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Authors

Concilio, Amy L
Loik, Michael E

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Elevated nitrogen effects on *Bromus tectorum* dominance and native plant diversity in an arid montane ecosystem

Amy L. Concilio & Michael E. Loik

Keywords

Cheatgrass; Downy brome; Great Basin Desert; Invasive species; Nitrogen deposition; Sagebrush steppe; Sierra Nevada

Abbreviations

ANOSIM = analysis of similarity; D' = Simpson's dominance index; $E_{1/D}$ = Simpson's evenness index; GB = grazed–burned; GU = grazed–unburned; H' = Shannon diversity index; N = nitrogen; UB = ungrazed–burned; SEM = SE of mean

Nomenclature

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Concilio, A.L. (corresponding author, amyconcilio@gmail.com) & **Loik, M.E.** (mloik@ucsc.edu): Department of Environmental Studies, University of California, 1156 High Street, Santa Cruz, CA, 95064, USA

Abstract

Questions: Dominance of the widespread fire-altering invasive grass, *Bromus tectorum*, is markedly reduced at upper elevations in the Great Basin Desert. Here, we evaluated whether increased anthropogenic nitrogen (N) deposition would have an effect on species composition and ecosystem invasibility by *B. tectorum* at high elevations, and whether *B. tectorum* cover was associated with decreased native plant diversity.

Location: Sagebrush steppe of the eastern Sierra Nevada, CA, US, at the western edge of the Great Basin Desert.

Methods: We set up 54 paired plots, half of which were exposed to elevated N deposition ($50 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at the time of snowmelt for 4 yr) and half acted as controls, in areas differing in disturbance history (grazed, burned and grazed–burned). We monitored species composition each summer from 2008 to 2011 and then compared species richness, Shannon's diversity (H'), Simpson's dominance (D'), Simpson's evenness ($E_{1/D}$), *B. tectorum* dominance and community similarity (with ANOSIM and SIMPER analyses) by N treatment and disturbance history.

Results: Species composition differed by disturbance history in all years (ANO-SIM, $P < 0.05$), and the grazed–burned plots consistently had the highest levels of *B. tectorum* dominance ($P \leq 0.0003$) and cover ($P \leq 0.0001$). *Bromus tectorum* cover was inversely related to native forb species richness ($r = -0.44$, $P < 0.0001$), H' ($r_s = -0.73$, $P < 0.0001$), $-\ln(D')$ ($r_s = -0.75$, $P < 0.0001$) and $E_{1/D}$ ($r_s = -0.49$, $P < 0.0001$). We found no evidence that increased N deposition would affect native plant diversity after 4 yr in this arid montane ecosystem, but the possibility of longer-term effects cannot be eliminated.

Conclusions: Results suggest that high-elevation plant communities are already experiencing invasion impacts even though changes to the fire cycle have not yet occurred. In the most disturbed areas, *B. tectorum* cover is approaching the threshold for increased fire risk, which could result in more severe impacts at high elevations.

Introduction

Increases in nitrogen (N) emissions and deposition have been occurring throughout the western US over the last half-century as a result of industry, agriculture and transportation (Fenn et al. 2003b), and are predicted to continue to increase on a global scale over the next few decades (Dentener et al. 2006). Plants in many temperate terrestrial ecosystems are N-limited and can be fertilized by

anthropogenic N, sometimes leading to dramatic increases in plant growth (Vitousek et al. 1997). However, plant responses to N can vary by functional type or species, and increased N can consequently be associated with changes in species composition (e.g. Weiss 1999; Harpole et al. 2007; McClean et al. 2011). Fast-growing plants, including many invasive species, generally respond to exogenous N with large increases in productivity because they can readily take advantage of excess resources (Davis et al. 2000).

Consequently, increased N deposition can facilitate the invasion of non-native plants and loss of native flora and associated fauna, particularly in low-nutrient ecosystems where natives are well adapted to infertile soils (e.g. Brooks 2003; Schwinning et al. 2005).

Although much research has investigated the ecological effects of N deposition on plant communities, there is a particular lack of understanding of how plant communities respond to N in arid and semi-arid systems (Adams 2003; Fenn et al. 2003a). Studies that have been conducted in western US deserts have shown that increased N deposition can increase the dominance of invasive annual plants (Brooks 2003; Allen et al. 2009; Rao & Allen 2010). In Joshua Tree National Park, for example, exotic grass accumulation can increase to levels that exceed the threshold for carrying fire at 3.2–9.3 kg N·ha⁻¹·yr⁻¹ in desert scrub habitats and at 3.0–6.3 kg N·ha⁻¹·yr⁻¹ in pinyon juniper habitats (Fenn et al. 2010; Rao & Allen 2010; Pardo et al. 2011). The western Great Basin Desert sagebrush steppe ecosystem receives an estimated 1–3 kg N·ha⁻¹·yr⁻¹; this is relatively low compared to deposition rates measured in other parts of California (Weiss 2006; Fenn et al. 2010) but slightly elevated compared to modelled pre-industrial estimates (0.25–1.00 kg N·ha⁻¹·yr⁻¹; Bobbink et al. 2010). For sensitive organisms and ecosystems, effects of increased N may be detectable at levels as low as 2–5 kg N·ha⁻¹·yr⁻¹ (Baron et al. 2000; Pardo et al. 2011; Song et al. 2012).

