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Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland

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Abstract. Grasslands managed for grazing are the largest land-use category globally, with a significant proportion of these grasslands occurring in semiarid and arid regions. In such dryland systems, the effect of grazing on native plant diversity has been equivocal, some studies suggesting that grazing reduces native plant diversity, others that grazing increases or has little impact on diversity. One impediment toward generalizing grazing effects on diversity in this region is that high levels of interannual variation in precipitation may obfuscate vegetative response patterns. By analyzing a long-term data set collected over a 20-yr period in a semiarid grassland, we explicitly evaluated the role of climate in regulating the effect of cattle grazing on plant communities, finding that climate interacted with grazing intensity to shape grassland communities. Community composition of plots that were intensively grazed varied considerably in response to climatic variation and native species richness was low relative to ungrazed and moderately grazed plots. Following a severe drought in 2002, exotic species richness rapidly increased in the high-intensity grazing plots. While this pattern was mirrored in the other treatments, exotic species richness increased to a greater extent and was slower to return to pre-drought levels in the high-intensity grazing plots. Overall, moderate grazing, even compared to grazing cessation, stabilized grassland communities through time, increased resilience to drought, and maintained the highest levels of native plant diversity and lowest levels of exotic diversity. These findings suggest that grazing, at moderate levels, may support grassland resilience to climate change in semiarid regions. However, grazing that exceeds tolerances, particularly in combination with extreme climatic events, like drought, can alter plant composition over relatively long timescales and possibly increase invasibility by nonnative species.

Key words: cattle grazing; climate change; drought; exotic species; plant diversity; resilience; southwestern United States.

Introduction

Within grassland systems, grazing by large vertebrate herbivores shapes plant community diversity (Floyd et al. 2003, Harrison et al. 2003, Hayes and Holl 2003), structure (Adler et al. 2001), and function (Belsky and Blumenthal 1997, Hayes and Holl 2003, Belnap et al. 2009), though the magnitude and direction of these effects varies considerably along environmental gradients and depends on the strength of grazing pressure (Milchunas and Lauenroth 1993, Bakker et al. 2006, Beck et al. 2015, Irisarri et al. 2015, Liu et al. 2015, Herrero-Jáuregui and Oesterheld 2018). Classic grazing theory (i.e., Milchunas et al.'s [1988] "Generalized theory of the effects of grazing on plant community and structure" and subsequent iterations), supported by empirical evidence, suggests that moderate levels of grazing will increase native plant diversity in highly productive, mesic systems with long evolutionary histories of grazing (Milchunas et al. 1998, Cingolani et al. 2005). In terms of mechanism, such theories, which incorporate aspects of the Intermediate Disturbance Hypothesis (IDH), posit that a small number of plant species will outcompete others for limiting resources and eventually attain dominance within the system in the absence of disturbance (Milchunas et al. 1988). Grazing at intermediate levels reduces competitive exclusion of rare species by decreasing the performance of dominant species. Thus, in grassland systems with long evolutionary histories of grazing, herbivory diversifies selective pressures through time and space, allowing the persistence of plants with alternative life history strategies (i.e., life histories that promote tolerance of herbivory, in addition to those adapted to rapidly acquire light, water, nutrients

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or other limiting resources). When disturbance is too great, however, weedy or ruderal species displace those that lack adaptations to high-disturbance regimes, again reducing diversity.

Levels of grazing that support high diversity in mesic systems would be predicted to negatively impact native diversity in drier, less productive systems lacking a long evolutionary history with large vertebrate herbivores, (Milchunas et al. 1988). Grazing in these systems, even at intermediate levels, is expected to reduce diversity by eliminating species with low tolerance of herbivory, while providing a lesser benefit in terms of competitive release to other species, as competition is considered a stronger determinant of community assemblage in high productivity systems where greater biomass results in a unidirectional competition for light (Kondoh 2001, Harpole et al. 2016). Within this framework, livestock grazing would be predicted to reduce diversity of semiarid grassland plant communities in the southwestern regions of the United States. These grasslands are characterized by low overall annual precipitation and high rainfall variability, resulting in frequent droughts (Belesky and Malinowski 2016). Evidence from the fossil record and other sources suggest that the number of large vertebrate herbivores was historically low until the introduction of cattle and sheep by European settlers in the 1800s (Betancourt and Davis 1984, Schwinning et al. 2008). Indeed, 19th century overgrazing has been linked to conversion of grasslands to shrublands (Bestelmeyer et al. 2011), soil erosion, desertification (Schlesinger et al. 1990), and spread of noxious invasive plants, (Mack 1981) when the co-occurrence of high-intensity grazing with other stressors, particularly drought, sufficiently degraded perennial plant cover to allow invasion or vegetative state change. These past changes broadly support theories suggesting that high levels of grazing will negatively impact native plant diversity. While some contemporary studies similarly document diversity declines associated with grazing in arid and semiarid systems (Floyd et al. 2003, Lezama et al. 2014), many find neutral (Jones 2000, Fensham et al. 2014) or even positive effects on plant diversity and ecosystem stability (Beck et al. 2015, Alberti et al. 2017).

One explanation for observed inconsistencies among grazing studies in semiarid regions is that high levels of interannual variability in precipitation potentially obscure grazing effects on plant communities (Fuhlendorf et al. 2001). A study conducted in a high rainfall year may yield dramatically different results than when performed in a drought year, due to alterations in grazing patterns (e.g., changes in forage selectivity and proportion of total aboveground plant biomass consumed) and competitive relationships among plants (Carmona et al. 2012). In these systems, data must be collected over a sufficient time period and sampled with sufficient frequency to observe vegetative response to a robust range of climatic conditions and to distinguish long-term from transient responses of grassland communities. Meeting these intensive data requirements is imperative, not only to better understand grazing impacts on plant diversity in semiarid grassland communities, but also to examine how these effects may be modified as climate changes. Adaptation of management practices to ensure resistance/resilience are particularly important in semiarid and arid regions, where many species exist at the limits of their physiological tolerances and where mismanagement of grazing could hasten conversion to alternative, potentially less desirable, states like shrublands or invasive-dominated systems (Schlesinger et al. 1990, Van Auken 2000, Peters et al. 2006, Knapp et al. 2008, D'Odorico et al. 2013, Kettenbach et al. 2017).

Here, we examine a 20-yr dataset of plant community response to experimental grazing in a semiarid grassland on the Colorado Plateau in northern Arizona. We build on a previous study, which documented a positive effect of moderate grazing on native plant diversity, while simultaneously observing a rapid increase of cheatgrass in intensively grazed treatments following drought (Loeser et al. 2007). Adding an additional 10-yr of data and applying novel analytical techniques permitted by this extended time horizon, we ask: (1) Do grazing and climate interact to affect native and nonnative plant diversity in this semiarid grassland? and (2) How does drought shape southwestern plant community composition in grazed systems? In particular, we track frequency of cheatgrass and other invasive plant species to determine whether previous documented increases in abundance resulted in an irreversible shift to an invasive plant dominated system. Finally, we consider these results in the context of a changing climate in order to inform grazing management in arid and semiarid grasslands.

