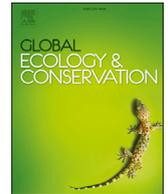




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Original Research Article

# Complex response of vegetation to grazing suggests need for coordinated, landscape-level approaches to grazing management

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## ABSTRACT

Management of domesticated ungulates on grasslands has the potential to affect ecosystem function at landscape to global scales. In the southwestern United States, introduction of livestock in the 1800s corresponded with grassland degradation and dramatic shifts in vegetation, including the rapid spread of invasive plant species. In contemporary grasslands, however, evidence increasingly suggests that responsible grazing may enhance plant diversity in the region, though positive effects on diversity may or may not offer corresponding benefits to ecosystem function. Here, we examined the effects of grazing on land cover and functional composition of a semiarid grassland over a 20-year period. We found that high intensity grazing increased exposed soil and shifted community composition toward a greater proportion of annual and exotic species. This was particularly apparent following a severe drought event that initiated a significant loss of perennial plant cover, especially forbs, and was followed by a nearly 4-fold expansion of exotic species. Plots that were grazed at moderate levels consistently exhibited the lowest proportion of exotic species and were similar in functional group composition to enclosure plots. However, moderate grazing did increase soil exposure relative to enclosure plots. These findings suggest that moderate grazing could provide benefits to grassland ecosystem diversity and correlated ecosystem services like invasive species control and pollination services, while simultaneously increasing erosion, reducing water infiltration and altering nutrient cycling, due to increased soil exposure and disturbance. The potential for grazing to exert antagonistic effects on ecosystem services, depending on site conditions and grazing intensity, suggests that livestock management decisions should be tailored to individual management and conservation goals that address the inherent spatiotemporal variability of arid grasslands.

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## 1. Introduction

European introduction of domesticated livestock in semiarid regions of the western United States in the 1800s was associated with large-scale, pervasive alterations in ecosystem structure, composition, and function (Fleischner, 1994; Mack, 1981; Schwinning et al., 2008). Evidence from pollen and vegetation preserved in packrat middens demonstrate a displacement of perennial grasses and species particularly palatable to livestock, such as winterfat (*Krascheninnikovia lanata*) and ricegrass (*Oryzopsis hymenoides*), with a concomitant increase in woody and/or better-defended species, like snakeweed (*Gutierrezia sarothrae*), rabbitbrush (*Ericameria nauseosa*), Russian thistle (*Salsola tragus*) and cheatgrass (*Bromus tectorum*), following European settlement of the western U.S. (Betancourt and Davis, 1984; DiTomaso, 2000; Fisher et al., 2009; Knapp, 1996; Mack, 1981; Schwinning et al., 2008; Van Auken, 2000). Prior to the 1800s, a paucity vertebrate herbivore fossils and lack of diversity and abundance of dung beetles, metrics which correlate with herbivore abundance, suggest southwestern grasslands experienced low grazing pressure (Betancourt and Davis, 1984; Schwinning et al., 2008). In present day, grazing remains an important disturbance in these systems; over 60% of the total land area in the Southwest is utilized as pasture (USDA, 2012), with an estimated 90% of semiarid grasslands managed for livestock grazing in some areas, such as the Colorado Plateau (Schwinning et al., 2008).

Classic grazing theory (i.e., Milchunas et al.'s 'Generalized theory of the effects of grazing on plant community and structure' and subsequent iterations) suggests that in dry, low productivity systems lacking a long evolutionary history with herbivores, like grasslands in arid and semiarid regions of the southwest, grazing should negatively impact native plant diversity (Milchunas et al., 1988; Milchunas et al., 1998; Milchunas and Lauenroth, 1993). This theory incorporates concepts from the Intermediate Disturbance Hypothesis, which posits that intermediate levels of disturbance prevents competitive exclusion of rare species, thus increasing biotic diversity. However, given a short co-evolutionary history with large herbivores, the tolerance of species within semiarid grassland systems is expected to be low, thus even low rates of grazing should result in diversity declines, due to attrition of grazing sensitive species (Milchunas et al., 1998; Milchunas and Lauenroth, 1993). Numerous studies conducted in contemporary rangelands, however, demonstrate neutral or positive effects of grazing on semi-arid grassland community diversity, despite herbivore densities exceeding pre-settlement levels (Alberti et al., 2017; Beck et al., 2015; Fensham et al., 2014; Jones, 2000). Cingolani et al. (2005) incorporated state-and-transition modeling concepts into Milchunas et al.'s generalized theory, suggesting that systems with short evolutionary grazing histories were less resilient to grazing, and hence, prone to irreversibly transition to alternative vegetation communities and structure. Hence, grazing may maintain diversity in contemporary southwestern ranges, since these systems fundamentally differ from pre-colonial rangelands and represent grazing tolerant species assemblages; a hypothesis supported by palynological data that shows shifts in vegetation following domesticated livestock introduction (Betancourt and Davis, 1984; Fisher et al., 2009; Knapp, 1996; Mack, 1981; Schwinning et al., 2008; Van Auken, 2000).