Plant community composition in the western Great Basin sagebrush steppe ecosystem could shift toward a higher proportion of grasses with increases in available N. Of particular concern is the spread of *Bromus tectorum* L. (also known as cheatgrass or downy brome), an invasive annual grass that has become ubiquitous throughout the Intermountain West (Mack 1981). When *B. tectorum* cover exceeds a threshold in density, it changes fuel dynamics, triggering a more rapid fire cycle and displacing native flora and fauna (Stewart & Hull 1949; Knapp 1996; Brooks et al. 2004; Link et al. 2006). At high elevation in the eastern Sierra Nevada, *B. tectorum* invasion has been limited possibly by low temperatures, snowpack or growing season length (Chambers et al. 2007; Griffith & Loik 2010). However, agents of global change, such as climate change and increased anthropogenic N deposition, may facilitate the spread of some invasive species (Dukes & Mooney 1999). Numerous field and greenhouse studies have demonstrated that *B. tectorum* can respond to N additions with increased growth (e.g. Kay 1966; Bilbrough & Caldwell 1997; Monaco et al. 2003). However, few studies have evaluated subsequent effects on native species richness or cover in the Great Basin Desert (but see Beckstead & Augspurger 2004) and none have been conducted at the high elevation *B. tectorum* range margin in the eastern Sierra Nevada.

We were interested in better understanding how plants in a high elevation, arid ecosystem would respond to increased N deposition, and as a result whether *B. tectorum* dominance over native species would increase. There is evidence that ecosystem response to N is likely to vary with disturbance and land-use history (Aber & Driscoll 1997; Foster et al. 2003; Lu et al. 2011), so we evaluated plant response to N in areas with different disturbance histories representative of the region (grazed, burned and grazed–burned). Our objectives were to determine whether: (1) increases in N deposition would affect *B. tectorum* cover, herbaceous species richness or diversity, *B. tectorum* dominance over other herbaceous species, or plant community composition; (2) plant responses to increased N would vary on an inter-annual scale; (3) plant responses to increased N would vary across the landscape; and (4) *B. tectorum* cover was negatively related to native species diversity under ambient or increased levels of N. To address these questions, we conducted an *in-situ* experiment using paired plots that received ambient and elevated levels of N over a period of 4 yr from 2008–2011. We hypothesized that increased N would lead to decreased biodiversity and increased dominance of *B. tectorum* in years of high rainfall, and that responses would vary across different landscape conditions.

Methods

Study site

This research was conducted at the Sierra Nevada Aquatic Research Laboratory (which is part of the University of California Valentine Eastern Sierra Reserve) and adjacent Inyo National Forest land (37°36'51" N 118°49'47" W; 2149–2169 m a.s.l.) on the eastern slope of the Sierra Nevada, about 16 km south of Mammoth Lakes, CA, US. A weather station on site has been monitoring climate since 1987; during that time, annual precipitation ranged from 156 to 674 mm (mean = 313 mm; Fig. 1a). The climate is Mediterranean and most precipitation (ca. 75%) falls in the form of snow between November and March (Fig. 1b). Air temperature reaches an average minimum in January of –5 to –10 °C and maximum in July of about 20 °C.

The site is near the ecotone of Great Basin Desert sagebrush and Sierra Nevada mixed conifer forest ecosystems. This research took place in the sagebrush zone, at the upper elevation limits of *B. tectorum* invasion. Dominant species include the shrubs *Artemisia tridentata* and *Purshia tridentata*. Open space makes up most of the land cover (ca. 50–75%), whereas forbs and grasses represent ca. 5–30% cover. There are no native annual grasses at the site, but a number of native perennial bunchgrasses are present, including: *Achnatherum hymenoides*, *A. nevadensis*, *Elymus*

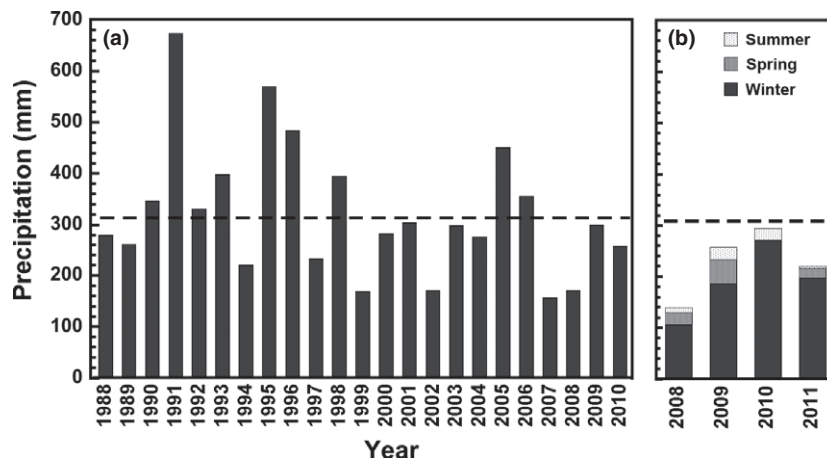


Fig. 1. Inter-annual and seasonal precipitation patterns at the study site. (a) Total annual precipitation measured from 1988 to 2010 (dashed line represents the 24-yr average) and (b) total seasonal precipitation measured from October of the previous year to March of the year of interest (winter), April–June (spring) and July–September (summer). Data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra University of California Natural Reserve, <2 km from our study plots.

elymoides and *Hesperostipa comata*. A complete list of annual and perennial forbs can be found in Orr & Howald (2000).