Methods

Study area

This study was conducted in a semiarid, high-elevation (2,160 m) grassland bordered by ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests in north-central Arizona on the Colorado Plateau. In this region, precipitation generally occurs during the summer monsoons (15 June–30 September) arriving from the eastern, tropical Pacific (Gulf of California/Gulf of Mexico) or during the winter as frontal systems arriving from the northern or western Pacific (Gulf of Alaska) in approximately equal amounts. Generally, the wettest month is August and the driest month is June (Schwinning et al. 2008). During the 20-yr (1997–2017) study period, total annual precipitation varied between 327 and 694 mm and average annual temperature varied between 6.9°C and 9.7°C (Table 1). The study area is underlain by Vertisol soils, characterized as containing a high proportion of shrink-swell clay, which causes extensive mixing of the uppermost soil horizons. Prior to European settlement, grazing pressure on Colorado Plateau grasslands was

Table 1. Climate conditions at the Reed Lake field site for all years in which plant surveys were conducted during the 20-yr study period from 1997 to 2017.

		Annual mean growing season temperature (°C)		January mean temperature (°C)		July mean temperature (°C)		
Year	Total annual precipitation (mm)	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	PDSI June
1997	397.2	15.7	−0.7	4.0	−8.5	27.8	7.5	−2.9
1998	694.1	14.7	−0.9	6.5	−7.2	27.7	10.3	1.5
1999	400.2	16.7	−1.0	9.6	−7.6	24.7	11.0	−3.1
2000	391.3	17.1	0.2	8.4	−7.4	28.7	9.7	−4.5
2001	446.3	16.8	−0.2	4.1	−9.5	27.1	10.2	−1.8
2002	**327.3**	**17.3**	**0.0**	**6.8**	**−7.9**	**29.1**	**13.0**	**−6.6**
2003	454.1	17.0	0.7	10.7	−5.0	29.7	12.0	−4.6
2004	600.9	15.5	−0.3	4.4	−8.0	27.3	8.9	−4.6
2005	610.5	16.2	0.2	5.2	−5.7	29.2	10.0	4.6
2006	396.4	16.5	−0.3	7.7	−9.4	27.4	12.4	−5.3
2007	443.9	16.9	0.1	3.0	−10.3	28.6	12.0	−5.3
2008	479.1	16.6	−0.2	2.8	−11.3	27.4	12.0	−1.5
2011	525.8	16.2	−0.6	7.0	−10.4	27.5	10.6	−2.9
2014	525.4	17.5	1.0	10.4	−6.4	27.6	11.8	−4.8
2017	439.7	17.6	1.9	3.0	−5.6	27.4	12.1	−0.8

Notes: Annual climate summaries, as well as mean temperature conditions for the coldest (January) and warmest (July) month of the year, are shown. The final column displays the Palmer Drought Severity Index, (PDSI), a measure of relative dryness that varies between −10 (dry) and +10 (wet), for the historically driest month of the year, June. The year 2002 has set in boldface type to highlight the high temperatures and low precipitation that resulted in drought that growing season.

believed to be low, given a paucity vertebrate herbivore fossils and lack of diversity and abundance of dung beetles, metrics that correlate with herbivore abundance (Betancourt and Davis 1984, Schwinning et al. 2008). Regional historic accounts indicate that extensive grazing by cattle and sheep occurred in Arizona during 1870–1890 (Schwinning et al. 2008). There is no indication that this site would have differed from other grasslands in the region in terms of historical grazing pressure. Cattle stocking rates have steadily decreased since the late 1800s, and from the 1950s onward, have been maintained at low to moderate densities (see description of grazing treatments Experimental design). Other grazers occur red at the site, including mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*). While cattle fencing may also reduce elk presence within fenced areas (Gross and Knight 2000), pellet counts conducted at this site did not indicate that visitation rates varied significantly among treatments (Loeser et al. 2007). However, pellet counts were not conducted every year of the study, so grazing by wild ungulates within exclosures/enclosures may, at times, have been lower than ambient levels experienced by the moderate use areas.

Experimental design

Grazing treatments were established on randomly selected 1-ha plots located at least 100 m apart in 1997 following initial vegetation surveys. At the time of plot establishment, ranchers managed cattle so that they consumed roughly 50% of the aboveground biomass, maintaining a stocking rate of approximately 0.5 cow-calf pairs/ha for 14 d/yr (~0.2 Animal Unit Months (AUM)/ha; Loeser et al. 2007). Grazing management in the study area evolved from a blending of traditional, season-long rest-rotation techniques (Hormay and Evanko 1958), typical of the region, and a more rapid rotation schedule inspired, in part, by the ranchers' exposure to holistic management (Savory and Butterfield 1999; K. Metzger, *personal communication*). This ambient grazing method became the moderate grazing-level treatment (MOD) in our study, because it was intermediate in intensity to complete grazing cessation and the high-intensity treatment. We constructed three 1-ha livestock exclosures to serve as a no-cattle grazing treatment (EXC), and three 1-ha livestock enclosures to increase grazing levels above ambient conditions. Within these high-grazing-level treatment (HIGH) plots, ranchers aimed to remove approximately 80% of the aboveground biomass in one short-duration, high-impact event to simulate herding behavior, where impact is highly concentrated in space and time, followed by long periods (in our case 1 yr) with little or no grazing. The stocking rate in HIGH plots was, on average, approximately 200 cow–calf pairs/ha for 12 h/yr annually, with grazing time never exceeding 24 h (~3.3 AUM/ha; Loeser et al. 2007). Periodically (e.g., in the drought year, 2002), drought conditions reduced vegetation to such an extent that cattle were transported to another site and thus did not graze the MOD or HIGH plots. Actual stocking rates, therefore, varied between 0 and 0.5 cow–

calf pairs/ha for 14 d/yr in the moderate grazing treatment and 0–400 cow–calf pairs/ha for 12 h/yr in the high-intensity treatment. Cattle breached one of the three exclosures twice during this 20-yr period. However, in each case, the exclosure was grazed for no more than a 24-h period, resulting in a grazing intensity below moderate levels.

To monitor vegetation change through time, we established Modified-Whittaker plots (Stohlgren et al. 1995). The Modified-Whittaker plot design included a series of subplots of exponentially increasing size, in this case 1, 10, and 100 m^2, nested within a 1,000-m^2 plot, thus allowing researchers to examine how metrics of species diversity varied as a function of sample area (Fig. 1). Plant surveys were conducted annually until 2008, when survey frequency was reduced to once every 3 yr. Vegetation data were collected in July, following the onset of the monsoonal rains. While vegetation sampling at additional time points during the year to capture intra-annual variation in vegetation due to species-specific phenology would be ideal, such a sampling regime was not tractable over this 20-yr study period. For this reason, sampling was timed to capture peak biomass production in the region, at a time when both cool and warm season grasses were present. At plot sizes >1 m^2, simple incidence data were collected in the form of species lists. At the 1-m^2 subplot level, a 50-point frequency frame was used to assess ground cover and to provide a more structured estimate of species occurrence. We repeated vegetation surveys for three replicate blocks for each treatment (Data S1).

Data analysis

Diversity metrics and cover analyses.—In order to analyze data on species diversity through time, Hill numbers or the effective number of species of the diversity order $q = 0$ (species richness), 1 (exponential Shannon entropy), and 2 (inverse Simpson index) were calculated at the plot level for all years and all treatments using the package iNext in R (Hill 1973, Hsieh et al. 2016). Species were scored as present/absent within the 1-m^2 subplots and incidence data were used to calculate diversity indices for each replicate plot. In addition to observed Hill numbers, we extrapolated these parameters to asymptotic species diversity estimates using sample completeness, which estimates false absences based on the number of rare species within an assemblage (Chao et al. 2014). Standardizing diversity metrics by extrapolation may improve comparisons among assemblages, because assemblages vary in terms of their species pools, and diversity estimates are highly sensitive to sample size and completeness (Chao and Jost 2012).