Such grazing theories provide a framework for understanding grazing impacts on taxonomic diversity, but may or may not apply to functional diversity. Livestock undoubtedly select for particular plant traits, both directly, through consumption and trampling of plant material and indirectly, through changes in nutrient and water availability that result from redistribution of nutrients (e.g., grazing in combination with waste elimination) and alterations to the physical environment (e.g. soil compaction, erosion). Thus, grazing may simultaneously increase taxonomic diversity, while reducing functional diversity as plant communities shift in composition towards a greater abundance of species possessing traits that promote avoidance or tolerance of herbivory, disturbance, or the physical environment created by livestock (Carmona et al., 2012; De Bello et al., 2006; Eldridge et al., 2016; Hanke et al., 2014). Indeed, grazed systems appear to include greater proportions of plants characterized by short stature, prostrate growth form, rosette or stoloniferous habit, annual life history, high light requirement for growth and survival, and early season seed production (Díaz et al., 2007; Pakeman, 2004). Moreover, grazing consistently increases spatial heterogeneity of vegetation (Adler et al., 2001), exposes bare soil (Hanke et al., 2014; Jones, 2000), and damages biocrusts (Belnap et al., 2009; Eldridge et al., 2016; Neff et al., 2005), potentially increasing rates of soil erosion and leading to nutrient and evaporative moisture loss. Taken together, such grazing-mediated changes in plant composition, cover, and heterogeneity may alter ecosystem function and compromise key services, such as water purification, erosion control, carbon sequestration, and nutrient cycling (Costanza et al., 1997). Given the spatial extent of grasslands, which cover more than a quarter of the terrestrial surface of the earth, determining the full suite of ecological impacts of grazing and managing grazing to maximize ecosystem function emerges as a critical goal, which crosscuts issues of ecosystem integrity and food security (Godfray et al., 2010; Herrero and Thornton, 2013).

Our 20-year study of grazing impacts on plant diversity in a high elevation, semiarid grassland found that cattle grazing at moderate levels increased native species richness, while decreasing exotic species richness, relative to both grazing cessation and high intensity grazing treatments (Loeser et al., 2007; Souther et al., 2019). While moderate-grazing levels had an overall positive effect on plant diversity, it remains unclear how grazing affects the relative abundance of broad plant functional classifications and land cover type in this grassland. Here we expand our understanding of the ecological impacts of grazing beyond plant diversity response, asking: How does grazing influence ground cover and vegetative functional groups through time? In particular, we examine grazing impacts on exotic species, contrast results with plant diversity findings, and interpret results in the context of ecosystem function under drier, more variable climatic conditions projected to occur as climate changes.

## 2. Methods

### 2.1. Study site

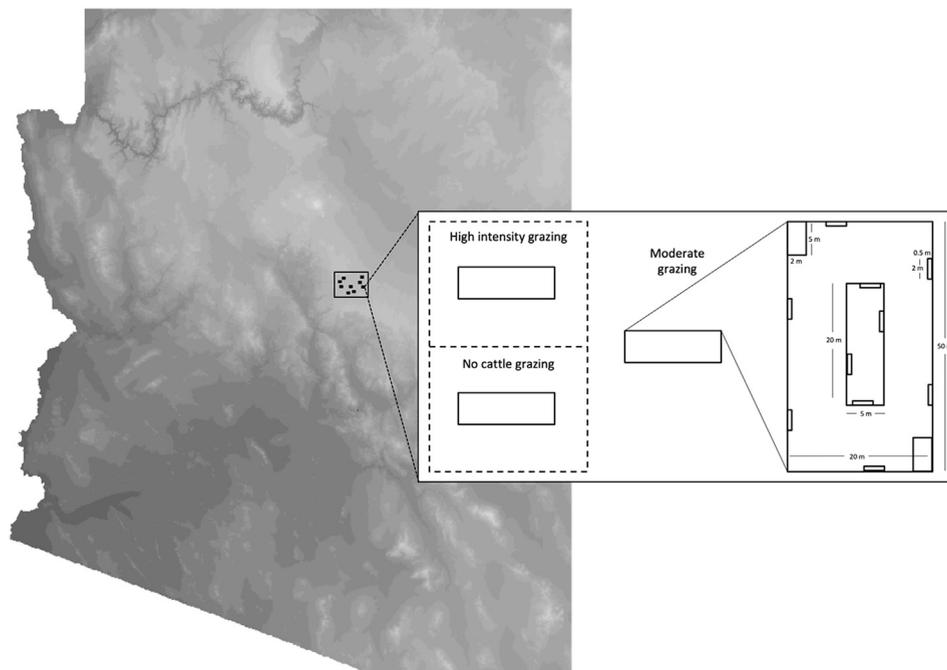
Plots were located in a high elevation (2160 m), semiarid grassland on the Colorado Plateau near Flagstaff, Arizona (Fig. 1). The study area is underlain by Vertisol soils, characterized as containing a high proportion of shrink-swell clay, which causes extensive mixing of the uppermost soil horizons. Vegetative communities at the site consisted principally of grasses and forbs, with few shrubs. Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forest surrounds the site, but trees do not occur within the study area. The 5 dominant plant species within the grassland include: *Pascopyrum smithii* (Rydb.) Barkworth & D. R. Dewey, *Artemisia caruthii* Alph. Wood ex Carruth, *Elymus elymoides* (Raf.) Swezey, *Bouteloua gracilis* (Kunth) Lag. Ex Griffiths, and *Heliomeris longifolia* (B. L. Rob & Greenm.) Cockerell.

### 2.2. Climate

In this region, interannual variation in precipitation is high (Table 1), with precipitation primarily occurring as winter snowfall or as summer monsoonal rainfall in approximately equal measure. In winter, precipitation arrives from the Gulf of Alaska and the Pacific Ocean, and during the summer, precipitation occurs in the form of monsoonal storms that arrive from the tropical Pacific (Pacific, Gulf of California, Gulf of Mexico). Current inter-annual variation in precipitation has been linked to La Niña and El Niño events and multi-decadal drought cycles linked to the Pacific Decadal Oscillation (Schwinning et al., 2008). Temperatures during the late Wisconsin (ca. 21,000–10,400 yrs. B.P.) were 7 deg C cooler than current temperatures (Anderson, 1993). As was the case globally, the region warmed during the Holocene (beginning ca. 10,400 year B.P.), when the Ponderosa pines forests were first observed in this region (Anderson, 1993). The years from 3000 to 1700 B.P. were the wettest in recent history (Polyak and Asmeron, 2001). Since that time, there have been periods of extreme drought, termed megadroughts that occurred in the 10th – 13th centuries (a.k.a. medieval droughts). The 19th and 20th centuries are generally characterized by anomalously high precipitation, though there have been notable multi-year droughts during this time (e.g., 1930's dustbowl, 1950's Southwest drought, and the 1980 and 1988 droughts) (Schwinning et al., 2008). Climate projections for the region indicate that drought events will increase in both frequency and severity (IPCC, 2013).