Field methods

In 2007, we set up 54 permanent 1 m × 2 m plots evenly distributed among three different disturbance types: grazed–unburned (GU), ungrazed–burned (UB) and grazed–burned (GB). The GU area has been grazed by cattle or sheep at least since the 1940s (in recent years at <0.25 calf/cow pairs·ha⁻¹ for about 1 mo each year) and has not burned in recent history (April Barron, USDA Forest Service, pers. comm. 5 Mar 2012). The UB area was burned on 7 Jan 1999 as part of a research project and rested from grazing since then with livestock exclusion fencing (Daniel Dawson, director of the Sierra Nevada Aquatic Research Laboratory, pers. comm., 11 Feb 2012). The GB area is directly adjacent to UB and was burned in the same fire, but located outside of the enclosure. It has been grazed with the same frequency and intensity as the GU area, both before and after the fire. Undisturbed sagebrush steppe sites (no grazing, no burning) are rare in the region, so it was not possible to fully replicate this combination. Nine sets of paired plots were placed per disturbance area. One plot of each pair received ambient N and the other received supplemental N. Paired plots were located a minimum of 0.5 m and maximum of 5.0 m apart from one another, and at least 10 m from any other plot.

Because our focus was on herbaceous species, we placed plots so that they included an equal representation of the same habitat types. Previous research has identified three dominant microhabitats as distinct growing environments for herbaceous species at the site: inter-shrub spaces

(INTR), spaces under *Artemisia tridentata* shrubs (ARTR) and spaces under *Purshia tridentata* shrubs (PUTR; Griffith 2010). We aimed to place plots so that they had equal representation of these three microhabitats consistent with broader landscape patterns (which was ca. 25% ARTR, ca. 25% PUTR and ca. 50% INTR). In the GB area, *Artemisia tridentata* was sparse and many of the plots had a distribution that was closer to 10% ARTR, 40% PUTR, 50% INTR. Some had 0% ARTR. In every case, however, plots were paired such that if ARTR was missing from a plot it was also missing from its paired plot.

Each year, 50 kg·ha⁻¹ N was added to half of the plots in the form of urea [CO(NH₂)₂]. We added urea rather than ammonium nitrate due to its easy accessibility and safe handling. We confirmed that both nitrate and ammonium (the two main forms of plant available N) were elevated with urea additions through resin probe analysis (not shown here). We added N at the time of snowmelt to simulate natural patterns of nutrient delivery into the soils. In areas that experience sustained snow cover, deposited N accumulates on the snow and then infiltrates into the soil profile at the time of snowmelt (Williams & Melack 1991; Bowman 1992). Fertilizer applied in dry form would have likely been dispersed by wind, so we dissolved urea (equivalent to 10 g N) with 6 L of water (equivalent to a 0.03 mm storm event) and added it evenly across each N addition plot, using water from Convict Creek about 1 km away. We ensured that any treatment effects were due to supplemental N rather than water by adding an equivalent amount of water to control plots at the time of N additions.

We measured soil nutrient status at the beginning and end of the experiment using two different methods. Cation and anion plant root simulator (PRS) probes (Western Ag

Innovations, Saskatoon, SA, CA) were inserted in the ground for 3 mo from 1 Jul to 1 Oct 2007 to estimate plant available N. Each probe's membrane area was 17.5 cm² (including both sides of the membrane, each of which was ca. 2-cm wide by 4-cm long), and we inserted each probe vertically into the soil to a depth of 10 cm. Probe measurements were made in only three of the nine replicate plot pairs in each disturbance area (3 replicates × 2 N treatments × 3 disturbance areas = 18 total samples) because of cost limitations. Probes were analysed by Western Ag Innovations for plant available N (NO₃⁻ + NH₄⁺). In 2011, three 2.2-cm diameter × 10-cm deep samples were collected per plot in the inter-shrub space. Samples were combined by plot, then sieved, dried and analysed for total carbon (C) and N (Elementar Vario MAX CNS analyser, Hanau, DE). We measured pH of these same samples using a 1:1 mix of dry soil and deionized water with a digital pH meter (model 220; Corning Science Products, Corning, NY, US).

Vegetation was measured each year in June, 2008–2011. Foliar cover of each plant species was visually estimated in two 1 m × 1 m quadrats per plot using modified Daubenmire (1959) cover classes: 0–1, 1–5, 5–10, 10–25, 25–50, 50–75 and 75–100%. The mid-point of the cover class was averaged by plot (from the two quadrats) for each species.

Data analysis

We calculated species richness (total number of species per plot) and evenness for each plot each year. Species evenness was calculated using the Shannon diversity index (H'), Simpson's dominance index (D') and Simpson's evenness index ($E_{1/D}$; Peet 1974). Shannon's diversity values were transformed before statistical analyses by calculating $e^{H'}$ so that the values covered a wider range (Margurran 2004). We used Kemp's transformation on Simpson's dominance values, calculated as $-\ln(D')$, which is a common transformation independent of sample size and recommended by Margurran (2004 and references therein). In addition to common diversity metrics, we also calculated *B. tectorum* dominance over other herbaceous species in the community for each plot as (*B. tectorum* cover/total herbaceous cover)*100%, where total herbaceous cover was the total cover of all non-woody species within each plot.

We used repeated measures analysis of variance (JMP v. 9.0; SAS Institute Inc., Cary, NC, US) to test whether the following response variables were significantly different by N treatment within each disturbance area over the 4 yr of the study: percentage cover *B. tectorum*, percentage cover native grasses, percentage cover native forbs, species richness of native grasses, species richness of native forbs, total native herbaceous species richness, *B. tectorum* dominance and the diversity indices H' , $-\ln(D')$, and $E_{1/D}$. We tested

differences by disturbance history and by year for *B. tectorum* cover using one-way ANOVA. Some variables were log transformed to meet assumptions of ANOVA.