Once Hill numbers were calculated, we used linear mixed effects models (R package lme4, function lmer) to determine whether grazing treatment, year, or the interaction of these two factors affected species diversity. Within these models, plot was treated as a random effect and the equation structured to account for the repeated measurement of these plots through time ($n = 3$). Models were fit using restricted maximum likelihood (REML) due to small sample size. Because species richness and percent cover calculations do not require a measure of evenness, we were able to calculate richness/cover at the 1-m^2 subplot level, and include these data as a subsample of the larger plots in the linear mixed effects models ($n = 3$). For these analyses, model main effects included treatment, year, and the interaction of these factors, with subplot nested within plot included as a random effect. Pairwise comparisons of treatment effects within each year of study were conducted using Tukey's Honestly Significant Difference (HSD) post hoc test (R package lsmeans).

We used multiple regression to determine if climatic factors drove interannual variation in native and exotic species richness. In order to account for the dependency of diversity on the vegetative state of the community the previous year, we calculated the change in species richness from the previous year for each treatment as the dependent variable for all analyses. Initial attempts to build explanatory models using backward and forward model selection resulted in overly complex, uninformative models. Based on ecological studies of the region and given the observable, profound effects of the 2002 drought on vegetation, we used the Palmer Drought Severity Index (PDSI), calculated for the driest month of the year, June, as the explanatory variable in the final models. The PDSI combines temperature and precipitation data to estimate relative dryness in relation to baseline data, in this case 1990 to 2000. PDSI is standardized to vary between −10 (dry) and +10 (wet). For each model, we explored both linear and polynomial fits. The 2002–2003 drought-recovery transition was an outlier for both native and exotic species richness for all treatment groups. Because we were interested in assessing deterministic climatic drivers of species richness with this analysis, the 2002–2003 transition, which bracketed this anomalous drought event, was excluded from models.

Community-level analyses of the 2002 drought event.—A severe drought in 2002 had observable, negative impacts on vegetation. In order to examine the effect of this drought event, we compared community composition for each treatment at three time points: (1) 2001, the pre-drought year, (2) 2003, the post-drought year, and (3) 2017, the final year of the study. To test for community compositional differences, we pooled survey data (treated as abundance data, see Royle and Nichols 2003) collected in the 10 1-m^2 subplots to the plot level, and performed a PERMANOVA analysis using 1,000 permutations and Bray-Curtis distance as a measure of dissimilarity in the R package vegan with the adonis function. To visualize differences in community composition among treatments, we used nonmetric multidimensional scaling (NMDS; R package vegan), which condenses information on community composition into

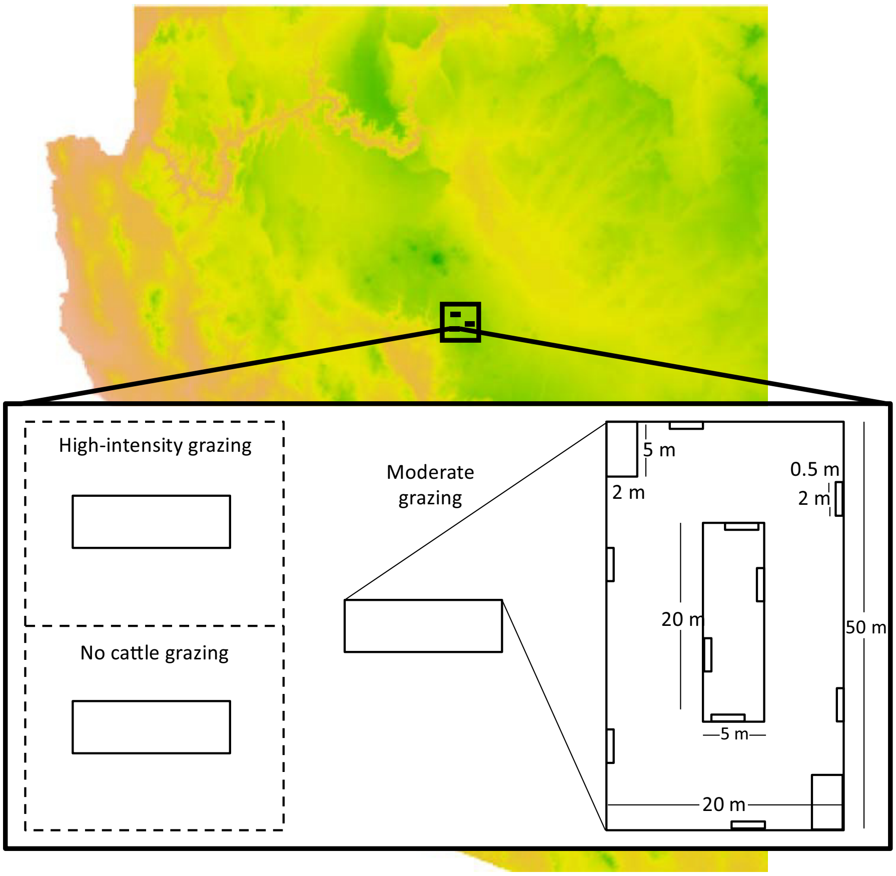

FIG. 1. Schematic illustrating Modified-Whittaker plot design for vegetation surveys, and the approximate location of plots in a semiarid grassland in Arizona. Within the inset plot design graphic, dashed lines on the left side of the figure indicate fence lines and solid lines indicate positioning of the survey plots. Plots were established in the center of the exclosure/enclosure areas to avoid edge effects. On the right side of the inset figure, solid lines demarcate survey areas, which included 10 1-m^2, two 10-m^2, and one 100-m^2 subplots nested within the entire 1,000-m^2 survey area.

a pair of synthetic orthogonal axes. Within this ordination space, proximity indicates similar species composition. We calculated the contribution of individual species to the Bray-Curtis dissimilarity distance between communities using function simper in R package vegan to determine which species drove differences in pairwise comparisons of plant communities.

RESULTS

Species diversity changes among grazing treatments through time

Interannual variation, presumably driven by climate, affected all metrics of native species diversity, including richness ($q = 0$; $F_{14,134} = 21.162$, $P < 0.001$; $F_{14,134} = 14.494$, $P < 0.001$; observed and extrapolated, respectively), exponential Shannon entropy ($q = 1$; $F_{14,134} = 11.560$, $P < 0.001$, $F_{14,134} = 2{,}795.980$, $P < 0.001$; observed and extrapolated), and inverse Simpson index ($q = 2$; $F_{14,134} = 11.017$, $P < 0.001$, $F_{14,134} = 202.130$, $P < 0.001$; observed and extrapolated). Grazing, however, did not affect measures of native plant diversity, with the exception of observed species richness ($q = 0$), in which the effect of grazing on species richness depended on year ($F_{28,134} = 1.897$, $P = 0.009$). Overall, diversity metrics $q = 0$, 1, 2 measured at the plot level were highly correlated (Appendix S1: Fig. S1). We were able to measure species richness with greater precision than other diversity metrics by sampling subplots in a structured manner. When subplots were treated as samples nested within plots, the effect of grazing on native species richness again depended on year ($F_{28,134} = 1.793$, $P = 0.007$; Fig. 2) as was observed in plot-level estimation of species richness; however, a statistically significant main effect of grazing was also detected ($F_{2,134} = 4.637$, $P = 0.012$) in addition to the main effect of year ($F_{14,134} = 79.329$, $P < 0.001$). The interactive effect appears to be driven by species richness in the high-intensity grazing treatment, which varied in response to interannual differences to a greater extent relative to the other treatments. When high-intensity grazing is removed from the model, main effects of grazing

