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Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass

Kirk W. Davies

Abstract Exotic plants are generally considered a serious problem in wildlands around the globe. However, some argue that the impacts of exotic plants have been exaggerated and that biodiversity and other important plant community characteristics are commonly improved with invasion. Thus, disagreement exists among ecologists as to the relationship of exotic plants with biodiversity and native plant communities. A better understanding of the relationships between exotic plants and native plant communities is needed to improve funding allocation and legislation regarding exotic plants, and justify and prioritize invasion management. To evaluate these relationships, 65 shrub–bunchgrass plant communities with varying densities of an exotic annual grass, *Taeniatherum caput-medusae* (L.) Nevski (medusahead), were sampled across 160,000 ha in southeastern Oregon, United States. Environmental factors were generally not correlated with plant community characteristics when exotic annual grass density was included in models. Plant diversity and species richness were negatively correlated with exotic annual grass density. Exotic annual grass density explained 62% of the variation in plant diversity. All native plant functional groups, except annual forbs, exhibited a negative

relationship with *T. caput-medusae*. The results of this study suggest that *T. caput-medusae* invasions probably have substantial negative impacts on biodiversity and native plant communities. The strength of the relationships between plant community characteristics and *T. caput-medusae* density suggests that some exotic plants are a major force of change in plant communities and subsequently threaten ecosystem functions and processes. However, experimental studies are needed to fully substantiate that annual grass invasion is the cause of these observed correlations.

Keywords Biodiversity · Conservation · Invasive plants · Medusahead · Species richness · Sagebrush

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Introduction

Invasive plants are generally considered to be a serious threat to wildlands around the world (D'Antonio and Vitousek 1992; DiTomaso 2000; Mack et al. 2000). Exotic annual grasses are of particular concern in arid and semi-arid regions of western North America, Africa, Asia, and Australia (Purdie and Slatyer 1976; Mack 1981; Hobbs and Atkins 1988, 1990; D'Antonio and Vitousek 1992; Young 1992; Brooks et al. 2004; Milton 2004; Liu et al. 2006; Davies and Svejcar 2008). Invasion by exotic grasses is concerning because they often increase fire frequency and negatively impact native vegetation (Torell et al. 1961; Hughes et al. 1991; D'Antonio and Vitousek 1992; Brooks et al. 2004; Milton 2004). Increases in fire frequency are ecosystem-level changes that can further facilitate invasion and perpetuate the dominance of wildlands by exotic grasses (D'Antonio and Vitousek 1992).

Exotic plant invasions have been reported to decrease biodiversity, reduce productivity, degrade wildlife habitat, displace native plants, and alter ecosystem functions in wildlands (DiTomaso 2000; Mack et al. 2000; Simberloff 2005; Masters and Sheley 2001). However, some ecologists argue the impacts of exotic plants have been exaggerated and that biodiversity and other important plant community characteristics are commonly improved with invasion. For example, Sagoff (2005) contended that exotics were not degrading ecosystems and claims to the contrary were artifacts of arbitrarily excluding exotics from measures of ecosystem integrity or using the presence of exotic species as an indicator of decline. One of the issues is that there has been a general tendency to study treatments to control exotic plants rather than their ecological impacts (Olson 1999). However, recent efforts have investigated the effects of exotic plants on biodiversity and species richness (e.g., Brewer 2008; Gaertner et al. 2009; Flory and Clay 2010; Meffin et al. 2010). The results, however, have been inconclusive. Flory and Clay (2010) reported that invasion by an exotic grass decreased native species richness and diversity in bottomland forest openings. In a meta-analysis, Gaertner et al. (2009) concluded that exotic grasses generally caused insignificant reductions in species richness in Mediterranean-type ecosystems. Similarly, the introduction of an exotic forb in montane plant communities in New Zealand did not negatively affect species richness, evenness, or biodiversity (Meffin et al. 2010). Sagoff (2005) argued that exotic invasion may increase species richness, and Sax and Gaines (2003) reported that invasion commonly increases species richness at the local scale (plots of less than a few dozen hectares). The influence of exotic plants on biodiversity is important because biodiversity may influence nutrient retention, nutrient cycling, ecosystem stability, carbon storage, and productivity (Tilman et al. 1997; Hooper and Vitousek 1998; Tilman 1999). Decreases in biodiversity reduce plant community stability and degrade ecosystem functions and processes (Tilman 1999).

Little information is available that details the relationship between exotic annual grass invasion and biodiversity. Davies and Svejcar (2008) reported that plant species diversity and richness were much lower in exotic annual grass-invaded compared to non-invaded plant communities, but did not investigate the response of plant species diversity and richness to increasing exotic annual grass abundance. Belnap and Phillips (2001) reported that annual grass-invaded sites compared to non-invaded sites had less rich soil biota, but they did not evaluate the correlation between invasion and soil biota. Determining the relationship between exotic annual grass invasion and biodiversity will provide critical information needed to better

evaluate the influence of exotic annual grasses on ecosystem functions and processes.

Exotic annual grass invasions have the potential to impact native plant communities and the fauna dependent upon them (D'Antonio and Vitousek 1992; Davies and Svejcar 2008). However, the extent of the loss of important plant community components and reduction of biodiversity across a gradient of exotic annual grass abundance is unknown. For example, biological soil crusts are an important component of *Artemisia* plant communities (Belnap 2003; Ponzetti and McCune 2001), but the relationship between biological soil crusts and exotic annual grass invasion is largely known. Understanding the relationships between exotic annual grass invasion and plant community diversity, richness, and other vegetation characteristics is critical to recognizing the overall effect of exotic annual grass invasion and determining what components are lost at various stages of invasion. If, at some point, exotic annual grass invasion begins to eliminate a key component of the native plant community, it may be critical to implement restorative efforts before it is completely lost. For example, native plant species that have been displaced by invasive species may be unavailable for restoration projects (Davies and Svejcar 2008). In addition, if vegetation change ultimately alters the site, then restoration would be even less likely to succeed. Alterations to soils or disturbance regimes by invasive plants may make it improbable that native plant communities can reclaim a site (Cronk and Fuller 1995; D'Antonio and Meyerson 2002). Thus, information on the response of native plant communities as invasion progresses from low to high exotic plant abundance is needed.