To determine whether herbaceous species composition was different between N addition and control plots across the landscape, we used two-way crossed analysis of similarity (ANOSIM) tests with Bray–Curtis dissimilarities (PRIMER, v. 6; Primer-E Ltd, Ivybridge, UK). Factors were N treatment and disturbance history and a separate analysis was run for each year from 2008 to 2011. To determine which species were most important in driving differences between sample groups, we used a similarity percentages procedure, SIMPER (Clarke 1993; PRIMER v. 6). When using untransformed data, the SIMPER analysis tends to highlight differences in abundant species. Transforming data can help to identify differences in rare or smaller-statured plant species by reducing the weighting of dominant species (Clarke 1993). We ran analyses using both raw data and 4th root transformed data because we were interested in understanding differences in both rare and dominant species.

We used Pearson's correlation analysis to test relationships between *B. tectorum* cover and total native herbaceous species percentage cover, total native herbaceous species richness, native grass percentage cover, native grass species richness, native forb percentage cover and native forb species richness. We used the non-parametric equivalent, Spearman's rank-order correlation, to test relationships between *B. tectorum* percentage cover and each of the diversity metrics [H' , $-\ln(D')$ and $E_{1/D}$] because it was clear from scatter plots that the data were heteroscedastic and that their relationships with *B. tectorum* cover were non-linear (Quinn & Keough 2002). Correlation analyses were run using data from all plots within each year, and then on subsets of data separated by disturbance area. To further test relationships between diversity and *B. tectorum* invasion, we calculated percentage change from 2008 to 2011 by plot for each diversity metric and compared them to initial *B. tectorum* cover (Pearson's correlation analyses). We then calculated percentage change in *B. tectorum* from 2008 to 2011 by plot and compared it to initial diversity within the plots (Pearson's correlation analyses). These analyses were designed to test whether increased diversity conferred greater resistance to invasion, whether invasion impacted diversity, or both. We used R software for all correlation analyses (v 2.14.1.; R Foundation for Statistical Computing, Vienna, AT).

Results

We found that N addition treatments succeeded in approximately doubling plant available N and increasing total N (Table 1). However, the increased N did not significantly

Table 1. Chemical characteristics of soils, including total nitrogen (N; %), total carbon (C; %), C:N, plant available N ($\mu\text{g } 10 \text{ cm}^{-2} \text{ mo}^{-1}$)*, and pH for each site in control and N addition plots. Values in parentheses are SEM. Differences between N addition and control plots are indicated with *P*-values (ANOVA comparisons with site as a blocking factor), while NS means no significant difference.

Site	%N	%C	C:N	NO ₃ + NH ₄	pH
Control plots					
UNGRAZED-BURNED	0.20 (0.02)	3.06 (0.27)	15.4 (0.25)	63 (27)	5.87 (0.05)
GRAZED-UNBURNED	0.20 (0.02)	3.41 (0.32)	17.3 (0.44)	31 (3.9)	5.68 (0.07)
GRAZED-BURNED	0.19 (0.01)	2.86 (0.17)	14.7 (0.31)	50 (3.4)	5.99 (0.07)
Nitrogen addition plots					
UNGRAZED-BURNED	0.23 (0.01)	2.95 (0.40)	12.7 (0.75)	97 (23)	6.60 (0.09)
GRAZED-UNBURNED	0.24 (0.02)	3.47 (0.56)	14.3 (0.37)	67 (21)	6.32 (0.08)
GRAZED-BURNED	0.24 (0.01)	3.17 (0.30)	13.5 (0.28)	98 (27)	6.53 (0.09)
Effect of disturbance history (<i>P</i> -value)	NS	NS	0.0002	NS	0.0021
Effect of N treatment (<i>P</i> -value)	0.046	NS	<0.0001	0.008	<0.0001

*Plant available N was measured with resin probes with a membrane area of 17.5 cm² inserted 10 cm into the soil. Probes were collected after 3 mo of exposure in the field and extracted for inorganic N by Western Ag Innovations (Saskatoon, SK, CA).

impact cover of *B. tectorum*, cover of native species, dominance of *B. tectorum* or species richness, regardless of disturbance history or year (Fig. 2). Further, there was no difference in community composition by N treatment in any year (Table 2).

We identified inter-annual differences in *B. tectorum* cover ($P < 0.0001$ in UB, GU and GB) and herbaceous species richness ($P = 0.0005$ in UB and $P < 0.0001$ in GU and GB; Fig. 2). Species richness generally decreased and *B. tectorum* cover increased over time, the latter particularly from 2008 to 2009 (Figs 2 and 3a). Consequently, *B. tectorum* dominance over native herbaceous species increased by 170% in UB ($P = 0.02$), 330% in GU ($P = 0.0002$) and 135% in GB ($P = 0.02$) between 2008 and 2009. Within the UB plots, species richness appeared to be declining at a greater rate in N addition plots than controls (Fig. 2d); however, results from the repeated measures ANOVA showed no difference by treatment ($F = 2.06$, $P = 0.169$).

We found that *B. tectorum* cover varied across the landscape by disturbance history ($P < 0.0001$; Fig. 3). The GB site consistently had the highest *B. tectorum* cover ($P \leq 0.0001$ for all years), the highest *B. tectorum* dominance over native species ($P \leq 0.0003$ for all years), and the lowest native herbaceous species richness in 2008 ($P = 0.09$) and 2011 ($P = 0.001$) but not 2009 or 2010 (Figs 2 and 3b). Analyses of similarity confirmed that there were significant differences in community composition between the areas (Table 2), and SIMPER analyses highlighted which species contributed to the differences (Appendices S1, S2). Using untransformed data, *B. tectorum* was the species that contributed the most to dissimilarity between communities in 11 out of 12 comparisons, ranging from a contribution of 23–57% (the exception was one instance in 2008 in which it contributed 15% of the dissimilarity between UB and GU; Appendix S1). Differences

Table 2. Summary of two-way ANOSIM tests of herbaceous plant community composition by N treatment (plus N, ambient N) and disturbance history (grazed, burned and grazed–burned) from 2008 to 2011. All data were transformed to the 4th root.