### 2.3. Grazing history

Analysis of desiccated dung specimens found in caves in the Colorado Plateau indicate the presence of megaherbivores (Pleistocene megafauna), including mammoths (*Mammuthus* sp.), bison (*Bison* sp.), Shasta ground sloths (*Nothrotheriops*



**Fig. 1.** This study was conducted near the southern border of the Colorado Plateau in north-central Arizona. Three sets of grouped plots representing three grazing levels, no grazing (EXC), moderate-grazing (MOD), and high intensity-grazing (HIGH), were randomly established across an actively-grazed grassland in 1997. Vegetation change through time was monitored within monumented modified-Whittaker plots.

**Table 1**

Climate conditions for all years in which plant surveys were conducted during the 20-year study period from 1997 to 2017. 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  $+$  (wet), for the historically driest month of the year, June. The year 2002 has been bolded and italicized to highlight the high temperatures and low precipitation that resulted in drought that growing season.

Year	Total annual precipitation (mm)	Annual mean maximum growing season temperature ( $^{\circ}\text{C}$ )	Annual mean minimum growing season temperature ( $^{\circ}\text{C}$ )	Mean maximum temperature in January ( $^{\circ}\text{C}$ )	Mean minimum temperature in January ( $^{\circ}\text{C}$ )	Mean maximum temperature in July ( $^{\circ}\text{C}$ )	Mean minimum temperature in July ( $^{\circ}\text{C}$ )	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
<b>2002</b>	<b>327.3</b>	<b>17.3</b>	<b>0.0</b>	<b>6.8</b>	<b>-7.9</b>	<b>29.1</b>	<b>13.0</b>	<b>-6.6</b>
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

*shastensis*), shrub-oxen (*Euceratherium collinum*), and Harrington's mountain goats (*Oreamnos harringtoni*); all, except the bison, becoming locally extinct around 11,000 years B.P. (Mead and Agenbroad, 1989; Meadi and Agenbroad, 1992). This follows the global pattern of extinction of megafauna during the late Pleistocene, attributed to rapidly changing climate in combination with human population expansion that resulted in habitat modification, disruption of megafaunal population connectivity, and over-harvesting (Cooper et al., 2015). Despite the presence of megafauna, scarcity of megafauna fossils and historical lack of *Onthophagus* dung beetles (a genus with ca. 34 species occurring east of the Rockies, where grasslands supported large numbers of herbivores) indicate that large herbivores occurred in low numbers (Mack and Thompson, 1982). Scarcity of permanent surface water is believed to have limited densities of smaller herbivores, like elk (*Cervus canadensis merriami*), pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). During the latter half of the 19th century, regional historic accounts indicate extensive grazing by domesticated cattle and sheep introduced by Europeans (Schwinning et al., 2008). While the precise grazing history of this particular site was not documented, there is no indication that this site would have differed from other grasslands in the region in terms of historical grazing pressure. Ranching remains an important livelihood today, though stocking rates are much lower than in the past (Schwinning et al., 2008). Development of springs and tanks as water sources for livestock also allowed undomesticated native herbivores, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and pronghorn antelope (*Antilocapra americana*), to increase in abundance concomitant with livestock introduction (Schwinning et al., 2008). These species occur at this study site and have access to all plots, though pellet counts indicate grazing by wild herbivores was similar among treatments (Loeser et al., 2007).

#### 2.4. Experimental design

In 1997, plots were randomly established across an active rangeland, positioned to capture representative areas of pasture (e.g., avoiding water sources), and an initial vegetation survey conducted to document pre-treatment conditions (Fig. 1). At the time plots were created, the stocking rate for this grassland was approximately 0.5 cow-calf pairs\*hectare<sup>-1</sup> for 14 days\*year<sup>-1</sup> (ca. 0.2 AUM\*ha<sup>-1</sup>) with a 50% biomass removal target (Loeser et al., 2007). This grazing management regime, which evolved from blending traditional, season-long rest-rotation techniques (Hormay and Evanko, 1958) with a more rapid rotation schedule inspired by the ranchers' exposure to holistic management (Savory and Butterfield, 1999), became the moderate grazing-level treatment (MOD); so-called because it is intermediate in intensity to complete grazing cessation and the high intensity treatment. We constructed a total of 6, 1-ha fenced areas. Three served as livestock enclosures to prevent cattle grazing (EXC), and 3 were enclosures, stocked to increase grazing levels above ambient conditions. Within the high grazing-level treatment (HIGH) plots, ranchers aimed to remove approximately 80% of the aboveground biomass in one short-duration, high impact event. This grazing regime is meant to mimic herding behavior, where impact is highly concentrated in space and time, followed by long periods (in our case 1 year) with little or no grazing. The stocking rate in HIGH plots was, on average, ca. 200 cow-calf pairs\*hectare<sup>-1</sup> for 12 h\*year<sup>-1</sup> annually, with grazing time never exceeding 24 h (ca. 3.3 AUM\*ha<sup>-1</sup>) (Loeser et al., 2007). The high intensity treatment implemented in this experiment exceeded typical levels managed for in this region. However, this intensity level was not incongruent with recommendations of holistic management and likely occurs at grazing hotspots within the landscape (i.e., at water sources). 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 any plots. Cattle breached one of the three enclosures twice during this 20-year period. However, in each case, the enclosure was grazed for no more than a 24-h period, resulting in a grazing intensity far below moderate levels.