This information would help direct exotic plant legislation and policy. A better understanding of the relationship between exotic annual grasses and native plant communities is also needed to prioritize restoration efforts and to determine the ecological cost of allowing invasions to progress from low to high population infestations. In the interim, resource allocations and legislation for exotic plant management will continue to be founded on inadequate information as long as the impacts of these exotics on ecosystem services are not quantified (Lacey and Olson 1991).

The objectives of this study were to determine plant diversity response to increasing exotic annual grass abundance and the relationship between native plant communities and exotic annual grass density. *Taeniatherum caput-medusae* (L.) Nevski (medusahead) invasions in *Artemisia* Nutt. (sagebrush) steppe plant communities provide an opportunity to investigate the relationship of native plant communities and plant diversity to exotic annual grass abundance. *Taeniatherum caput-medusae* is an exotic annual grass invading western North America rangelands,

and rapidly expanding the area of land it inhabits (Hironaka 1994; Davies and Johnson 2008). Thus, there is a gradient from low to high density *T. caput-medusae* invasions across *Artemisia* plant communities. I hypothesized that: (1) plant diversity and species richness would be negatively correlated to exotic annual grass density, (2) native vegetation would also decline as the invasion progresses from low to high annual grass density; however, individual plant functional groups may differ in their response, and (3) bare ground and biological soil crust would be negatively correlated to exotic annual grass density. These hypotheses are based on the assumption that *T. caput-medusae* invasion progresses from low to high density over time, and that *T. caput-medusae* increases wildfire frequency.

Materials and methods

Study area

The study was conducted in *Artemisia* steppe plant communities in southeastern Oregon, United States. The study area encompasses 160,000 ha of the eastern and western edge of the High Desert and Snake River Ecological Provinces, respectively (Anderson et al. 1998). Climate is characteristic of the northern Great Basin with cool, wet winters and hot, dry summers. Average annual precipitation is approximately 250–320 mm (Oregon Climatic Service 2009). Regional precipitation for 2007, 2008, and 2009 crop years (1 October–30 September) were 66, 80, and 110% of the 30-year average, respectively (Oregon Climatic Service 2009; Eastern Oregon Agricultural Research Center, unpublished data). Topography varied among the study sites and elevation ranged from 950 to 1,430 m above sea level. Slope varied from 0 to 14°, and aspect ranged from south to north. Livestock used the study area, but measurements occurred prior to livestock use in the sampling years. Current livestock use was similar across the entire study area, with moderate levels of utilization (40–50% consumption of herbaceous forage). Potential natural vegetation across the study sites was *Artemisia* overstory with an understory dominated by large perennial bunchgrasses. Dominant *Artemisia* species were either *A. tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh (Wyoming big sagebrush) or *A. arbuscula* Nutt. (low sagebrush). Common native perennial bunchgrasses included *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), *Achnatherum thurberianum* (Piper) Barkworth (Thurber needlegrass), *Festuca idahoensis* Elmer (Idaho fescue), and *Poa secunda* J. Presl (Sandberg bluegrass). *Taeniatherum caput-medusae* is common across the study area and is rapidly increasing the area of land it inhabits (Davies and Johnson 2008).

Experimental design

To evaluate the relationship between exotic annual grass density and plant communities, vegetation and environmental characteristics were sampled across a gradient of *T. caput-medusae* density. *Taeniatherum caput-medusae*-invaded plant communities were located by traversing non-graveled, two track dirt roads across a 160,000-ha landscape. Invaded locations were recorded with handheld global positioning units. Every *T. caput-medusae*-invaded plant community located was sampled, resulting in 65 sites with varying levels of exotic annual grass abundance. Areas within 200 m of the roads were excluded from sampling to remove any potential road effect. The road effect was probably minor because roads experienced limited traffic, as was evident by native vegetation frequently growing in the middle of the roads between the two tracks.

Measurements

Each *T. caput-medusae*-invaded site was sampled from late-May to mid-June in 2007, 2008, and 2009 using a randomly located 50 × 80 m (0.4 ha) plot. One 80-m transect was positioned on the long side of the plot and five 50-m transects were placed perpendicular to it at 20-m intervals. Shrub canopy cover by species was measured by line intercept (Canfield 1941) on each of the five 50-m transects. Canopy gaps less than 15 cm were included in shrub canopy cover measurements. Shrub density was determined by counting all individuals rooted in five 2 × 50-m belt transects at each site. Herbaceous canopy cover and density were measured by species inside 40 × 50-cm frames (0.2 m^2) located at 3-m intervals on each 50-m transect (starting at 3 m and ending at 45 m), resulting in 15 frames per transect and 75 frames per site. Bare ground and biological soil crust cover were also measured in the seventy-five 40 × 50-cm frames. Cover was estimated to a percent based on markings on the frames that divided it into 1, 5, 10, 25, and 50% segments. Cover and density estimates of plant functional groups were determined from individual species measurements. Perennial and total species richness were determined by counting species found in the seventy-five 40 × 50-cm frames at each site. Plant species diversity (Shannon diversity index) was calculated from species density measurements (Krebs 1998). Exotic plants were included in estimates of diversity and species richness. Herbaceous biomass production by functional group was measured by clipping all standing vegetation in 15 randomly located 1-m^2 frames per site at 57 of the 65 sites. Eight sites were not sampled because livestock had grazed the plots after cover and density measurements but before biomass production could be measured. Biomass samples

were oven-dried, and then the current year's growth was separated from the previous years' growth and weighed.