Year	Factor	<i>R</i>	<i>P</i>
2008	N treatment	−0.035	0.760
	Disturbance history	0.236	0.002
2009	N treatment	−0.040	0.775
	Disturbance history	0.251	0.001
2010	N treatment	−0.080	0.985
	Disturbance history	0.211	0.001
2011	N treatment	−0.008	0.511
	Disturbance history	0.215	0.001

in all native grasses combined contributed between 21% and 37%, and all forbs combined contributed between 8% and 33% to dissimilarities. Using fourth root transformed data, a higher number of species contributed to dissimilarities (an average of 17 ± 0.3 species over all years and disturbance areas as opposed to 11 ± 0.7 with untransformed data; Appendix S2). Notably, forbs contributed much more to the total dissimilarities (39–65%). Most forbs at the site are small in stature and do not contribute much to the total biomass or vegetative cover of the system, so it was expected that their role in the community might be overlooked if we were to use raw data alone for analyses.

We found that *B. tectorum* cover was negatively correlated to biodiversity indices in 2009, 2010 and 2011 (we present data from 2011 as an example in Fig. 4). The strength of these associations appeared to be driven by differences in richness of native forbs. Forb species richness was negatively correlated to *B. tectorum* cover ($r = -0.44$, $P = 0.0008$), while grass richness was not ($P = 0.25$). Neither forb cover nor grass cover were related to *B. tectorum* cover ($P = 0.17$, $P = 0.38$, respectively). Further comparisons of *B. tectorum* cover and biodiversity were made

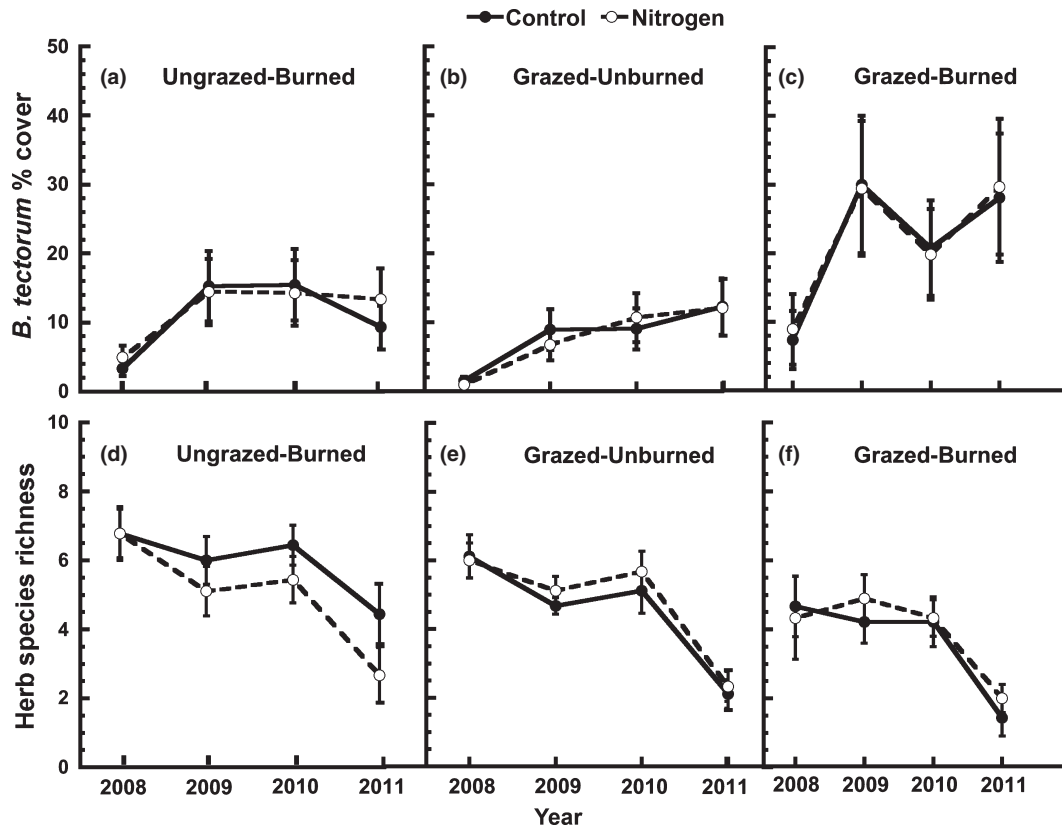


Fig. 2. Mean *Bromus tectorum* cover (a–c) and herbaceous species richness (d–f) measured from 2008 to 2011 in control and N addition plots in areas that were burned (a, d), grazed, (b, e) and grazed-and-burned (c, f). Bars are 1 SEM.

