RL (2007) A conceptual framework for preventing the spatial dispersal of invasive plants. Weed Sci 55:178–184

Dickson JH (1998) Plant introductions in Scotland. Pages 38–44 *in* Lambert RA, ed. Species History in Scotland. Introductions and Extinctions Since the Ice Age. Edinburgh: Scottish Cultural Press

Ehleringer JR, Schwinning S, Gebauer R (1999) Water use in arid land ecosystems. Pages 347–365 *in* Press MC, Scholes JD, Barker MG, eds. Physiological Plant Ecology. Boston: Blackwell Science

Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77:248–258

Godefroid S, Koedam N (2003) Identifying indicator plant species of habitat quality and invasibility as a guide for peri-urban forest management. Biodivers Conserv 12:1699–1713

González AL, Kominoski JS, Danger M, Ishida S, Iwai N, Rubach A (2010) Can ecological stoichiometry help explain patterns of biological invasions? Oikos 119:779–790

Gooden B, French K, Turner PJ, Downey PO (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. Biol Conserv 142:2631–2641

Grice AC (2004) Weeds and the monitoring of biodiversity in Australian rangelands. Austral Ecol 29:51–58

Hall JPJ, Wood JA, Harrison E, Brockhurst MA (2016) Source-sink plasmid transfer dynamics maintain gene mobility in soil bacterial communities. Proc Natl Acad Sci USA 113:8260–8265

Hester SM, Cacho OJ (2009) The spread of a biological invasion in space and time: modelling active and passive surveillance. Pages 4298–4304 *in* Proceedings of the 18th World IMACS Congress and MODSIM09 International Congress on Modelling and Simulation. Cairns, Australia: Modelling and Simulation Society of Australia and New Zealand and International Association for Mathematics and Computers in Simulation

Hironaka M (1994) Medusahead: natural successor to the cheatgrass type in the northern Great Basin. Pages 89–91 *in* Proceedings—Ecology and management of annual rangelands. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station

Horvath TG, Lamberti GA, Lodge DM, Perry WL (1996) Zebra mussel dispersal in lake-stream systems: source-sink dynamics? J N Am Benthol Soc 15:564–575

Jepson Flora Project (2017) Jepson eFlora. http://ucjeps.berkeley.edu/eflora. Accessed: December 22, 2017

Kaltenecker JH, Wicklow-Howard M, Rosentreter R (1997) Microbiotic crusts of the Lemhi Resource Area and their effect on soil-water relationships in sites recovering from long-term grazing. Salmon, ID: U.S. Department of the Interior Bureau of Land Management. 58 p

Leffler AJ, Leonard ED, James JJ, Monaco TA (2014) Invasion is contingent on species assemblage and invasive species identity in experimental rehabilitation plots. Rangeland Ecol Manag 67:657–666

Macdonald IAW (1994) Global change and alien invasions: implications for biodiversity and protected area management. Pages 199–209 *in* Solbrig OT, Van Emden HM, Van Oordt PGW, eds. Biodiversity and Global Change. Paris: CAB International/IUBS

MacDougall AS, Boucher J, Turkington R, Bradfield GE (2006) Patterns of plant invasion along an environmental stress gradient. J Veg Sci 17:47–56

Mack RN, Simberloff D, Londsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Mackey A (2014) Developing a Decision Support Tool for Ventenata (*Ventenata dubia*) Integrated Pest Management in the Inland Northwest. Master's thesis. Moscow, ID: University of Idaho. 81 p

Marshall TJ, Holmes JW (1988) Soil Physics. 2nd ed. New York, NY: Cambridge University Press. 374 p

Miller HC, Clausnitzer D, Borman MM (1999) Medusahead. Pages 271–281 *in* Sheley RL, Petroff JK, eds. Biology and Management of Noxious Rangeland Weeds. Corvallis, OR: Oregon State University Press

Miller TW, Northam FE, Callihan RH (1998) Forage cultivar performance on rangeland twelve years after seeding. Kona, HI: Western Society of Weed Science. P 4

Morris EK, Caruso T, Buscot F, Fischer M, Hancock C, Maier TS, Meiners T, Müller C, Obermaier E, Prati D, Socher SA, Sonnemann I, Wäschke N, Wubet T, Wurst S, Rillig MC (2014) Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol Evol 4:3514–3524