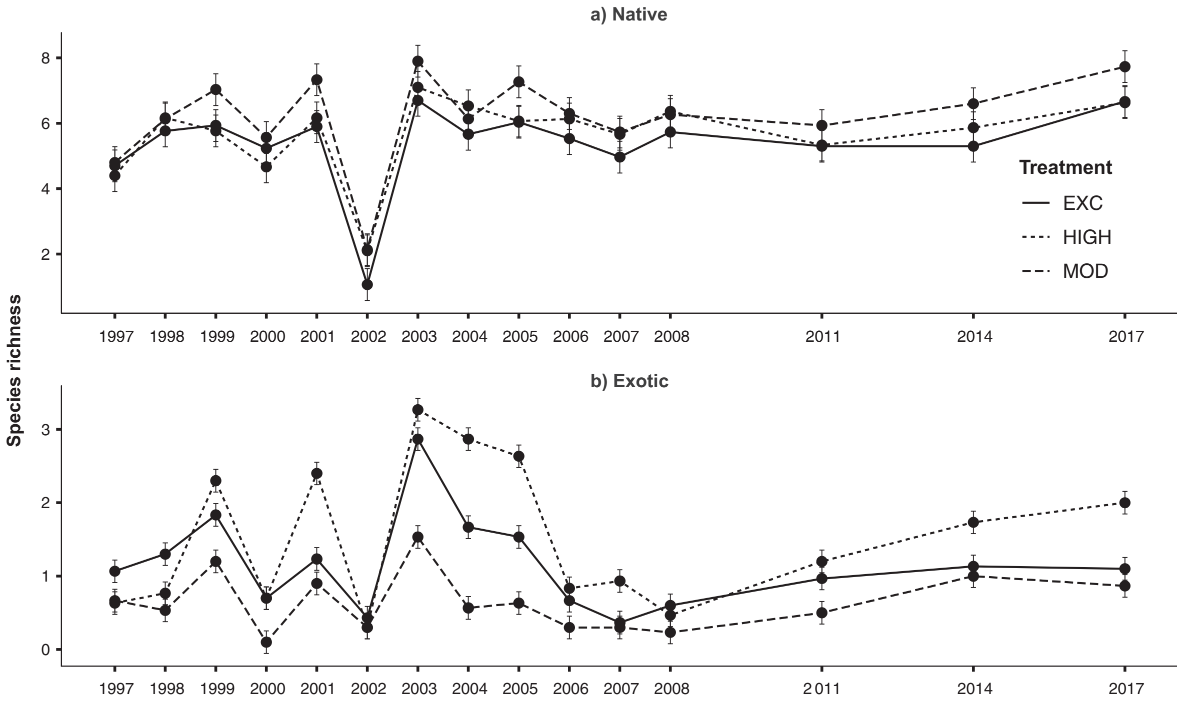

FIG. 2. (a) Native species richness and (b) exotic species richness varied by grazing treatment through time. Values are mean ± SE. The *y*-axes for native and exotic species are on different scales, since native species were more abundant in the system. In 1997, the pretreatment year, native species richness did not differ among treatments, but exotic species richness was higher in the exclosure (EXC) plots by chance. By 2000, moderately grazed (MOD) plots had significantly higher native species richness relative to exclosure and high-intensity grazing (HIGH) plots, and maintained higher levels of richness relative to one or both of these treatments in most years. In terms of exotic species richness, generally, moderate-grazing plots had the fewest exotics and the high-intensity grazing plots the most, while exclosure plots possessed numbers of exotic species intermediary to both grazing treatments.

($F_{2,134}$ = 5.115, P = 0.032) and year ($F_{14,134}$ = 22.574, P < 0.001) are still apparent, but not the interaction ($F_{28,134}$ = 0.940, P = 0.516). Regardless of whether the high-intensity grazing treatment was included in the model, native species richness varied dramatically among years, reaching a low in 2002 when an extreme drought occurred (Table 1), but rapidly rebounding to pre-2002 levels the following year (Fig. 2). Generally, native species richness was higher in the moderate grazing treatment, relative to the exclosure and the high-intensity grazing treatment (Fig. 2).

We also examined changes in exotic species richness using data collected at the subplot level. As in the case of native species, exotic species richness varied through time ($F_{14,134}$ = 502.320, P < 0.001; Fig. 2). Again, the effect of study year on exotic species was likely driven by climate and depended on grazing treatment ($F_{28,134}$ = 9.060, P < 0.001; Fig. 2). In the drought year, 2002, exotic species richness across all grazing treatments was considerably reduced from the previous year. Following this drought, however, exotic species richness reached a zenith across all grazing treatments, though the magnitude of increase varied by treatment. Differential rates of increase among treatments resulted in nearly twice the exotic species richness in the exclosure and high-intensity plots relative to the moderately grazed plots following the drought. Increase of exotic species richness was greatest in the high-intensity grazing treatment plots, in which exotic species richness increased by nearly 11 times the previous year's average, followed closely by increases in the exclosure plots of around seven times the 2002 average. In moderately grazed areas, exotic species richness increased at a significantly lesser rate, though this change represented a nearly fivefold increase from 2002 levels. While moderately grazed plots returned to pre-drought numbers of exotic species by 2004, the exotic species richness in the exclosure and high-intensity grazing plots remained elevated for an additional 2 yr before declining. Notably, however, exotic species richness returned to pre-drought levels for all treatments by 2006. Differential response through time among grazing treatments was again apparent in the latter part of the study (2008–2017), during which time the high-intensity grazing treatment increased in exotic species richness relative to both the moderate and exclosure plots. In general, moderate grazing plots exhibited the lowest exotic species richness ($F_{2,134}$ = 38.904, P < 0.001) and richness was less variable, whereas the high-intensity grazing plots had the highest exotic species richness and experienced pulses of exotics depending on, presumably, annual climatic conditions (Fig. 2).

In order to speculate on response of plant communities to increases in aridity projected by climate models, we related changes in native and exotic plant diversity to the Palmer Drought Severity Index (PDSI). An index of drought, PDSI, calculated as the departure of evaporative demand in the month of June from mean conditions at the study site, varied between a minimum of −6.6 to a maximum of 4.6 on a scale of −10 to 10, with negative numbers indicating drier conditions (Table 1). June PDSI appeared to be a driver of native, and to a lesser extent, exotic species richness in this system (Fig. 3). In the exclosure plots, relative dryness explained as much as 73.5% of the variation in native species richness with deviations from average conditions in the 1901–2000 base period, either drier or wetter, reducing richness (Fig. 3). Generally, across all grazing treatments, declines in native species richness were observed in response to increasing relative dryness. Notably, climate had decreasing predictive power as grazing intensity increased, amplifying variability of native species richness response to climate.