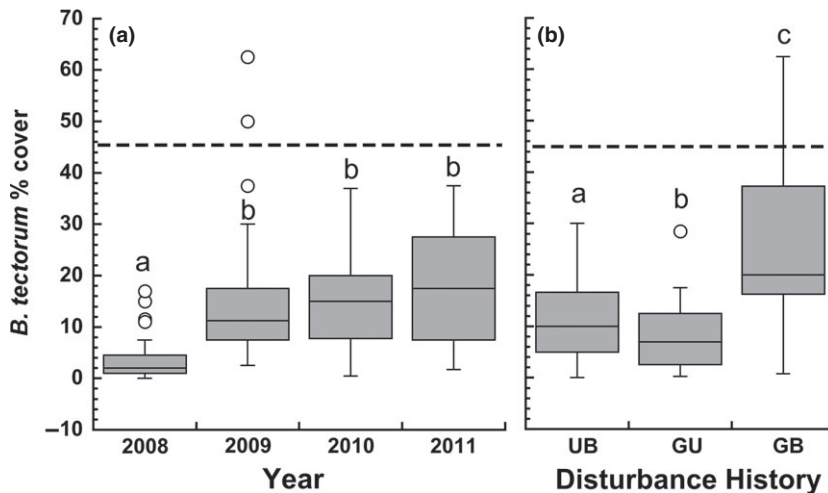


Fig. 3. Box plots of *Bromus tectorum* cover by (a) year and (b) disturbance history (UB, ungrazed burned, GU, grazed unburned, GB, grazed burned). Boxes represent median and 25% and 75% quartiles; bars represent minimum and maximum values; dots are outlier values. Different letters signify significantly different means within each panel. A dashed line is drawn at the predicted threshold in *B. tectorum* cover when fire risk approaches 100% (Link et al. 2006).

within each disturbance area. In both GU and UB, initial forb species richness measured in 2008 was negatively correlated to the percentage change in *B. tectorum* cover

from 2008 to 2011 (Fig. 5a, c). In both GU and UB, change in *B. tectorum* cover was also related to initial e^{H^r} ($r = -0.53$, $P = 0.02$ and $r = -0.54$, $P = 0.02$,

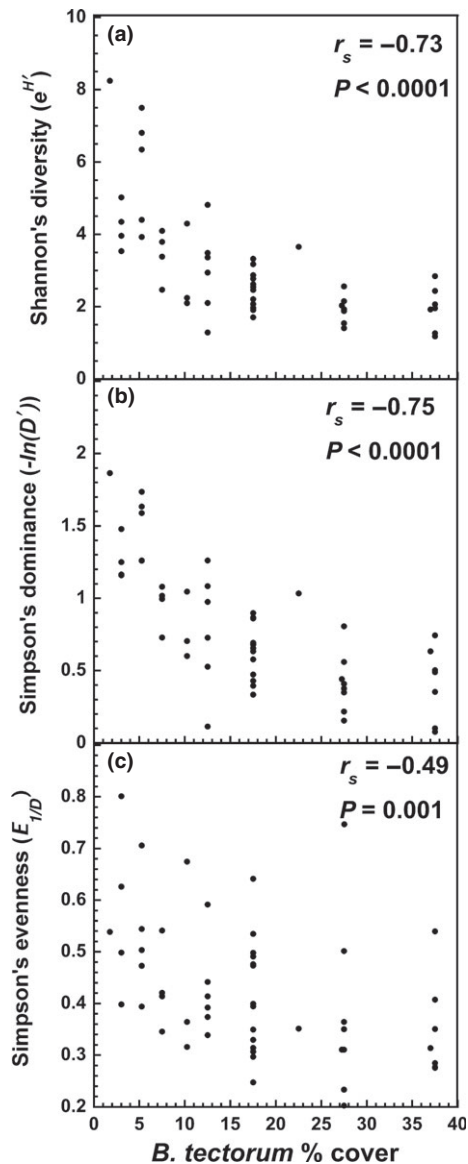


Fig. 4. Relationships between *Bromus tectorum* cover and (a) Shannon's diversity, (b) Simpson's dominance and (c) Simpson's evenness. Spearman's rank correlation coefficient and corresponding P -value associated with each monotonic relationship appear in the upper right corner of each panel.

respectively) and $-\ln(D')$ ($r = -0.46$, $P = 0.05$ and $r = -0.57$, $P = 0.01$, respectively), but not $E_{1/D}$ ($r = -0.01$, $P = 0.95$ and $r = 0.21$, $P = 0.41$, respectively). Conversely, initial *B. tectorum* cover measured in 2008 was negatively related to the percentage change in forb species richness in GU plots (Fig. 5d). This trend was not significant in UB plots (Fig. 5b). Initial *B. tectorum* cover was not correlated to any of the other diversity indices in GU or UB. Percentage change correlations were not significant in GB plots.

Discussion

We did not detect an effect of N addition on plant community composition or *B. tectorum* dominance over 4 yr in this high-elevation shrub steppe ecosystem. Plants in arid environments may be less responsive to nutrient additions because they are primarily limited by water (Noy-Meir 1973). Still, studies in arid and semi-arid ecosystems have measured changes in species richness and vegetative composition with increased N deposition (Brooks 2003; Schwinning et al. 2005; Allen et al. 2009; Pasquini & Vourlitis 2010; Rao & Allen 2010; Zeng et al. 2010; Song et al. 2012). Four of these seven studies measured plant response to a higher level of N ($\geq 100 \text{ kg} \cdot \text{ha}^{-1}$) than what we used in our manipulations; we may have measured a response by increasing the amount of N added. We might also expect to see a response to N (even at lower levels) during years of higher spring precipitation; during the 4 yr of our study, total annual precipitation was below the 24-yr average (Fig. 1). Additionally, some longer-term studies have shown that plant response to N can vary over time (Kay 1966; Inouye & Tilman 1995; Faust et al. 2012), and we might expect to measure shifts in the plant community after repeated N additions over a longer time period. N availability, even with the N additions, was relatively low compared to soils in other study locations (e.g. Dobermann et al. 1994). It should be noted, however, that our manipulations delivered available N at more than ten times the background rate. Such an increase is unlikely to occur in the near future, although there may be pockets receiving higher input – such as along roadsides.