A Modified-Whittaker plot design, which includes a series of subplots of exponentially increasing size nested within a large plot, was used to survey vegetation (Fig. 1) (Stohlgren et al., 1995). We surveyed three replicate 1000 m<sup>2</sup> plots per grazing treatment, within which were nested ten 1 m<sup>2</sup>, two 10 m<sup>2</sup>, and one 100 m<sup>2</sup> subplots. We used a 50-point frequency frame to estimate ground cover of the 10, 1 m<sup>2</sup> subplots. Vegetation surveys took place in July, prior to grazing, but following the onset of the summer monsoonal period, which delineates the growing season for many species in the region. We conducted surveys annually until 2008, when survey frequency was reduced to every 3 years.

## 2.5. Analyses

Using cover data collected in the 10, 1 m<sup>2</sup> subplots, we calculated percent ground cover as the number of sample points for each cover category (bare ground, vegetation, and litter) divided by the total number of frequency frame sample points. For vegetative classes examined in this study (perennial forb, perennial grass, annual forb, annual grass, native species, exotic species, C3 grasses, C4 grasses, and N-fixing legumes), we calculated percent cover (i.e., proportion of vegetation that consisted of each functional group/species) in an analogous way, but using the total sample points in which vegetation was observed as the denominator. In order to determine whether cover changed through time as a function of grazing treatment, we analyzed data using linear mixed effects models with grazing treatment, year, and grazing treatment\*year as fixed effects and subplot nested within block ( $n = 3$ ) as a random effect (R-package 'lme4', function 'lmer'). The error was structured to account for repeated sampling of subplots through time. Models were fit using Restricted Maximum Likelihood (REML) due to small sample size. When necessary, these data were arcsine square root transformed to improve normality. Tukey's Honestly Significant Difference (HSD) post-hoc analysis (R-package 'lsmeans') was used to test pairwise comparisons of grazing treatments.

We used multiple regression to determine if climatic factors drove interannual variation in vegetative cover detected in the analyses described above. In order to account for the dependency of plant cover on the vegetative state of the community the previous year, we calculated the change in cover from the previous survey year for each treatment as the dependent variable for all analyses. Thus, response variables included change in proportion bare ground, perennial grass, annual grass, perennial forb, annual forb, and exotic cover. Due to the relatively low abundance and variation of C3/C4 grasses and N-fixing species through time, we did not include these cover types in our analyses. Initial attempts to build statistical models to explore climate effects on vegetation using backwards and forwards 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 predictor variable in all models relating climatic variation through time to change in plant cover. The metric 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).

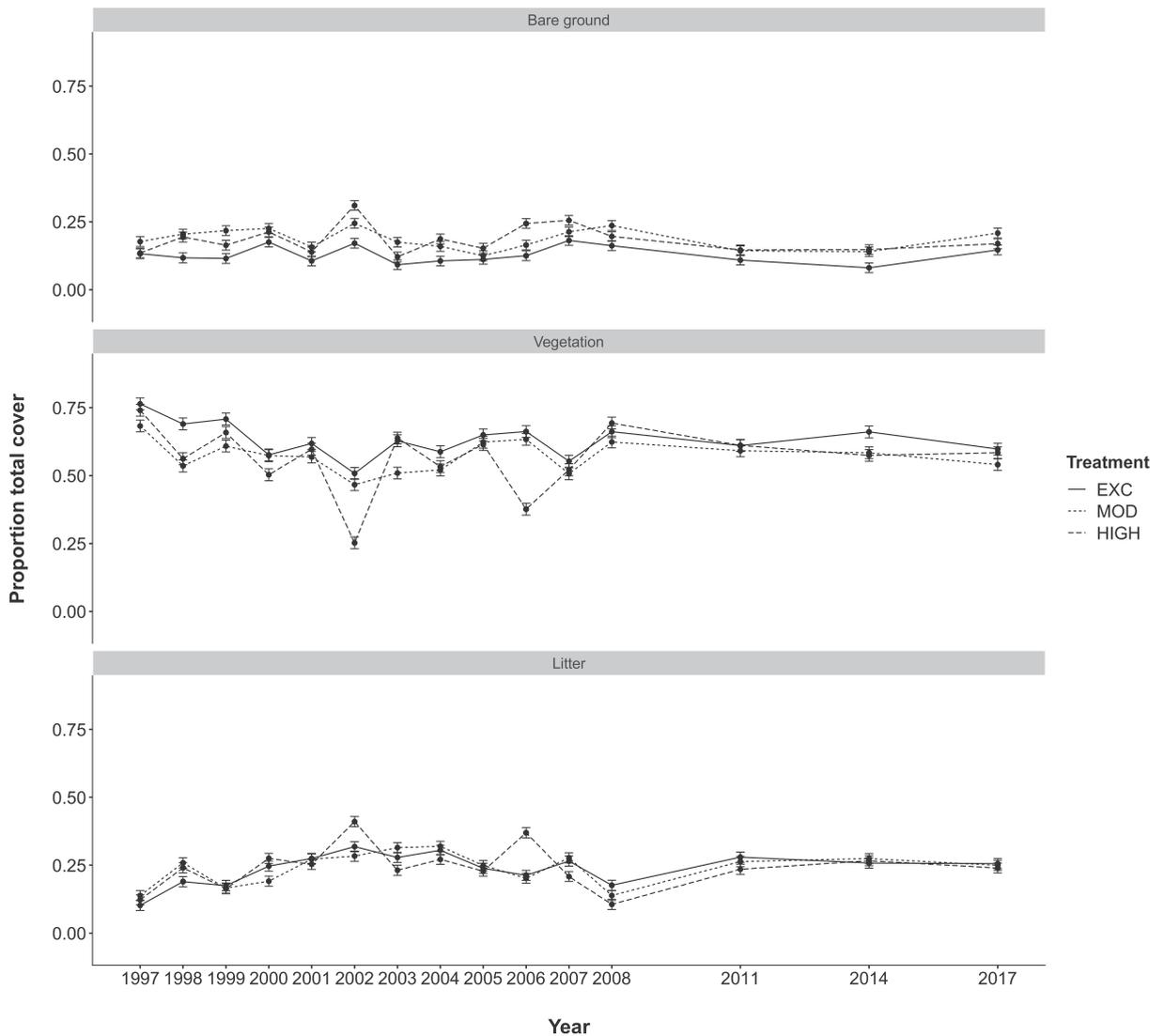
For each model, we explored both linear and polynomial fits. The 2002–2003 drought-recovery transition was an outlier for all treatment groups and was excluded from analyses. Given the unique effects of the drought, we wanted to examine the role of this stochastic climatic event in shaping vegetative communities. To do this, we classified years 1998, 1999, 2000, 2001 as pre-drought and 2003, 2004, 2005, 2006, 2007, 2008, 2011, 2014, and 2017 as post-drought and again used Generalized Linear Models (GLMs) to test for treatment by time period effects on various types of vegetative cover and native and exotic species richness; richness calculated as a simple count of the number of species. We parameterized all models to include main effects of grazing treatment and time period, averaging across blocks for each treatment, so that the unit of replication was a year. This design is necessarily unbalanced (4 pre-drought years, 9 post-drought years). Generalized Linear Models tolerate unequal sample sizes, though our likelihood of making a Type II error, stating that there are no differences among groups when in reality differences exist, is likely elevated due to small pre-drought sample size (Cnaan et al., 1997).