Community-level differences among grazing treatments through time

Given the effect of the 2002 drought on species richness, we narrowed our analysis to specifically examine community composition before and after the drought (years of analysis = 2001, 2003, pre- and post-drought years, and 2017, the final year of the study) for each grazing treatment. Pre- and post-drought plant communities were not significantly different in the cattle exclosure and moderately grazed plots ($F_{2,8} = 2.062$, $P = 0.105$, stress = 0.131; $F_{2,8} = 1.204$, $P = 0.332$, stress = 0.124, respectively; Fig. 4). However, drought did alter plant community composition in high-intensity grazing plots ($F_{2,8} = 2.826$, $P = 0.033$, stress = 0.149, Fig. 4). As of 2017, compositional differences persisted, and the 2017 plant community aligned in an intermediate position between pre- and post-drought years along NMDS axes, suggesting a slow return to pre-drought conditions. These differences in plant community composition in the high-intensity grazing treatment preceding and following the drought were driven by changes in abundance of both native and exotic species. Exotic species, *Sisymbrium altissimum* L. and *Bromus tectorum*, explained 15.7% and 4.1% of the variation between the 2001 and 2003 plant communities, respectively, and were the first and third most important species driving community differences over this time period. To put these changes into context, subplots contained an average of zero *S. altissimum* and 9.3 *B. tectorum* detections in 2001, with this number increasing to 116.7 and 39.7, respectively, in 2003. Over the long term, from 2001 to 2017, changes in the abundance of the native grass *Elymus elymoides* (Raf.) Swezey, which decreased from an average count of 147.7 to 30 detections per subplot in the final year of the study, explained 16.6% of the dissimilarities between communities (Table 2).

Changes in individual native species cover through time among grazing treatments

In order to better understand vegetative community change through time, we examined the role of grazing on individual species through time. Consistently across

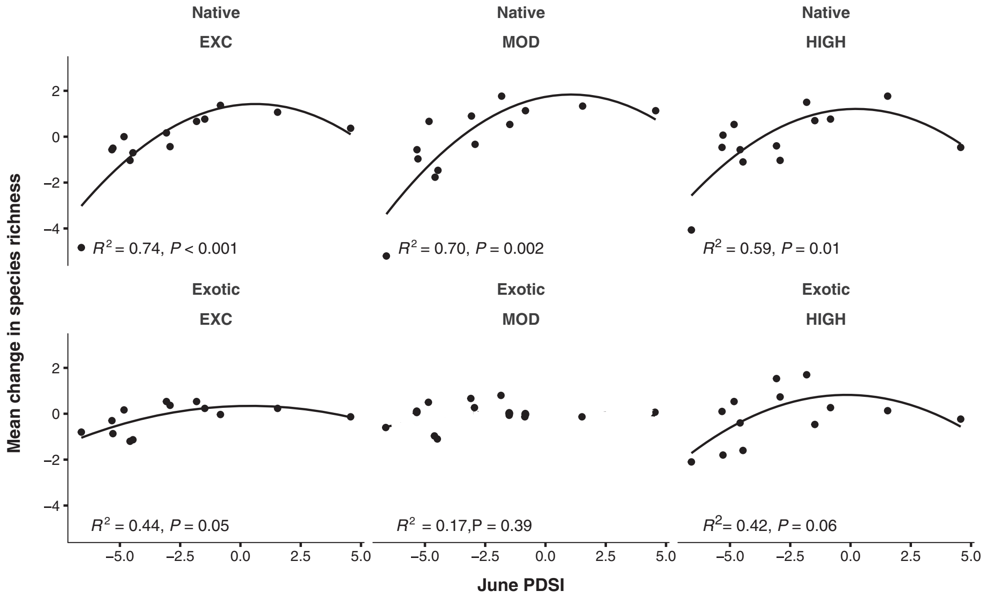

FIG. 3. The relationship between change in species richness from one growing season to the next and the Palmer Drought Severity Index (PDSI) in the month of June for native and exotic plant species in each grazing treatment.

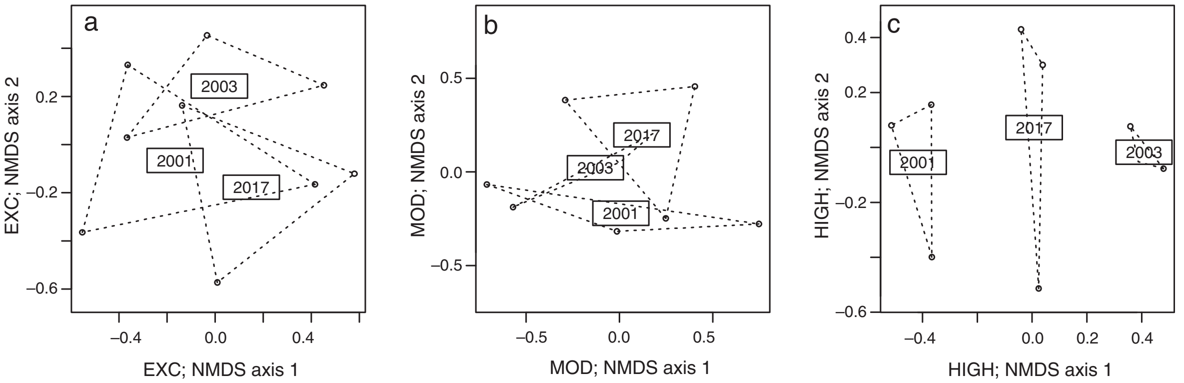

FIG. 4. Species composition for (a) exclosure (EXC), (b) moderate (MOD), and (c) high-intensity (HIGH) grazing plots in 2001, the year preceding the 2002 drought, 2003, the year immediately post-drought, and 2017, the final year of the study. The dotted line indicates the outer hull of the distribution of sites used in NMDS.

TABLE 2. Percent contribution to community dissimilarity of top 10 most influential species to differences in pairwise comparisons of 2001, 2003, and 2017 plant communities in the high-intensity grazing treatment.

		Mean richness			
Species	Comparison years	Time point 1	Time point 2	Contribution (%)	*P*
Sisymbrium altissimum	2001–2003	0	116.7	15.7	0.009
Elymus elymoides	2001–2003	147.7	51	13.1	0.039
Bromus tectorum	2001–2003	9.3	39.7	4.1	0.025
Pascopyrum smithii	2001–2003	89	97.3	3.4	0.8571
Artemisia caruthii	2001–2003	53.7	35.7	2.8	0.5644
Brassica tourneforti	2001–2003	15.3	0	2.1	0.021
Tragopogon dubius	2001–2003	0.7	14	1.8	0.017
Bouteloua gracilis	2001–2003	10	6.3	1.6	0.8741
Erigeron divergens	2001–2003	1.7	10.7	1.3	0.1009
Heliomeris longifolia	2001–2003	6.7	1.3	0.7	0.9141
Elymus elymoides	2001–2017	147.7	30	16.6	0.003
Heliomeris longifolia	2001–2017	6.7	49.3	5.9	0.1538
Pascopyrum smithii	2001–2017	89	125.3	5.5	0.1249
Melilotus officinalis	2001–2017	3.7	19.3	2.3	0.0609
Brassica tourneforti	2001–2017	15.3	0	2.2	0.006
Bouteloua gracilis	2001–2017	10	15.3	2.1	0.3057
Artemisia caruthii	2001–2017	53.7	67	1.9	0.8511
Bromus tectorum	2001–2017	9.3	14.3	1.6	0.991
Aristida purpurea	2001–2017	2.7	9.3	1.2	0.1089
Gutierrezia sarothae	2001–2017	0.3	5.7	0.8	0.0569
Sisymbrium altissimum	2003–2017	116.7	0	15.8	0.016
Heliomeris longifolia	2003–2017	1.3	49.3	6.2	0.038
Pascopyrum smithii	2003–2017	97.3	125.3	4.7	0.4306
Artemisia caruthii	2003–2017	35.7	67	4.2	0.011
Elymus elymoides	2003–2017	51	30	4	1
Bromus tectorum	2003–2017	39.7	14.3	3.5	0.1199
Melilotus officinalis	2003–2017	0.3	19.3	2.6	0.02
Tragopogon dubius	2003–2017	14	0.3	1.9	0.009
Bouteloua gracilis	2003–2017	6.3	15.3	1.8	0.7103
Erigeron divergens	2003–2017	10.7	1.7	1.3	0.0999