Aspect and slope in degrees were measured in the field for each site with a compass and clinometer, respectively. Because aspect is circular in nature, it was converted to cos(aspect). Elevation for each site was determined from topographical maps of the study area. Topographical position (toe slope, side slope, valley, etc.) was recorded for each site. Soil texture (0–30 cm) was measured using the hydrometer method (Gee and Bauder 1986). Precipitation (long-term estimated average) for each site was determined from 50-mm precision climatic maps (NRCS 1998).

Statistical analysis

Stepwise multiple linear regressions were used to evaluate the relationships of plant diversity, richness, biomass production, cover and density to environmental characteristics and exotic annual grass density using SAS v.9.1 (SAS Institute, Cary, NC, USA). Explanatory factors that were not significant contributors (as determined using stepwise selection at $\alpha = 0.05$) were excluded from the final models. Because stepwise multiple linear regressions generally selected models with exotic annual grass density as the only significant explanatory factor, non-linear mechanistic models with a zero asymptote (exponential decay) were used to explore these relationships using SAS v.9.1 (SAS Institute). Mechanistic models are advantageous because they provide a physical understanding of the system and often require few parameters (Box et al. 2005). Because mechanistic models require few parameters, they also provide estimates of the fitted response with smaller variance compared to empirical models (Box et al. 2005). The exponential decay model was:

$$y = ae^{-bx} \tag{1}$$

where a = initial quantity of the response variable (y) when T. caput-medusae is absent (y_0), e = exponential function, b = decay rate, and x = T. caput-medusae density.

Density of T. caput-medusae was selected as the explanatory variable instead of its cover or biomass production because density is repeatable among different observers, and the period of time when accurate measurements can be taken is longer. Correlations between response variables and T. caput-medusae density using the exponential decay model were considered significant at $\alpha = 0.05$. For some of the analyses, species measurements were grouped into the following plant functional groups: P. secunda, large perennial bunchgrasses, T. caput-medusae, perennial forbs, Artemisia, and annual forbs. Poa secunda was separated from the other perennial bunchgrasses

because of its smaller stature and earlier phenological development (Davies 2008; James et al. 2008). Plant functional groups are a common and useful classification of plants based on physiological and morphological characteristics (Lauenroth et al. 1978).

Results

Taeniatherum caput-medusae density was the only explanatory variable selected for model inclusion using stepwise multiple linear regression ($P < 0.05$), except it was not correlated with annual forb cover, density, and biomass production and perennial forb density ($P > 0.05$). None of the environmental explanatory variables were correlated with annual forb cover, density, and biomass production ($P > 0.05$). Elevation was positively correlated with perennial forb density ($P = 0.02$) and explained 7% of its variation ($R^2 = 0.07$). Prior to the inclusion of T. caput-medusae density in the models, elevation was correlated with most of the vegetation response variables (data not presented; $P < 0.05$, $R^2 = 0.04$–0.10), whereas other environmental explanatory variables were not consistently correlated to response variables.

Diversity and density

Plant species diversity (Shannon diversity index) was negatively correlated with T. caput-medusae density (Table 1; Fig. 1a; $P < 0.001$). Taeniatherum caput-medusae density explained 62% of the variation in plant diversity ($R^2 = 0.622$). Total species richness and perennial species richness both decreased with increasing T. caput-medusae density (Fig. 1b, c; $P < 0.001$). Taeniatherum caput-medusae density explained 29 and 34% of the variation in species and perennial species richness, respectively ($R^2 = 0.293$ and 0.339, respectively).

In general, the density of plant functional groups decreased as T. caput-medusae density increased (Table 1; Fig. 2). Large perennial bunchgrass and P. secunda densities were negatively correlated with T. caput-medusae density (Fig. 2a, b, respectively; $P < 0.001$). At approximately 250 T. caput-medusae plants m^{-2}, large perennial bunchgrass and P. secunda densities were zero at some sites. Approximately 47 and 40% of the variation in large perennial bunchgrass and P. secunda densities were explained by T. caput-medusae density, respectively ($R^2 = 0.466$ and 0.401, respectively). Perennial and annual forb densities were not related to T. caput-medusae density ($P = 0.964$ and 0.064, respectively). Perennial herbaceous and total native herbaceous densities were negatively correlated to T. caput-medusae density (Table 1; $P < 0.001$ and 0.009, respectively). Taeniatherum caput-medusae

Table 1 Non-linear mechanistic models of the relationships between native vegetation density and diversity and *Taeniatherum caput-medusae* (L.) Nevski density

Response variable	Model	R^2	P value
Poa secunda	$y = 17.3080e^{-0.0033x}$ (2.1796) (0.0009)	0.4013	<0.001
Large perennial bunchgrass	$y = 11.9570e^{-0.0036x}$ (1.2666) (0.0008)	0.4657	<0.001
Perennial forb	NS	NS	0.964
Annual forb	NS	NS	0.064
Perennial herbaceous	$y = 40.8690e^{-0.0024x}$ (4.8601) (0.0006)	0.3018	<0.001
Total native herbaceous	$y = 150.8199e^{-0.0014x}$ (21.3333) (0.0005)	0.1277	0.009
Artemisia	$y = 0.7651e^{-0.0042x}$ (0.1246) (0.0015)	0.2755	0.008
Diversity (H)	$y = 1.7210e^{-0.0015x}$ (0.0840) (0.0002)	0.6219	<0.001
Perennial species richness	$y = 14.6060e^{-0.0012x}$ (0.9903) (0.0002)	0.3386	<0.001
Total species richness	$y = 19.5532e^{-0.0006x}$ (0.9775) (0.0001)	0.2926	<0.001

Standard errors of estimated variables are given in parentheses for each relationship

NS not significant, *x T. caput-medusae*, *y* response variable

density explained 30 and 13% of the variation in perennial herbaceous and total native herbaceous densities, respectively ($R^2 = 0.302$ and 0.128, respectively). *Artemisia* density also decreased with increasing *T. caput-medusae* density (Fig. 2c; $P = 0.008$). Approximately 28% of the variation in *Artemisia* density was explained by *T. caput-medusae* density ($R^2 = 0.276$). *Artemisia* density decreased to approximately zero when *T. caput-medusae* density exceeded 600 plants m^{-2}; however, *Artemisia* could be absent from some sites at lower *T. caput-medusae* densities.