## 3. Results

### 3.1. Land cover response to grazing through time

The effect of grazing on the proportion of bare ground, litter, and vegetation depended on year ( $F = 3.2689$ ,  $p < 0.0001$ ,  $F = 6.186$ ,  $p < 0.0001$ ,  $F = 9.638$ ,  $p < 0.0001$ ; respectively; Fig. 2).

Notably, moderate and high intensity grazing treatments, which consistently possessed a greater proportion of bare ground relative to enclosure plots, did not differ from each other in proportion of bare ground and vegetative cover in most years. However, high intensity grazing plots increased in the proportion of bare ground to a greater degree relative to other treatments in drought years, particularly 2002 and 2006. The proportion of bare ground, vegetation, and litter in the high intensity grazing plots was twice as variable among years ( $\sigma^2 = 0.0027$ , 0.0148, 0.0063; respectively) relative to the moderate ( $\sigma^2 = 0.0014$ , 0.0034, 0.0035; respectively) and enclosure plots ( $\sigma^2 = 0.0010$ , 0.0042, 0.0033; respectively), which were the least responsive to environmental changes. To put this range of variation into context, the proportion of bare ground, averaged across blocks for each treatment, varied between 8.1 and 18.1%, 12.5 and 24.5%, and 12.1 and 31.1% for the enclosure, moderate, and high-intensity grazing plots, respectively. Generalizing across years, grazing influenced the proportion of bare ground ( $F = 7.5586$ ,  $p = 0.0009$ ), which was lowest in the enclosure plots, and the proportion of vegetation ( $F = 10.591$ ,  $p < 0.0001$ ), which was highest in the enclosure plots, but not the proportion of litter ( $F = 0.0647$ ,  $p = 0.9374$ ; Fig. 2). For all



**Fig. 2.** Proportion of total ground cover comprised by bare ground, litter, and vegetation for grazing treatments from 1997 (pre-treatment year) to 2017 (+/-SE).

ground cover types, there was high inter-annual variation in the proportion of bare ground, litter, and vegetation ( $F = 20.6064$ ,  $p < 0.0001$ ,  $F = 38.152$ ,  $p < 0.0001$ ,  $F = 43.573$ ,  $p < 0.0001$ , respectively; Fig. 2). The highest proportion of bare ground and lowest proportion of vegetation occurred in the drought year, 2002, for all treatments.

### 3.2. Shifts in plant functional groups

#### 3.2.1. Exotic species

The effect of grazing on proportion of native to exotic species depended on year ( $F = 8.1075$ ,  $p < 0.0001$ ; Fig. 3). Differential response of grazing treatments to annual conditions is clearly apparent following the 2002 drought, when the rate of increase in exotic plant cover was roughly twice as great in the high-intensity grazing plots relative to the moderate grazing treatments. Moderately grazed plots quickly returned to pre-drought exotic cover levels, while plant communities in the high intensity grazing treatment recovered more slowly. Interestingly, exotic species response in the enclosure plots was intermediate to that observed in the MOD and HIGH plots. In 2011, the proportion of exotics again increased in the enclosure plots, so that exotics comprised around 15% of vegetative cover, contrasted to the grazed plots in which exotic cover less than 5% of the vegetation. Across all grazing treatments, exotic cover reached its maximum in 2003, and was near zero in 2000, 2002, 2006, and 2007. Overall, moderately grazed plots contained the lowest proportion of exotics ( $F = 12.9851$ ,  $p < 0.0001$ ; Fig. 3).