Note: P values indicate the probability of estimating an equal or larger average contribution to community dissimilarity in 1,000 random permutations of data.

treatments and through time, the dominant native species in this high-elevation grassland were the perennial C_3 grass species *Elymus elymoides* and *Pascopyrum smithii* (Rydb.) Barkworth & D. R. Dewey, the perennial C_4 grass *Bouteloua gracilis* (Kunth) Lag. Ex Griffiths, the perennial forb *Artemisia caruthii* Alph. Wood ex Carruth, and the annual forb *Heliomeris longifolia* (B. L. Rob & Greenm.) Cockerell. For all five of these native species, the effect of grazing on their percent cover depended on year (Fig. 5; Appendix S1: Table S2). *Elymus elymoides* declined markedly in the drought year, 2002, in both grazing treatments. To a lesser extent, *A. caruthii* and *B. gracilis* (moderate treatment only, exclosure and high-intensity plots exhibited consistently low *B. gracilis* cover) also appear to have been negatively impacted by drought conditions, with proportion vegetative cover of these species declining in the post-drought year, 2003. Unlike the other dominant grasses in this system, *P. smithii* cover increased in 2002 in the HIGH grazing treatment and was unaffected by drought in the MOD or EXC treatments. Indeed, we begin to observe divergence of the high-intensity grazing treatment from the exclosure and moderate grazing treatments in the latter portion of the study in terms of the percent cover of *P. smithii* and *A. caruthii,* with *P. smithii* occurring in consistently higher proportions and *A. caruthii* in lower proportions in the high-intensity grazing treatment relative to the exclosure and moderately grazed plots. Another notable pattern, the annual plant species, *H. longifolia*, which occurred in relatively low numbers in the years preceding the drought, rapidly proliferated following 2003, eventually comprising 40% of the total vegetative cover in the HIGH treatment by 2011.

Changes in individual exotic species cover through time among grazing treatments

Individual exotic species responded idiosyncratically to grazing through time. Among exotic species, the response of *Bromus tectorum*, *Melilotus officinalis* (L.) Lam., *Sisymbrium altissimum*, and *Tragopogon dubius* Scop. to grazing depended on year (Fig. 6; Appendix S1: Table S3). This was not the case for *Convolvulus arvensis* L. and *Lactuca serriola* L., though there was a tendency for the proportion of these species to be influenced by grazing alone (Appendix S1: Table S3). *Bromus inermis* Leyss., *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Linaria dalmatica* (L.) Mill., and *Poa pratensis* L. were observed in this system in surveys at the 10–1,000 m^2 plot level but occurred in such low frequencies at the 1-m^2 plot level as to render the data unanalyzable. Rather than persisting continuously in appreciable quantities, the proportion of exotic species increased in pulses and then returned to near 0 levels across all species and all grazing treatments. During expansion events, the rate of increase in proportion of vegetative cover occupied by exotics was greatest in the high-intensity treatment plots for all exotic species, except for *M. officinalis*, for which coverage peaked in the exclosure plots. Moderately grazed plots consistently contained the lowest proportion of exotic species relative to the exclosures and high-intensity grazing treatment plots. The 2002 drought affected the proportional abundance of some exotic species, but not others. *Bromus tectorum*, *S. altissimum*, and *T. dubius* increased following 2002, while *M. officinalis* remained virtually absent from the system. In 2011 and 2017, *M. officinalis* occupied around 15% of the vegetative cover in the exclosure plots, driving the pulse of exotics observed in the latter half of the study. While the average percent cover of exotics across 30 subplots reached as high as 30% of the total vegetative cover (*Sisymbrium altissimum*, HIGH treatment, Fig. 6), the spatial distribution of exotics was patchy, so that exotics were virtually absent in some plots, but occurred in quite high quantities in others. For instance, *B. tectorum*, *M. officinalis*, *S. altissimum*, and *T. dubius* comprised up to 75%, 79%, 74%, and 23% of the total vegetation of individual 1-m^2 plots, respectively.

Discussion

Grazing impacts in semiarid systems

Moderate levels of grazing had an overall positive effect on native species richness (q = 1) in this semiarid grassland, though we did not detect an effect on other diversity metrics (q = 1 and 2); a pattern observed in other grazing studies (Lyseng et al. 2018). Species richness weights rare and common species equally, as opposed to exponential Shannon entropy and inverse Simpson, which incorporate a measure of evenness and are therefore more sensitive to changes in abundant species. Given this, species richness measures may capture grazing impacts when such effects manifest primarily in the gain or loss of rare species. Notably, when species were analyzed individually, grazing did alter cover of common species in this system, perhaps indicating that subsampling increased precision and reduced statistical noise for richness and cover measurements, thus permitting detection of grazing effects on these metrics.

Plots that experienced moderate levels of grazing exhibited consistently higher native and lower exotic species richness relative to plots exposed to high-intensity grazing and from which cattle were excluded. Following the 2002 drought, plant communities in the moderate grazing treatment were resilient, native and exotic species richness quickly returning to pre-drought levels. Other studies conducted in semiarid grasslands support these findings, either documenting positive effects of moderate levels of grazing on native plant diversity (reviewed in Jones 2000) and drought resilience (Sprinkle et al. 2006), or little or no increase in diversity following grazing cessation (Chew 1982, Valone et al. 2002); though grazing impacts in these systems appear to be highly site specific (Jones 2000). In productive, mesic systems, an intermediate level of disturbance is presumed to maintain diversity by limiting competitive exclusion of rare species by species that attain dominance under stable environmental conditions (Milchunas et al. 1988, Cingolani et al. 2005, Yuan et al. 2016). In arid and semiarid grasslands, particularly those that are not believed to have evolved over long time scales in tandem with large vertebrate herbivores, grazing that exceeds low levels is predicted to decrease diversity