Cover

Native vegetation cover, in general, decreased with increasing *T. caput-medusae* density (Table 2; Fig. 3). Large perennial bunchgrass and *P. secunda* cover were negatively correlated with *T. caput-medusae* density (Fig. 3a, b, respectively; $P < 0.001$). Approximately 55 and 51% of the variation in large perennial bunchgrass and *P. secunda* cover was explained by *T. caput-medusae* density, respectively ($R^2 = 0.548$ and 0.510, respectively). Perennial forb cover was negatively correlated with *T. caput-medusae* density ($P = 0.007$), but annual forb cover was not correlated with *T. caput-medusae* density ($P = 0.757$). *Taeniatherum caput-medusae* density explained 19% of the variation in perennial forb cover ($R^2 = 0.191$). Total perennial herbaceous and total native herbaceous cover were negatively correlated with *T. caput-medusae* density ($P < 0.001$), which explained approximately 60% of their variation ($R^2 = 0.610$ and 0.605, respectively). *Artemisia* cover decreased as *T. caput-medusae* density increased ($P < 0.001$). *Taeniatherum caput-medusae* density explained 46% of the variation in *Artemisia* cover ($R^2 = 0.464$). Total native vegetation

cover was negatively correlated to *T. caput-medusae* density (Fig. 3c; $P < 0.001$). Almost 70% of the variation in native vegetation cover was explained by *T. caput-medusae* density ($R^2 = 0.695$). Bare ground and biological soil crust cover also decreased with increasing *T. caput-medusae* density ($P < 0.001$). *Taeniatherum caput-medusae* density explained 81 and 29% of the variation in bare ground and biological soil crust cover, respectively ($R^2 = 0.812$ and 0.288, respectively).

Biomass production

Native herbaceous biomass production generally decreased with increasing *T. caput-medusae* density (Table 3; Fig. 4). Large perennial bunchgrass biomass production was negatively correlated with *T. caput-medusae* density (Fig. 4a; $P < 0.001$). *Taeniatherum caput-medusae* density explained 54% of the variation in large perennial bunchgrass biomass production ($R^2 = 0.537$). *Poa secunda* and perennial forb biomass production also decreased with increasing *T. caput-medusae* density ($P < 0.001$ and 0.011, respectively). Approximately 32 and 15% of the variation in *P. secunda* and perennial forb biomass production was explained by *T. caput-medusae* density ($R^2 = 0.324$ and 0.151, respectively). Perennial herbaceous and total native herbaceous biomass production decreased with increasing *T. caput-medusae* density (Fig. 4b, c, respectively; $P < 0.001$). Greater than 60% of the variation in perennial herbaceous and total native herbaceous biomass production was explained by *T. caput-medusae* density ($R^2 = 0.648$ and 0.640, respectively). Perennial herbaceous and total native herbaceous biomass decreased relatively rapidly as *T. caput-medusae* density increased to about 300 plant m^{-2} and then decreased less rapidly between 300 and 700 *T. caput-medusae* plants m^{-2}.

(a)

$y = 1.7210e^{-0.0015x}$
$R^2 = 0.6219$
$P < 0.0001$

(b)

$y = 19.5532e^{-0.0006x}$
$R^2 = 0.2926$
$P < 0.0001$

(c)

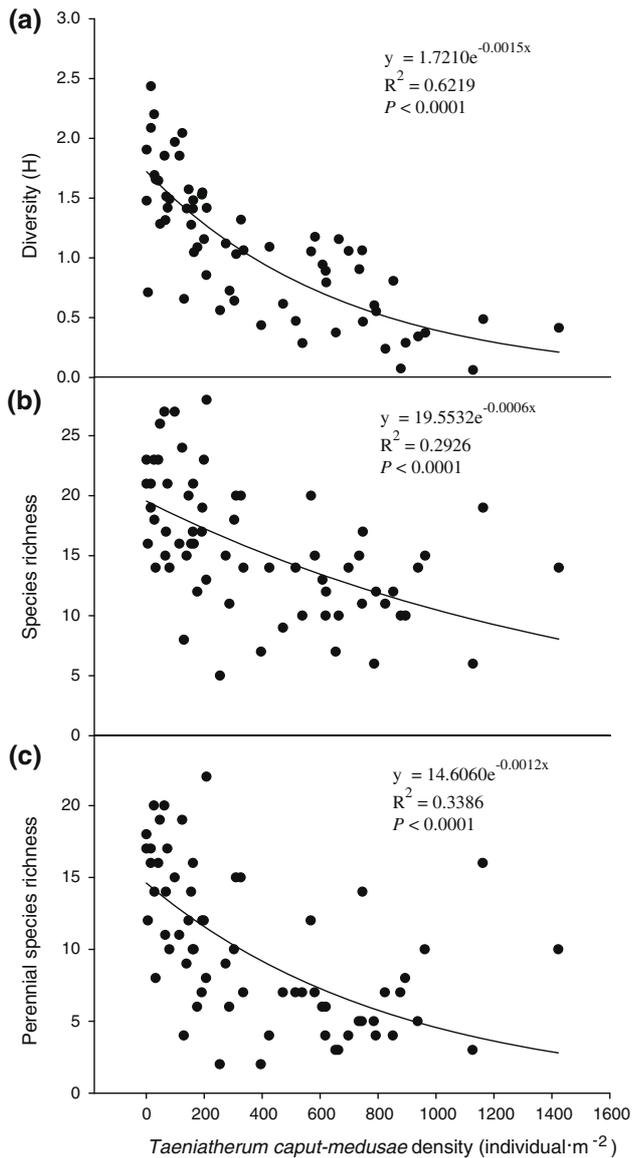$y = 14.6060e^{-0.0012x}$
$R^2 = 0.3386$
$P < 0.0001$