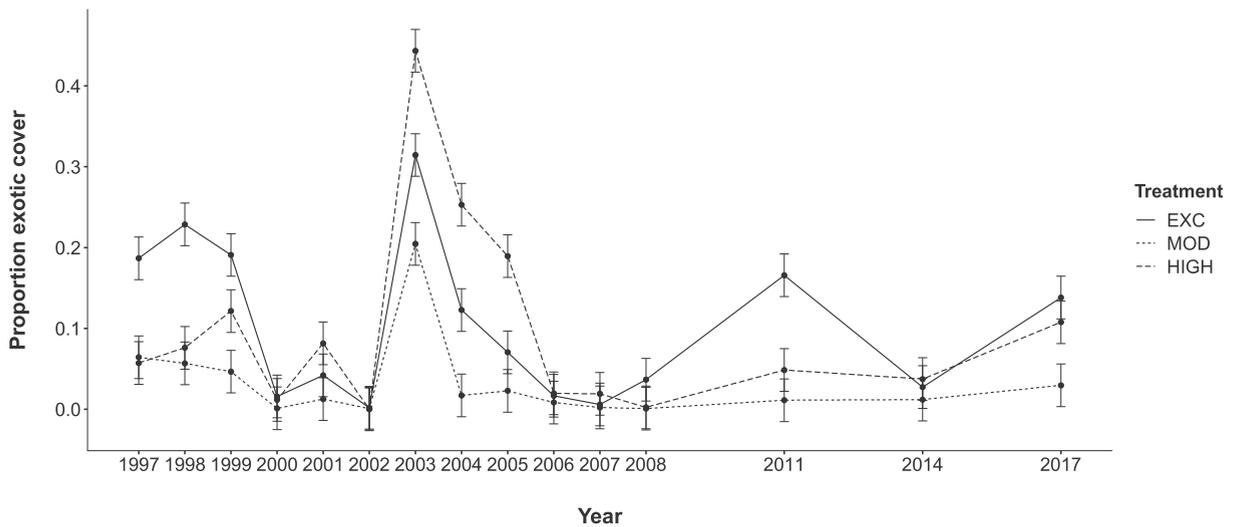


Fig. 3. Proportion of total vegetative cover consisting of exotic species for each grazing treatment from 1997 (pre-treatment year) to 2017 (+/-SE).

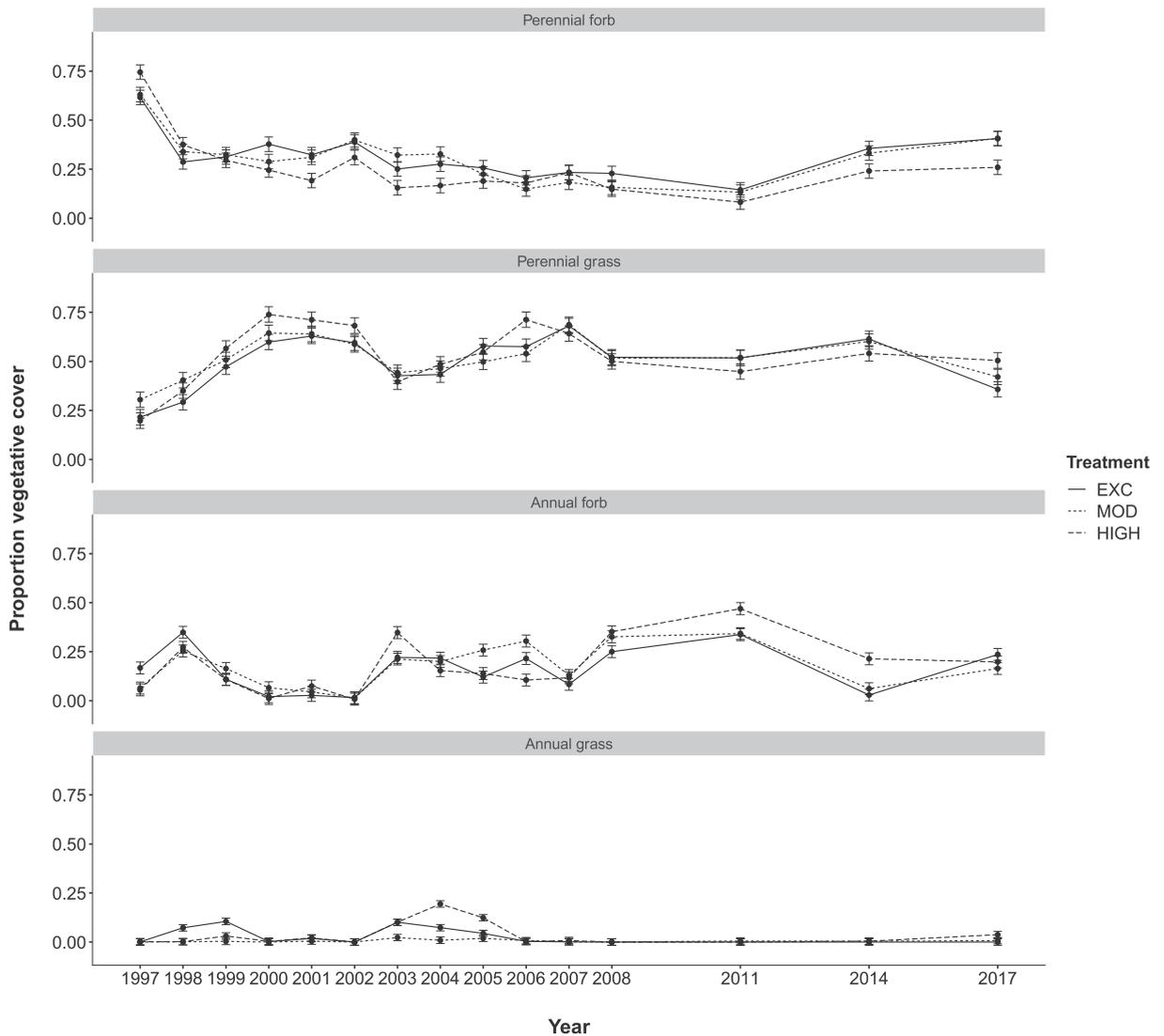
### 3.2.2. Growth form and life history

The effect of grazing on the proportion of annual and perennial forbs and grasses depended on year ( $F = 4.882$ ,  $p < 0.0001$ ;  $F = 3.258$ ,  $p < 0.0001$ ;  $F = 7.2799$ ,  $p < 0.0001$ ;  $F = 2.186$ ,  $p < 0.0004$ ; annual forb, perennial forb, annual grass, perennial grass, respectively; Fig. 4). Generally, this interaction appears to be driven by differences in the magnitude of response to inter-annual variation among grazing treatments, rather than differences in directionality of responses. For example, following the 2002 drought, the proportion of perennial herbs declined and the proportion of annual forbs and grasses increased at a greater rate in the high intensity grazing treatment relative to the moderate and enclosure treatments (Fig. 4). The percent cover of all vegetation types varied annually ( $F = 48.072$ ,  $p < 0.0001$ ,  $F = 59.871$ ,  $p < 0.0001$ ,  $F = 19.0291$ ,  $p < 0.0001$ ,  $F = 40.662$ ,  $p < 0.0001$ ; annual forb, perennial forb, annual grass, perennial grass, respectively; Fig. 4), with several notable patterns. For all vegetation types, interannual response of the vegetative cover appears more variable in the high intensity grazing treatments ( $\sigma^2 = 0.0180$ , 0.0238, 0.0034, 0.0227; annual forb, perennial forb, annual grass, perennial grass, respectively) relative to the moderate ( $\sigma^2 = 0.0118$ , 0.0161, <0.0001, 0.0106; annual forb, perennial forb, annual grass, perennial grass, respectively) and enclosure treatments ( $\sigma^2 = 0.0126$ , 0.0125, 0.0016, 0.0178; annual forb, perennial forb, annual grass, perennial grass, respectively).