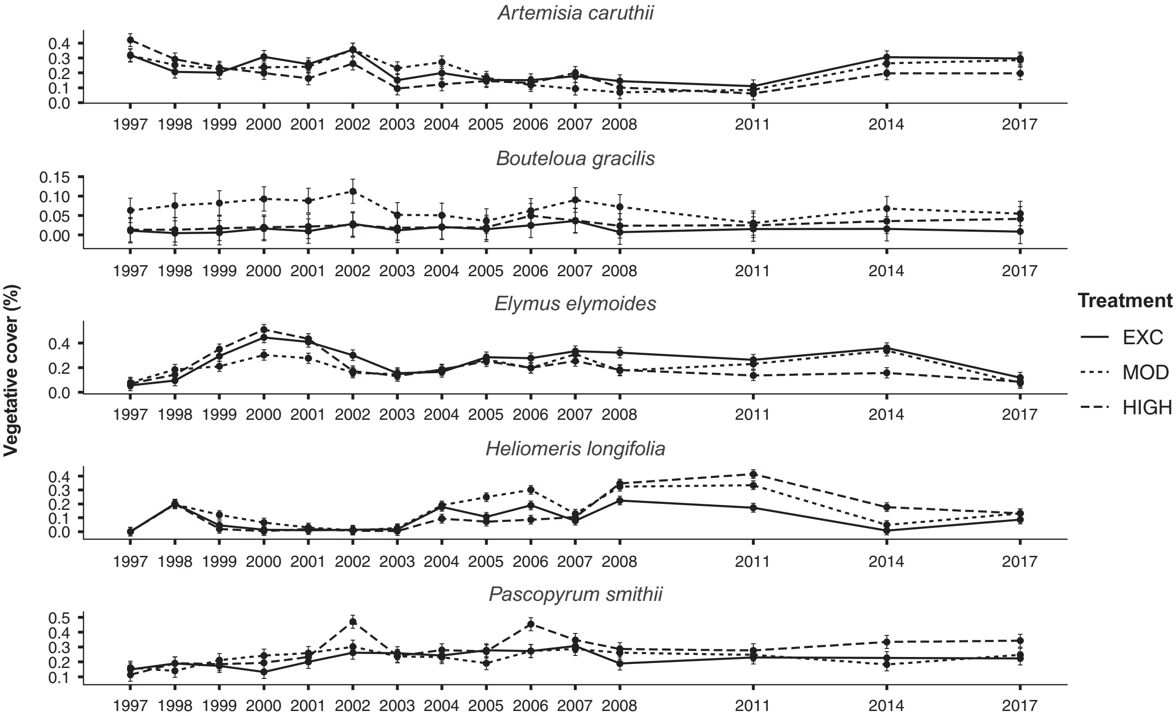

FIG. 5. Response of the five most common native species in in this grassland to grazing from 1997 (pretreatment) to 2017. Values are mean ± SE. *Artemesia caruthii* is a perennial forb; *Bouteloua gracilis* is a perennial C_4 grass; *Elymus elymoides* and *Pascopyrum smithii* are perennial C_3 grasses; *Heliomeris longifolia* is an annual forb. The *y*-axes for individual species are on different scales, since some species were more abundant in the system.

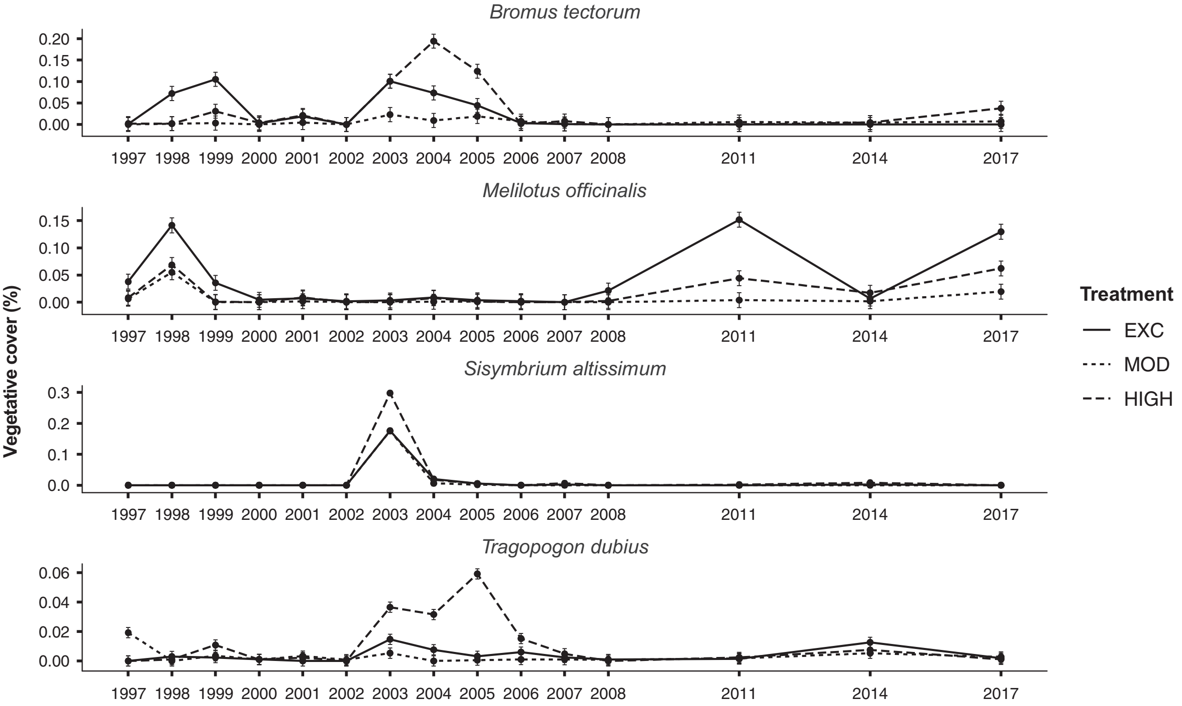

FIG. 6. Response of exotic species in this grassland to grazing from 1997 (pretreatment) to 2017 (±SE). The effect of grazing on cover of exotic species, *Bromus tectorum*, *Melilotus officinalis*, *Sisymbrium altissimum*, *Tragopogon dubius*, varied through time. The *y*-axes for individual species are on different scales, since some species were more abundant in the system.

(Milchunas et al. 1988). As no universal scale for grazing intensity has been established, it is difficult to place our study system in the context of Milchunas et al.'s grazing intensity–diversity relationships. However, cattle grazing at current levels in our system, in combination with grazing by wild ungulates, whose populations have expanded due to development of surface water sources, likely exceeds pre-European settlement grazing pressure (Schwinning et al. 2008). Notably, accurately characterizing prehistoric coevolutionary relationships between grassland communities and herbivorous megafauna may be an impossible endeavor, with some suggesting that the intermountain west was likely subjected to similar grazing pressures as elsewhere in the continental United States (Burkhardt 1996).