Fig. 1 The relationship of **a** diversity, **b** perennial species richness, and **c** total species richness with *Taeniatherum caput-medusae* (L.) Nevski density

(a)

$y = 11.9570e^{-0.0036x}$
$R^2 = 0.4657$
$P < 0.0001$

(b)

$y = 17.3080e^{-0.0033x}$
$R^2 = 0.4013$
$P < 0.0001$

(c)

$y = 0.7651e^{-0.0042x}$
$R^2 = 0.2755$
$P < 0.0076$

Fig. 2 The relationship of **a** large perennial bunchgrasses, **b** *Poa secunda* J. Presl, and **c** *Artemisia* densities with *Taeniatherum caput-medusae* (L.) Nevski density

Discussion

Plant species diversity, most native plant functional groups, and biological soil crust declined exponentially with increasing exotic annual grass density. However, not all native plant functional groups were negatively correlated with exotic annual grass density. This study suggests that exotic annual grass invasions can progress to a level that markedly reduces the likelihood of successful restoration because native plant community components are either severely degraded or completely absent. The results of this study also suggest that increasing dominance by exotic annual grasses negatively impacts biodiversity and other important components of plant communities; however,
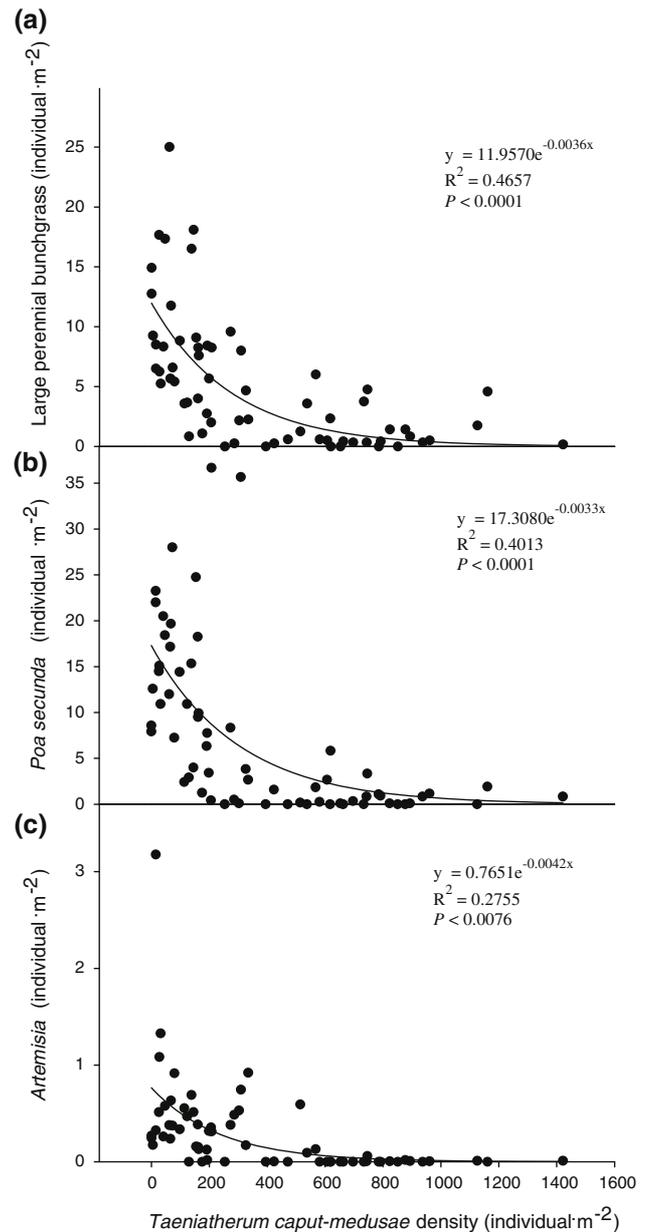
experimental studies will be needed to fully substantiate that exotic annual grass invasion is the causal mechanism.

While it is generally assumed that negative correlations between exotic and native plants are due to impacts of the invaders, the reverse is also possible given that variability in the initial success of invasion is often related to differences in plant community characteristics (Levine 2000; Naeem et al. 2000; Maron and Marler 2007). However, the general lack of correlations between native vegetation characteristics and environmental variables in invaded communities in this study suggests that *T. caput-medusae*

Table 2 Non-linear mechanistic models of the relationships between cover and *Taeniatherum caput-medusae* (L.) Nevski density