We measured inter-annual variation in *B. tectorum* cover, which was likely influenced by differences in annual precipitation and the advancing invasion of *B. tectorum*. In arid ecosystems, both wet and dry years can provide windows of opportunity for shifts in plant community composition (Holmgren et al. 2001; Loeser et al. 2007). *Bromus tectorum* exhibits boom and bust cycles in response to annual variation in precipitation (Mack & Pyke 1983; Bradley & Mustard 2005; Griffith & Loik 2010). In drought years, *B. tectorum* biomass can drop to close to zero, even in highly invaded areas (Stewart & Young 1939; Kay 1966). At our site, *B. tectorum* cover was lowest in 2008, which was the driest of the 4 yr. In 2009, the site received relatively more springtime precipitation, and *B. tectorum* cover and dominance increased dramatically in all plots during that year. Link et al. (2006) found that once *B. tectorum* reaches about 45% cover, the risk of fire approaches 100%. Some plots at our site surpassed this threshold in 2009. Another year of high spring precipitation could result in a larger portion of the landscape susceptible to fire and provide an opportunity for initiation of an invasive grass-fire cycle at this upper elevation range limit. In 2000,

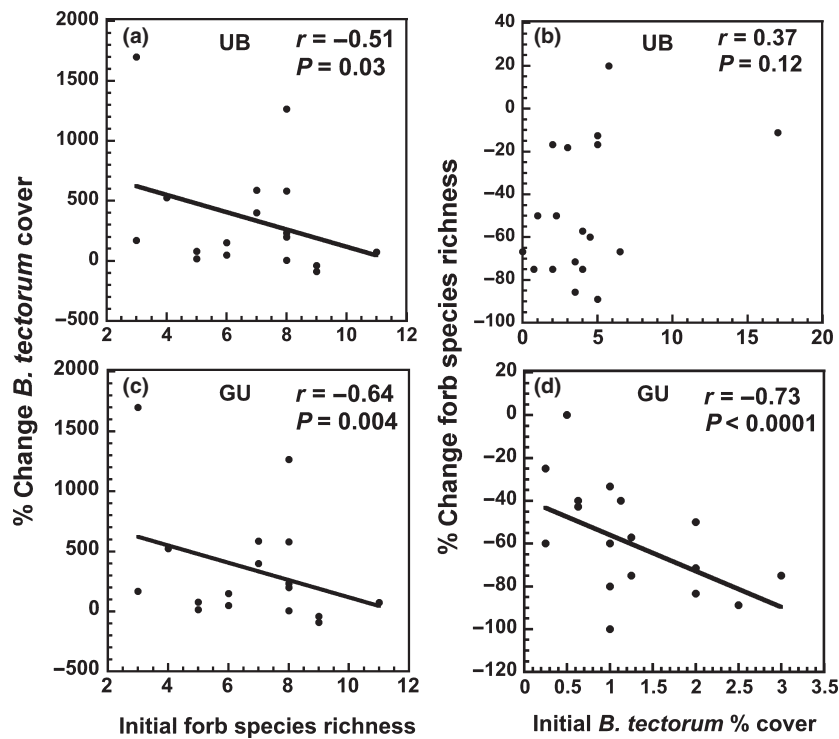


Fig. 5. Relationships between initial forb species richness (in 2008) and percentage (%) change in *Bromus tectorum* cover from 2008 to 2011 in (a) burned plots (UB) and (c) grazed plots (GU) and, conversely, between initial *B. tectorum* percentage cover (in 2008) and percentage change in forb species richness from 2008 to 2011 in (b) burned plots and (d) grazed plots. Pearson's correlation coefficient and corresponding *P*-value associated with each linear relationship appear in the upper right corner of each panel.

a flora of the Sierra Nevada Aquatic Research Laboratory UC Reserve, which is directly adjacent to our study site, described *B. tectorum* as occurring 'occasionally in disturbed areas along edge of entrance road near buildings' (Orr & Howald 2000; Section II, pg. 30). The increase in cover that *B. tectorum* achieved in just 9 yr is alarming at this elevation.

We found that plant community composition, species richness and *B. tectorum* dominance varied by disturbance history. It should be noted that these comparisons were made between one site only per disturbance history type and results should, therefore, be interpreted with caution. However, our findings were consistent with past research that reported differences in species composition between grazed, ungrazed, burned and unburned sagebrush steppe (West & Yorks 2002; Yeo 2005; Manier & Hobbs 2007; Davies et al. 2009). Plant community responses to disturbance may be influenced by differences in soil physical and chemical properties and herbivore pressure (Blank et al. 1994; Beever et al. 2006; Scholefield et al. 2007). For example, we expected that abundance of preferred forage species (i.e. perennial grasses) would be lower in grazed compared to ungrazed plots (West & Yorks 2002), and our results supported this hypothesis in every year except 2011. *Bromus tectorum* was most abundant in the

GB site compared to grazed or burned alone, which could be attributed to the increased disturbance. It is well known that disturbances can facilitate plant invasions, and that grazing and fire, in particular, can promote the spread of *B. tectorum* (Stewart & Hull 1949; Mack 1981; Knapp 1996; Loeser et al. 2007). Still, Davies et al. (2009) found a pattern opposite to our results: burning without grazing led to a large increase in *B. tectorum*, while burning with grazing did not. Likewise, while we found that species richness and diversity were consistently highest at the ungrazed site, Manier & Hobbs (2007) found that species richness was lower in ungrazed than grazed sites. Grazing exclosures at their sites were in place for much longer (42 yr) than ours, which probably influenced the direction and magnitude of the response. Grazing duration at our site is also relatively short term each year, which may also affect the response. Land-use history and site characteristics (including, e.g. the intensity and duration of grazing, past agricultural use, dominance of invasive species, and shrub and bunchgrass cover) can have a significant influence on the response of arid and semi-arid plant communities to disturbances (Loeser et al. 2007; Davies et al. 2009).