One explanation for the surprising tolerance of this and other semiarid grasslands to grazing is that plant traits that confer fitness in arid environments, such as small stature and drought deciduous leaves, also provide plants with a greater ability to avoid or tolerate herbivory than that predicted by Milchunas et al. (1988; Coughenour 1985, Adler et al. 2004, Sprinkle et al. 2006). A second explanation is that the introduction of vast numbers of domesticated livestock by European settlers in the 19th century may have favored the assemblage of plant communities more tolerant of grazing (Mack and Thompson 1982, Betancourt and Davis 1984, Westoby et al. 1989, Cingolani et al. 2005, Schwinning et al. 2008). Thus, grasslands in the semiarid west may have previously transitioned to an alternative state that differs from pre-European settlement plant communities, but is stable through time and resilient to grazing. Indeed, analyses of plant material preserved in packrat middens suggest a decline in species particularly palatable to livestock, such as winterfat (*Krascheninnikovia lanata*) and ricegrass (*Oryzopsis hymenoides*), with a concomitant increase in less palatable, better-defended species, like snakeweed (*Gutierrezia sarothrae*), rabbitbrush (*Ericameria nauseosa*), Russian thistle (*Salsola tragus*), and cheatgrass (*Bromus tectorum*), following European settlement of the western United States (Schwinning et al. 2008, Fisher et al. 2009). Cingolani et al. (2005) built on previous theory, suggesting that systems with short evolutionary grazing histories were less resilient to grazing, and hence, more prone to irreversibly transition to alternative vegetation communities and structure. Perhaps, contemporary grazing in this grassland provided an overall positive effect to native plant diversity via the same mechanism observed in systems with long evolutionary grazing histories: moderate levels of grazing freed resources, likely water and soil nutrients, by removing abundant species, and preventing competitive exclusion of rare species. Generally, we observed the greatest diversity and cover of exotic species and annual species (e.g., *Heliomeris longifolia*) in the high-intensity grazing treatment following the 2002 drought, further supporting literature that suggests that intensive grazing will advantage weedy species adapted to high levels of disturbance (Coughenour 1985, Milchunas et al. 1988, Adler et al. 2004).

While these findings suggest that livestock grazing, at intermediate levels, may be an important component of managing grassland plant communities for enhanced diversity and stability in this region (discussed further herein), grazing methodology for achieving this outcome requires further investigation. While targets for biomass removal remained constant in this study, these targets were met by varying both the density of cattle in a plot as well as grazing duration. Future research detangling the effects of cattle density and grazing duration on grassland biodiversity could further improve management practices. We present findings from a single grassland in northern Arizona. Examining among-site variation in ecological impacts of different levels of biomass removal would aid land managers in setting critical upper and lower bounds on grazing intensity in the southwestern United States and permit the development of generalizable recommendations for grazing management in semiarid grasslands. Finally, the observed effect may differ depending on livestock type and their specific dietary preferences (Li et al. 2017).

Climate and grazing impacts on vegetation

Grazing intensity and climate interacted to shape plant communities. High-intensity grazing increased variability of grassland response to interannual climatic variation in terms of both native and exotic species richness and overall community composition. In years that appeared to favor the expansion of exotic species (e.g., 1999, 2001, 2003, 2014; Fig. 2), exotic species richness in the intensively grazed plots increased more compared to the response within moderately grazed and ungrazed plots. While the number of exotic species consistently returned to low baseline levels following expansion events in the first half of the study, exotic richness has remained elevated in the high-intensity plots relative to other grazing treatments for the last three censuses (2011–2017). It is still unclear whether observed higher exotic richness represents a permanent change in community composition following 2002, or whether it is a transitory response. Droughts and other extreme weather events have been demonstrated to favor exotics by reducing resistance of the native plant community to invasion, sometimes producing soil-mediated legacy effects on vegetation that persist even when rainfall returns to normal levels (Jiménez et al. 2011, Diez et al. 2012, Meisner et al. 2013). However, abundance of exotic species in this system that proliferated following the 2002 drought, namely cheatgrass (*B. tectorum*), tumble mustard (*S. altissimum*), and yellow salsify (*T. dubius*), returned to and remains near zero with the exception of yellow sweet clover (*M. officinalis*), which has increased in recent years. The increase in *M. officinalis* principally occurred in the exclosure plots, likely because, as a preferred forage species, *M. officinalis* abundance was depressed by grazing pressure in the grazed plots (Currie et al. 1977).

Overall, this grassland has demonstrated remarkable resilience following invasion by species like *B. tectorum*, a species notorious for attaining dominance in other western grasslands (Mack 1981, Rimer and Evans 2006, Sperry et al. 2006, Bradley 2009). One explanation for observed resilience may be this site's robust perennial plant populations, which typically comprise 50–75% of the total plant cover, and has been shown to be the single most important factor in predicting resistance to *B. tectorum* invasion (Bradford et al. 2006, Chambers et al. 2007, 2014, Condon et al. 2011). There is some evidence that the perennial plant community may be deteriorating in the high-intensity grazing plots, where there has been a reduction in squirreltail (*E. elymoides*), a native perennial C_3 grass, and a concomitant increase in annual species, most notably the native species, longleaf false goldeneye (*H. longifolia*) and the nonnative species, yellow sweet clover (*M. officinalis*). This reduction in a native perennial grass, in combination with exotic species persisting in low numbers, may allow for the rapid expansion of nonnative species during future drought events.

Climate certainly appears to drive grassland response to grazing (Figs. 3, 4), but predicting plant community dynamics under future climate conditions in complex systems is challenging. While overall drier conditions negatively affect both native and exotic species, the impact of aridity on nonnative species appears to be less severe, and thus increasing aridity may favor exotic expansion events like that observed following the 2002 drought. Generally, climate change is projected to favor invasive species, which are often characterized by high phenotypic plasticity. Such plasticity allows exotics to persist in a dynamic climate under conditions that may exceed the range of climatic variation tolerated by native species (Willis et al. 2010, Davidson et al. 2011). Critically, stochastic events, like the 2002 drought, have the potential to interact synergistically with grazing to rapidly transform grassland communities in ways not predicted based on past climate–community relationships and to produce lasting effects on species composition and abundance.

Climate change in rangelands; implications for management

Native and exotic species richness varied considerably from year to year, presumably in response to climatic variation. When change in native species richness was regressed on a metric of drought, relative dryness explained approximately 73% of the variation in diversity in the exclosure plots when the post-year drought, 2003, was excluded from the data set. This suggests that, in general, drier conditions may be expected to reduce native species richness, though relative dryness explained less variation in the grazing treatments (particularly in high-intensity grazing plots) and was a generally poor predictor of exotic species richness. In semiarid systems, stochastic weather events, particularly droughts, which are projected to increase as a consequence of climate change (IPCC 2013), may be as important determinants of plant community composition as mean changes in precipitation and temperature. In this study, for instance, the 2002 drought precipitated an increase of exotic species diversity and incidence in intensively grazed grasslands, altering community composition to the present day. Predicting precise outcomes of increasing drought frequency is challenging, however, as extreme events can shape plant communities in unexpected ways that are not simple extrapolations of past vegetation–climate relationships.

Generally, we observed that moderate grazing maintained the highest levels of native species richness, the lowest levels of exotic species richness, and plant communities robust to the ecological impacts of drought. Adopting grazing strategies that promote resilience to climatic change may prevent erosion of native species diversity, while deterring the expansion of invasive species within semiarid systems. Critically, high-intensity grazing may select for disturbance-adapted species, and hasten the spread of invasive or weedy species. While the high-intensity treatment in this experiment exceeded typical levels managed for in this region, this intensity level was not incongruent with recommendations of holistic management and likely occurs at grazing hotspots within the landscape (e.g., at water sources). In this way, areas that experience intense biomass removal may act as points of establishment for invasive species, even in cases in which managers maintain stocking rates at moderate levels. Land managers interested in preventing nonnative species spread should target invasive species control efforts in areas of high-intensity grazing to prevent nonnative species establishment and spread to other pastures. Grazing management in a dynamic and directionally changing climate must be adaptive and responsive to field conditions (Jakoby et al. 2015). Specifically, stocking rates should be reduced in drought years to prevent conversion to exotic dominated grassland plant communities. While reduction of stocking rates may result in short-term economic losses, these losses will likely be recouped through enhanced long-term stability of grazing systems.

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SUPPORTING INFORMATION

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