Response variable	Model	R^2	P value
Poa secunda	$y = 6.1670\mathrm{e}^{-0.0038x}$ (0.6525) (0.0008)	0.5097	<0.001
Large perennial bunchgrass	$y = 16.0420\mathrm{e}^{-0.0039x}$ (1.5384) (0.0008)	0.5480	<0.001
Perennial forb	$y = 3.6643\mathrm{e}^{-0.0024x}$ (0.5331) (0.0008)	0.1910	0.007
Annual forb	NS	NS	0.757
Perennial herbaceous	$y = 26.0217\mathrm{e}^{-0.0037x}$ (2.1134) (0.0006)	0.6100	<0.001
Total native herbaceous	$y = 26.7758\mathrm{e}^{-0.0035x}$ (0.6525) (0.0008)	0.6050	<0.001
Artemisia	$y = 9.0554\mathrm{e}^{-0.0035x}$ (1.0334) (0.0009)	0.4639	<0.001
Total native vegetation	$y = 35.6793\mathrm{e}^{-0.0034x}$ (2.3251) (0.0005)	0.6951	<0.001
Bare ground	$y = 50.6700\mathrm{e}^{-0.0022x}$ (2.0438) (0.0002)	0.8119	<0.001
Biological soil crust	$y = 3.0635\mathrm{e}^{-0.0033x}$ (0.5030) (0.0012)	0.2884	<0.001

Standard errors of estimated variables are given in parentheses for each relationship

NS not significant, *x* *T. caput-medusae*, *y* response variable

invasion overwhelms environmentally driven differences among plant communities across the study area. Despite the influence of plant community characteristics on initial establishment rates of *T. caput-medusae* (Davies 2008), its demonstrated competiveness with native vegetation (Hironaka and Sindelar 1975; Young and Mangold 2008) and alteration of fire regimes may override the initial differences in plant community characteristics. The ability of *T. caput-medusae* to out-compete native vegetation and alter fire regimes to the detriment of native vegetation (Hironaka and Sindelar 1975; D'Antonio and Vitousek 1992; Davies and Svejcar 2008; Young and Mangold 2008) suggest the declines in native plants observed in this study were probably caused by increasing *T. caput-medusae* abundance. Native plants are often weakly competitive with highly competitive exotics, while these exotics substantially negatively impact natives (Maron and Marler 2008). For example, in an experimental plot study, a non-native grass decreased native plant biomass, species richness, and biodiversity (Flory and Clay 2010). Though disturbance history can have substantial impacts on native plant communities, and thus influence their susceptibility to invasion, the negative correlations between native plant communities and *T. caput-medusae* density were probably mainly the result of the impact of *T. caput-medusae* on native vegetation. Livestock use across the entire study area was similar, and plant communities dominated by *T. caput-medusae* were immediately adjacent to plant communities with few *T. caput-medusae* plants. Thus, differences in livestock use levels were probably not causing the measured differences in plant community characteristics. However, wildfires have probably promoted exotic annual grass invasion and simultaneously decreased native vegetation (Whisenant 1990; Hughes et al. 1991; Brooks et al. 2004). The relationship between wildfires and exotic annual grasses is a positive feedback cycle (D'Antonio and

Vitousek 1992); therefore, fire disturbance history is influenced by annual grass invasion. Exotic annual grass invasion increases fire frequency which perpetuates exotic annual grass dominance and facilitates the invasion of adjacent non-invaded plant communities (D'Antonio and Vitousek 1992). Thus, across the 65 plant communities sampled in this study, it seems likely that *T. caput-medusae* densities were indicative of invasion status, and, subsequently, plant communities were responding to pressure, including increased wildfire frequency, from *T. caput-medusae*. Though accurate, complete fire histories for all 65 sites were not available, anecdotal information suggest that the most heavily invaded sites burned more frequently than sites with less *T. caput-medusae*. The absence of sagebrush and abundant charred basal trucks of sagebrush in the heavily invaded plant communities suggest that fire was frequent enough to prevent sagebrush reestablishment. Plant communities with lower densities of *T. caput-medusae* had juvenile sagebrush, evidence that fire was not as common as it was in plant communities with higher *T. caput-medusae* densities.