Northam FE, Callihan RH (1994) New weedy grasses associated with downy brome. Pages 211–212 *in* Proceedings—Ecology and Management of Annual Rangelands. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station

Novak SJ, Cristofaro M, Maguire D, Sforza RFH (2015) The invasive grass ventenata (*Ventenata dubia*): a new threat for Nevada. http://agri.nv. gov/uploadedFiles/agrinvgov/Content/Plant/Noxious_Weeds/Documents/ Novak%20et%20al.%20Nevada%20Weed%20Management%20Association %20Conference%202015.pdf. Accessed: December 27, 2017

Pavek P, Wallace J, Prather T (2011) Ventenata biology and distribution in the Pacific Northwest. Page 107 *in* Proceedings of Western Society of Weed Science. Spokane, WA: Western Society of Weed Science

Pfeifer-Meister L, Cole EM, Roy BA, Bridgham SD (2008) Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia 155:357–366

Porter SD, Savignano DA (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 7:2095–2106

Preston DL, Henderson JS, Johnson PTJ (2012) Community ecology of invasions: direct and indirect effects of multiple invasive species on aquatic communities. Ecology 93:1254–1261

Prather T, Burke I (2011) Symposium: *Ventenata dubia*—an emerging threat to agriculture and wildlands? Pages 107–111 *in* Proceedings of Western Society of Weed Science. Spokane, WA: Western Society of Weed Science

Pyšek P, Bacher S, Chytrý M, Jarošík V, Wild J, Celesti-Grapow L, Gassó N, Kenis M, Lambdon PW, Nentwig W, Pergl J, Roques A, Sádlo J, Solarz W, Vilà M, Hulme PE (2010) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. Glob Ecol Biogeogr 19:317–331

Radosevich SR, Stubbs MM, Ghersa CM (2003) Plant invasions: process and patterns. Weed Sci 51:254–259

Rejmanek M, Pitcairn MJ (2002) When is eradiation of exotic pest plants a realistic goal? Pages 249–253 *in* Veitch CR, Clout MN, eds. Turning the Tide: The Eradication of Invasive Species. Gland, Switzerland/Cambridge, UK: International Union for Conservation of Nature, IUCN Species Survival Commission

Sardans J, Bartrons M, Margalef O, Gargallo-Garriga A, Janssens IA, Ciasis P, Obersteiner M, Sigurdsson BD, Chen HYH, Peñuelas J (2017) Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient-poor environments. Glob Change Biol 23:1282–1291

Shultz L (2012) Pocket Guide to Sagebrush. Petaluma, CA: Point Reyes Bird Observatory Conservation Science. 88 p

Simberloff D (2013) Invasive Species: What Everyone Needs to Know. 1st ed. New York: Oxford University Press. 352 p

Smith AD (1950) Sagebrush as winter feed for deer. J Wildl Manag 14:285–289

Stohlgren TJ, Barnett TD, Simonson SS (2003) Beyond North American weed management standards. http://irmaservices.nps.gov/datastore/v4/rest/ DownloadFile/434136?accessType=DOWNLOAD. Accessed: December 19, 2017

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Thuiller W, Gassó N, Pino J, Vilà M (2012) Ecological niche and species traits: key drivers of regional plant invader assemblages. Biol Invasions 14: 1963–1980

[USDI] U.S. Department of the Interior (2001) Biological Soil Crusts: Ecology and Management. Denver, CO: U.S. Department of the Interior Technical Reference 1730-2. 110 p

Usher MB (1989) Ecological effects of controlling invasive terrestrial vertebrates. Pages 463–489 *in* Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, eds. Biological Invasions: A Global Perspective. New York: Wiley

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veg Sci 18:35–42

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Wallace JM, Prather TS (2013a) Comparative demography of an exotic herbaceous annual among plant communities in invaded canyon grassland: inferences for habitat suitability and population spread. Biol Invasions 15:2783–2797

Wallace JM, Prather TS (2013b) Yellow starthistle control and forage response using aminopyralid and clopyralid combinations. San Diego, CA: Western Society of Weed Science. P 26

Warren RJ, Bahn V, Bradford MA (2012) Decoupling litter barrier and soil moisture influences on the establishment of an invasive grass. Plant Soil 367:339–346

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16:1192–1203