Perennial grasses increased after the establishment of the experiment and comprised roughly 66% of the vegetative cover for 3 consecutive years, until, after the 2002 drought, the proportion of perennial grasses dropped to 42.2%, similar to the current proportion of perennial grass (42.8%). In general, years following the drought were characterized by a higher than average proportion of annual to perennial species, particularly in the HIGH grazing treatment. There are two pulses of annual grasses, one occurring from 1998 to 1999 and the other from 2003 to 2005; the latter period of annual grass expansion followed the 2002 drought event and the former occurred after the 3rd driest year of the study, 1997. The proportion of annual forbs in the system was highly variable; the highest proportion occurring in 2011 when annual forbs comprised nearly 50% of the vegetation in the high intensity grazing plots and over a quarter of the vegetation overall. Grazing alone did not explain variation in annual forb or perennial grass cover ( $F = 0.4950$ ,  $p = 0.6111$ ;  $F = 0.6080$ ,  $p < 0.5469$ ; annual forb, perennial grass, respectively; Fig. 4), but did shape relative abundance of perennial forbs and annual grasses ( $F = 3.187$ ,  $p = 0.0463$ ;  $F = 5.9268$ ,  $p = 0.0004$ ; perennial forb, annual grass, respectively; Fig. 4), with the high intensity grazing treatment generally possessing greater proportions of annual grasses and lower proportions of perennial forbs than the other treatments.

### 3.2.3. Photosynthetic system

The effect of grazing through time on the proportion of C3 to C4 grasses depended on year ( $F = 1.9402$ , 0.0024; Fig. 5). When plots were established in 1997, the moderate grazing plots had a much lower proportion of C3 to C4 grasses, relative to the high intensity grazing plots and the enclosures. This chance difference gradually lessened through time, particularly following the 2002 drought, as the proportion of C4 grasses decreased in the moderate plots. There was a tendency for grazing alone to affect the ratio of C3 to C4 grasses ( $F = 3.0136$ ,  $p = 0.0544$ ). This difference among grazing treatments is, at least in part, driven by the initial state of the moderate grazing plots, which contained the highest proportion of C4 grasses, but is also explained by consistently low C4 grass cover in the enclosure plots. Climate alters the proportion of C3 to C4 grasses through time ( $F = 2.3903$ ,  $p = 0.0027$ ). For high intensity grazing and enclosure plots, the lowest proportion of C4 grasses occurred in 1999, the coolest year of our study (Fig. 5, Table 1). For the moderate grazing plots, the proportion of C4 grasses was lowest in 2005, the wettest growing season of this study period (Table 1).



**Fig. 4.** Variation in proportion of vegetative cover consisting of plant functional groups, perennial forbs, perennial grasses, annual forbs, and annual grasses, from 1997 (pre-treatment year) to 2017 for each grazing treatment (+/-SE).

### 3.2.4. Nitrogen-fixing species

The effect of grazing on the proportion of leguminous species (*Fabaceae*) depended on year ( $F = 5.3319$ ,  $p < 0.0001$ ; Fig. 6). Following 2008, the proportion of leguminous species increased to a greater extent in the enclosure plots relative to grazed plots. This general pattern was repeated in 2017. Grazing treatments did affect the proportion nitrogen-fixing species, such that leguminous species cover was greatest in the enclosure treatment and lower in the grazed plots ( $F = 24.2043$ ,  $p < 0.0001$ ). Across grazing treatments, pulses of leguminous species occurred in 1998, 2014, and 2017 ( $F = 16.3406$ ,  $p < 0.0001$ ), though temporal fluctuations in nitrogen-fixing species are not clearly linked to a particular climatic driver (Table 1).

### 3.2.5. Deterministic relationship with climate

Climate was a surprisingly poor predictor of cover changes through time (SI Table 2). Among analyses of the relationship between climate and the proportion bare ground, exotic plant, perennial grass, perennial forb, annual grass, and annual forb cover for each treatment, only forb cover in the high and moderate grazing intensity plots responded to climate in a predictable manner (SI Table 2, Fig. 7). In the high intensity grazing treatment, the proportion of annual forbs was negatively related to drought severity (i.e., increased linearly with precipitation). The relationship of perennial forb cover with drought severity was more complex. In the moderate treatment, generally, drought conditions favored perennial forbs, with the lowest proportion of forbs occurring during climatically typical years (i.e., not dry, not wet). The observed increase in forb