The progressive decline of plant species diversity and richness with increasing exotic annual grass density in this study is contrary to claims that exotics increase species richness and do not threaten biodiversity (e.g., Sagoff 2005). Although Sax and Gaines (2003) reported that diversity commonly increased with invasion at local and regional scales, the results of this study suggest that in some situations diversity declines substantially with invasion at the local scale. The strong, negative correlation between *T. caput-medusae* density and plant species diversity in this study suggests that exotic annual grass invasion may be exerting a prevailing influence on biodiversity. The fact that *T. caput-medusae* density explained more than 62% of the variation in plant diversity across 65 plant communities with varying site characteristics
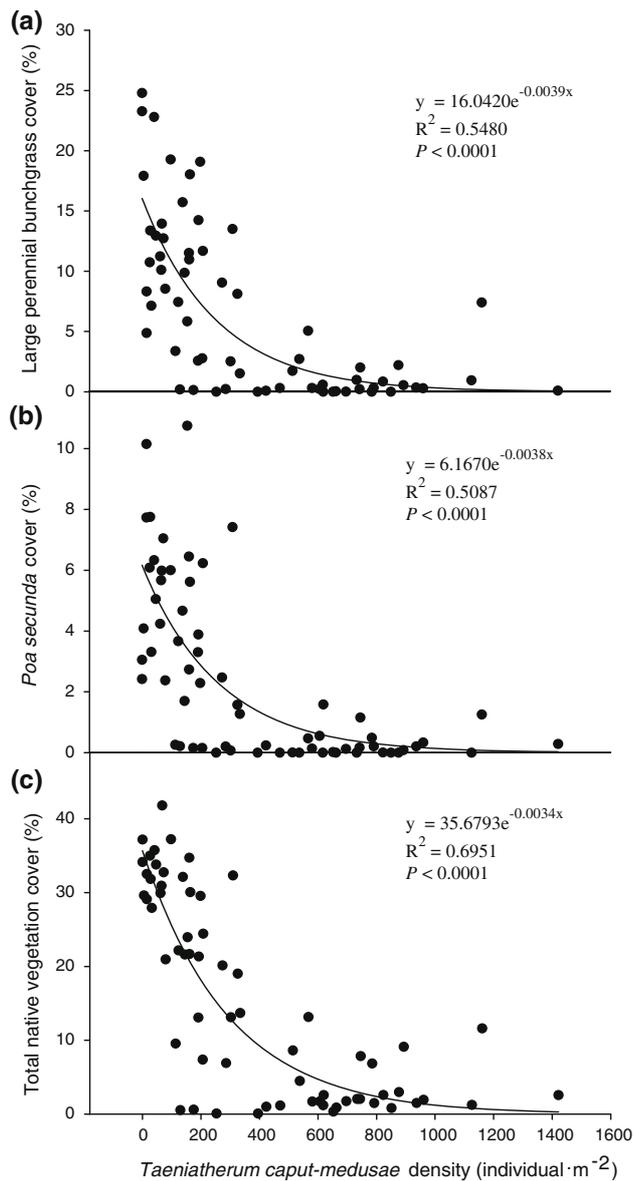
Fig. 3 The relationship of **a** large perennial bunchgrasses, **b** *Poa secunda* J. Presl, and **c** total native vegetation cover with *Taeniatherum caput-medusae* (L.) Nevski density
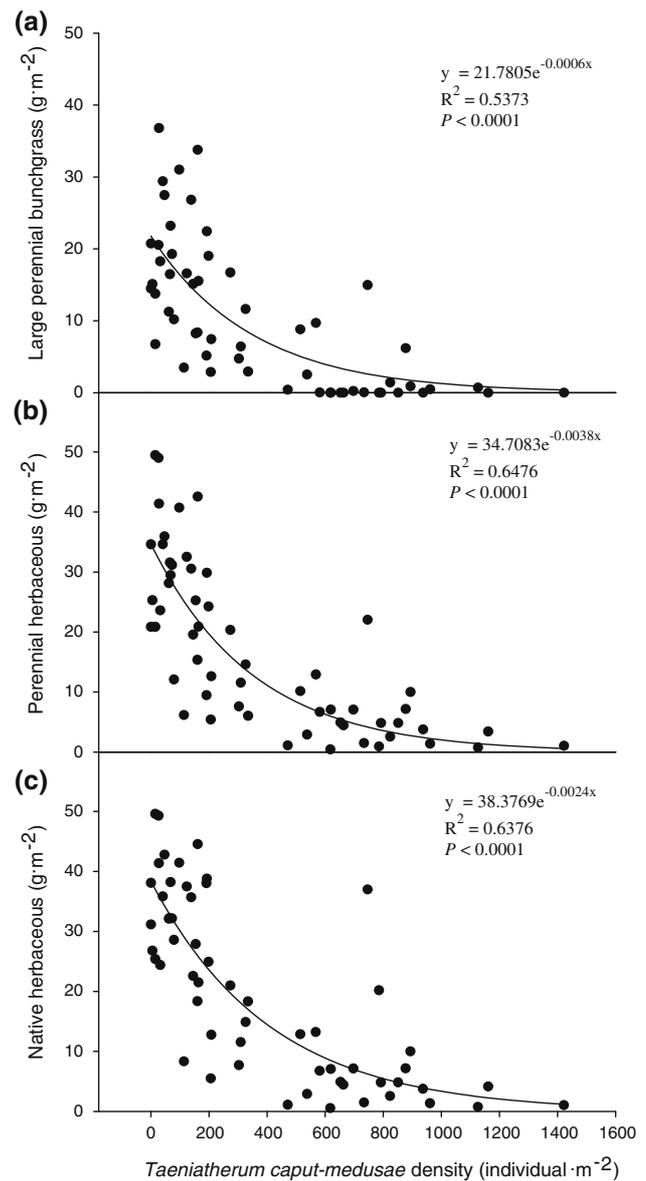
Fig. 4 The relationship of **a** large perennial bunchgrasses, **b** perennial herbaceous vegetation, and **c** total native herbaceous vegetation annual biomass production with *Taeniatherum caput-medusae* (L.) Nevski density

Table 3 Non-linear mechanistic models of the relationships between native vegetation annual biomass production and *Taeniatherum caput-medusae* (L.) Nevski density

Response variable	Model	R^2	P value
Poa secunda	$y = 5.4074e^{-0.0046x}$ (0.9235) (0.0017)	0.3236	<0.001
Large perennial bunchgrass	$y = 21.7805e^{-0.0028x}$ (2.0561) (0.0006)	0.5373	<0.001
Perennial forb	$y = 7.1952e^{-0.0016x}$ (1.050) (0.0006)	0.1502	0.011
Annual forb	NS	NS	0.280
Perennial herbaceous	$y = 34.7083e^{-0.0028x}$ (2.4464) (0.0005)	0.6476	<0.001
Total native herbaceous	$y = 38.3769e^{-0.0024x}$ (2.5643) (0.0004)	0.6396	<0.001

Standard errors of estimated variables are given in parentheses for each relationship

NS not significant, *x* *T. caput-medusae*, *y* response variable

provides an indication of how strong the influence of invaders may be on biodiversity. Exotic grasses and other invasive plants have negatively impacted biodiversity and native vegetation in other ecosystems. Exotic grasses have decreased biodiversity in longleaf pine savannas (Brewer 2008) and abandoned farm fields in bottomland hardwood forests (Flory and Clay 2010). Similarly, exotic plants have decreased diversity in European riparian habitats (Gerber et al. 2008) and grasslands (Moroń et al. 2009), North American forest communities (Adams and Engelhardt 2009), and Mediterranean-type ecosystems around the globe (Gaertner et al. 2009). The decline of plant species diversity related to increasing exotic annual grass density is concerning because declines in biodiversity may cause serious alterations to nutrient storage and cycling and ecosystem services (Tilman et al. 1997; Hooper and Vitousek 1998; Tilman 1999).