We found strong negative correlations between *B. tectorum* cover and biodiversity indices every year apart from

2008. These correlations were significant within the entire data set (i.e. across the landscape and including past disturbances and land use), but also within each disturbance area, implying that they did not simply result from disturbance. We have three hypotheses that could explain this trend: (H₁) areas of the landscape with higher diversity are more resistant to *B. tectorum* invasion; (H₂) *B. tectorum* invasion is negatively impacting native forbs through competitive displacement; and (H₃) some other driver (e.g. differences in physical or chemical properties of the soil) is influencing both *B. tectorum* cover and native species richness independent of one another. Ecological theory suggests that more diverse systems can confer increased resistance to invasion (Elton 1958) due to more complete utilization of limiting resources (Kennedy et al. 2002). Empirical research has provided evidence to both support (e.g. Tilman 1997; Naeem et al. 2000; Anderson & Inouye 2001) and refute (e.g. Robinson et al. 1995; Stohlgren et al. 1999; Floyd et al. 2006) this theory. We did find that the initial forb species richness in each plot was correlated to the change in *B. tectorum* percentage cover over the 4 yr of the study in both burned and grazed plots (but not GB plots), which suggests that more diverse plots may be more resistant to invasion and provides support for this hypothesis. However, this result was unexpected because many of the forb species at the site are small-statured annual plants that cover an insubstantial portion of the landscape (most covered <1% of plots). In the Intermountain West, ecosystem resistance to *B. tectorum* invasion would be expected to increase with increased functional diversity (rather than total species diversity), with perennial grasses playing an especially important role (D'Antonio et al. 2009; Brooks & Chambers 2011). Some studies elsewhere in the Great Basin reported inverse relationships between perennial grass cover and *B. tectorum* cover (West & Yorks 2002; Bates et al. 2005). However, we did not find relationships between grass richness or cover and *B. tectorum* cover in any year. In a manipulative experiment testing the effect of species richness on *Lolium* invasion, Lyons & Schwartz (2001) found that rare species had a disproportionately important effect on resistance to invasion compared to their biomass. Small-stature plants in the Great Basin may be more important for maintaining ecosystem function and resistance to invasion than might be expected.

At the burned site, the initial percentage cover of *B. tectorum* was inversely related to the change in species richness from 2008 to 2011. This suggests that *B. tectorum* invasion may contribute to declining species richness and provides support for H₂. It is well known that *B. tectorum* can replace native species after disturbance (Stewart & Hull 1949; Mack 1981; Knapp 1996), but not much evidence exists for displacement effects at the early stages of *B. tectorum* invasion, especially at high-elevation range margins.

In a Sonoran Desert plant community, Olsson et al. (2012) also measured negative impacts on native species richness after invasion of an exotic grass before initiation of a grass–fire cycle. However, over the first 11 yr of *B. tectorum* invasion into a sagebrush steppe community of eastern Oregon, no loss of forbs or perennial grasses was reported (Kindschy 1994). Although the time since invasion was similar, *B. tectorum* cover was relatively low (10%) at the eastern Oregon site compared to ours. Other studies have found effects on composition and abundance of soil biota and on nutrient cycling in response to recent *B. tectorum* invasion in perennial grass communities (Belnap & Phillips 2001; Sperry et al. 2006), which could have feedback effects on native plants.

Finally, some external factor may be influencing both forb richness and *B. tectorum* cover at these plots (H₃). For example, differences in nutrient availability can influence *B. tectorum* distribution across the landscape (Beckstead & Augspurger 2004; Miller et al. 2006; Gundale et al. 2008), and may also influence native plants. Invasion success has also been associated with differences in soil texture, rockiness, litter layer, shrub cover and bare ground (English et al. 2005; Miller et al. 2006; Adair et al. 2008; Gundale et al. 2008; Rao et al. 2011). Species richness did not vary by shrub cover or bare ground at our site (data not shown), but some of these other variables (which we did not measure) may have been responsible for spatial differences in community composition. The fact that we found differences in relationships between changes in *B. tectorum* cover and species richness depending on whether plots had experienced burning and/or grazing suggests that the mechanisms causing species decline may differ by disturbance and land-use history. More work is needed to address this question.

In summary, we did not find evidence that increased N deposition would affect species composition or the spread of *B. tectorum* at these high-elevation sagebrush steppe sites. However, our study was conducted during years of below-average precipitation; results would likely be different in wet years due to the interactive effects of N and precipitation on *B. tectorum* biomass (Concilio et al. 2013). Additionally, we recognize that some of the vegetation community patterns may be a result of change that has already occurred; unfortunately, we are unable to identify the extent of such changes. Interestingly, our data suggest that *B. tectorum* is advancing at high elevations and may be impacting native species richness before initiation of an invasive grass–fire cycle. During a year of high spring precipitation, *B. tectorum* surpassed the threshold for increased fire risk in some plots. Managers should monitor high-elevation populations of *B. tectorum*, especially during years of high precipitation, and be prepared to initiate fuel reduction or active restoration treatments (Brooks et al. 2004;

Diamond et al. 2009) to decrease the chances of a shift to an invasive grass–fire cycle.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Results from one-way SIMPER comparisons of herbaceous community composition by disturbance history and year. Data untransformed.

Appendix S2. Results from one-way SIMPER comparisons of herbaceous community composition by disturbance history and year. Data transformed to the 4th root.