In general, native plant functional groups exhibited a negative relationship with increasing exotic annual grass density in this study. However, the strength of the relationship between exotic annual grass density and native vegetation did vary by plant functional group. For example, variation in perennial bunchgrass cover, density, and production compared to other functional groups was better explained by exotic annual grass density. The stronger relationship between annual and perennial grasses is probably an indication of their overlap in resource use. Perennial bunchgrasses and exotic annual grasses overlap in their spatial and temporal acquisition of resources more than exotic annual grasses and native perennial forbs (James et al. 2008). However, the negative relationship between dominant perennial vegetation and exotic annual grass abundance, and limited evidence of a relationship between exotic annual grass and annual forbs, is contrary to the presumed effects of invaders. Less productive plants are expected to be excluded from plant communities with increasing competition from other plants (Lepš 2004). In these plant communities, *Artemisia* and perennial bunchgrass dominate the overstory and understory, respectively, and annual forbs constitute a minor subordinate (Davies et al. 2006; Davies and Bates 2010). Thus, if exotic annual grasses influence other vegetation solely through competition, less productive functional groups with similar life cycles (i.e., annual forbs) should have a strong negative relationship with exotic annual grasses, and less similar and more productive functional groups would be less influenced. The results of this study suggest the opposite occurs in exotic annual grass-invaded *Artemisia* plant communities. Evidence of a relationship between *T. caput-medusae* and annual forbs was lacking, and *Artemisia,* even though occupying a distinctly different niche, exhibited a strong negative association with increasing annual grass density. *Artemisia* is a long-lived, evergreen shrub that is removed

from the plant community by fire (Harniss and Murray 1973; Humphrey 1984; Wambolt et al. 2001), suggesting that the influence of *T. caput-medusae* on plant communities may be more related to its ability to make the environment more adverse (i.e., increased fire frequency) than to direct competitive interactions. The superior competitiveness of *T. caput-medusae* is probably an important factor driving its success (Hironaka and Sindelar 1975; Young and Mangold 2008); however, its influence on fire frequency may be of equal or greater importance. The strong negative correlations between *T. caput-medusae* density and native plants supports D'Antonio and Vitousek's (1992) assertion that exotic invasions that alter disturbance regimes can be especially damaging to native plant communities. Increased fire frequency is probably especially detrimental to native plant communities that have evolved with less frequent fires (Whisenant 1990; Hughes et al. 1991; Brooks et al. 2004).

The results of this study suggest that, based on correlative data, native plant communities were degraded by *T. caput-medusae* invasion, as evidenced by the decline of biological soil crust and most native plant functional groups with increasing *T. caput-medusae* abundance. Similarly, Maron and Marler (2008) reported that invasive plants substantially suppressed native vegetation. The negative relationship between *T. caput-medusae* and important native plant functional groups suggests that exotic plant invasions may also have impacts at higher trophic levels. For example, the decline of *Artemisia* with increasing *T. caput-medusae* would likely be detrimental to sage-grouse (*Centrocercus urophasianus*), an *Artemisia* obligate wildlife species whose breeding populations have declined by 17–47% since the mid-1900s (Wallestad et al. 1975; Connelly and Braun 1997; Connelly et al. 2000). The decrease in *Artemisia*-covered wildlands has been a major contributing factor to the decline of sage-grouse (Connelly et al. 2000; Aldridge et al. 2008). Thus, substantial declines of native plant functional groups with increasing exotic annual grass abundance suggest that exotic plant invasions may also have considerable indirect influences and degrade critical native fauna habitat. Similarly, Pawson et al. (2010) reported that a higher trophic level, grassland invertebrate assemblages, was negatively impacted by increasing exotic conifer density.

Native plant functional groups rapidly declined until *T. caput-medusae* density was approximately 200–600 individual m^{-2}, after which the rate of decay slowed. However, at these densities, native plant functional groups could be largely displaced from the plant community and the likelihood of successful restoration would probably decline. Lacking residual native vegetation in plant communities invaded by exotic plants may severely compromise the potential for successful restoration (Davies and Sheley

2011). In fact, the loss of some plant functional groups and species may be irreversible because of a lack of available propagules for restoration (Davies and Svejcar 2008). Restoration efforts applied after substantial loss of native species will probably be less successful because more plant community components will need to be simultaneously repaired. The results of this study also suggest that after a certain point many of the negative impacts of invasion have been realized and few subsequent critical changes in the plant community will occur as invasion progresses. These plant communities should probably receive a lower priority for restoration than plant communities declining relatively rapidly with increasing exotic plant abundance.

Conclusions

Taeniatherum caput-medusae density had a strong negative correlation to plant species diversity and richness, most native plant functional groups, and biological soil crusts. The negative correlation between *T. caput-medusae* density and plant diversity suggests that exotic annual grasses are degrading ecosystem function and integrity. The decline of important native plant functional groups suggests that exotic annual grass invasion may also be degrading native fauna habitat, especially for those species that depend upon endemic habitat elements. The exponential decline of important components of the native plant communities in relation to increasing exotic annual grass density suggests a finite window of restoration opportunity prior to the loss of native plant propagules. Thus, restoration efforts may benefit from being prioritized based on exotic annual grass abundance. The near, or in some situations complete, elimination of several native plant functional groups and substantial decline in plant species diversity at high *T. caput-medusae* densities suggest that the negative impacts of invasion on native plant communities can be severe. Exotic annual grass invasion appears to become a driver of ecosystem functions and processes as native vegetation is excluded and biodiversity decreases. However, experimental studies will need to be conducted to conclude that exotic annual grass invasion is the cause of the decline in diversity and native plant functional groups.

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