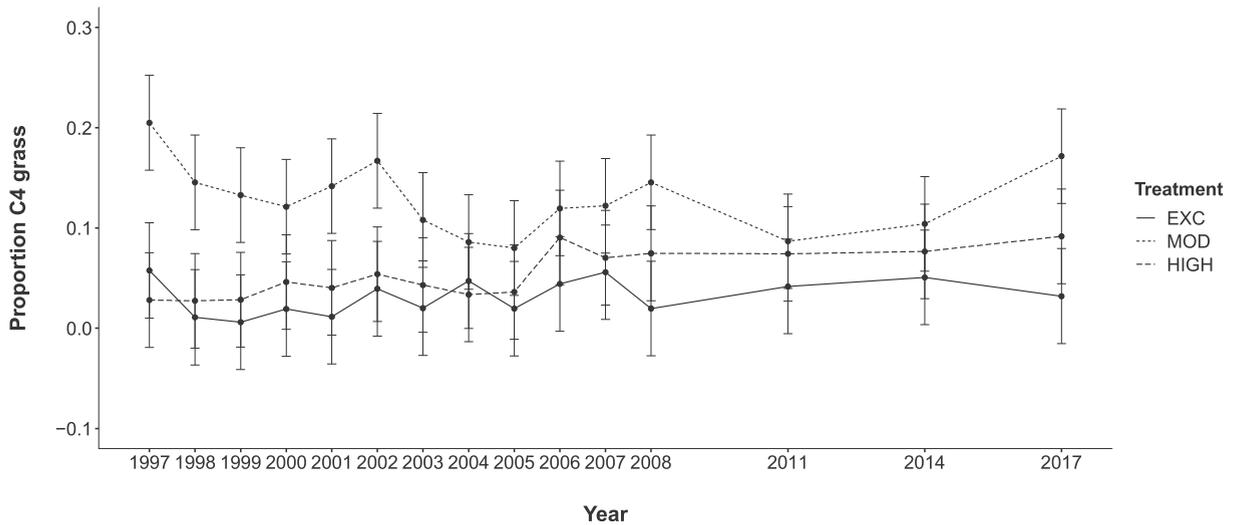


Fig. 5. Change in proportion of grasses consisting of C4 grasses from 1997 (pre-treatment year) to 2017 for each grazing treatment (+/- SE).

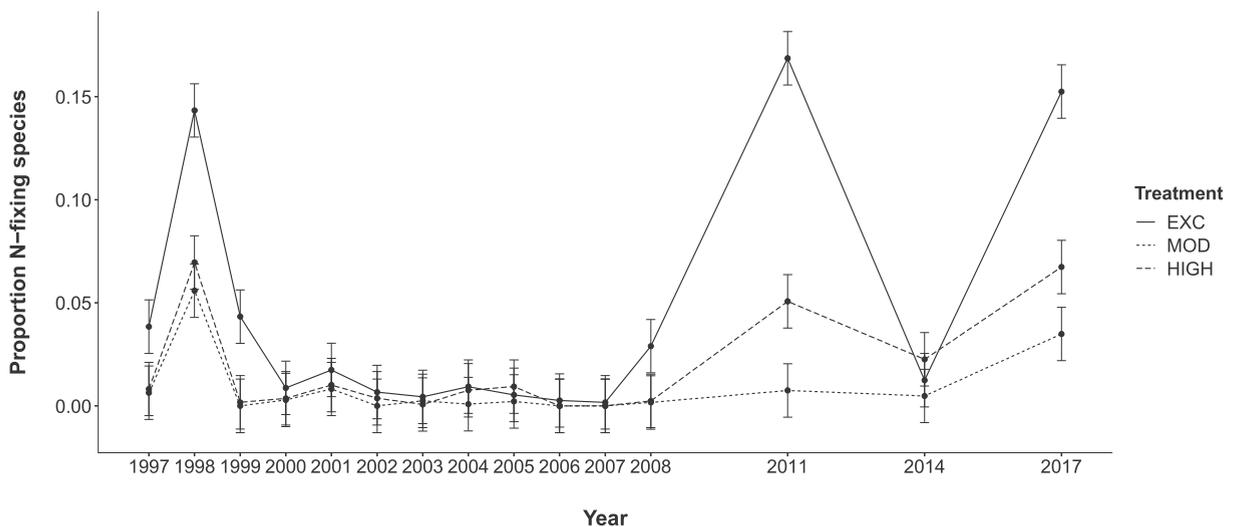
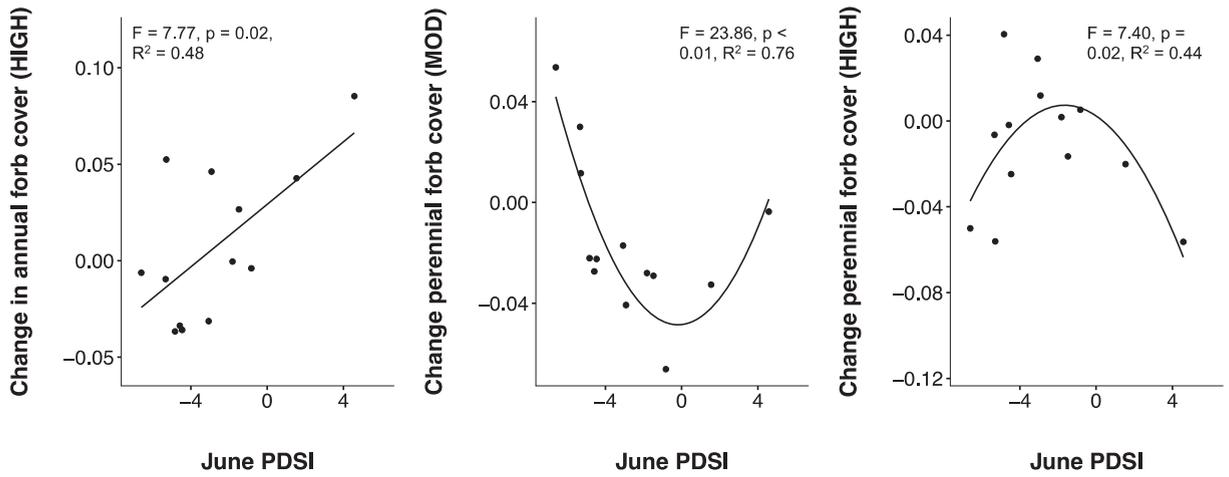


Fig. 6. Proportion of total vegetative cover comprised by plants in the nitrogen-fixing *Fabaceae* plant family from 1997 (pre-treatment year) to 2017 for each grazing treatment (+/-SE).

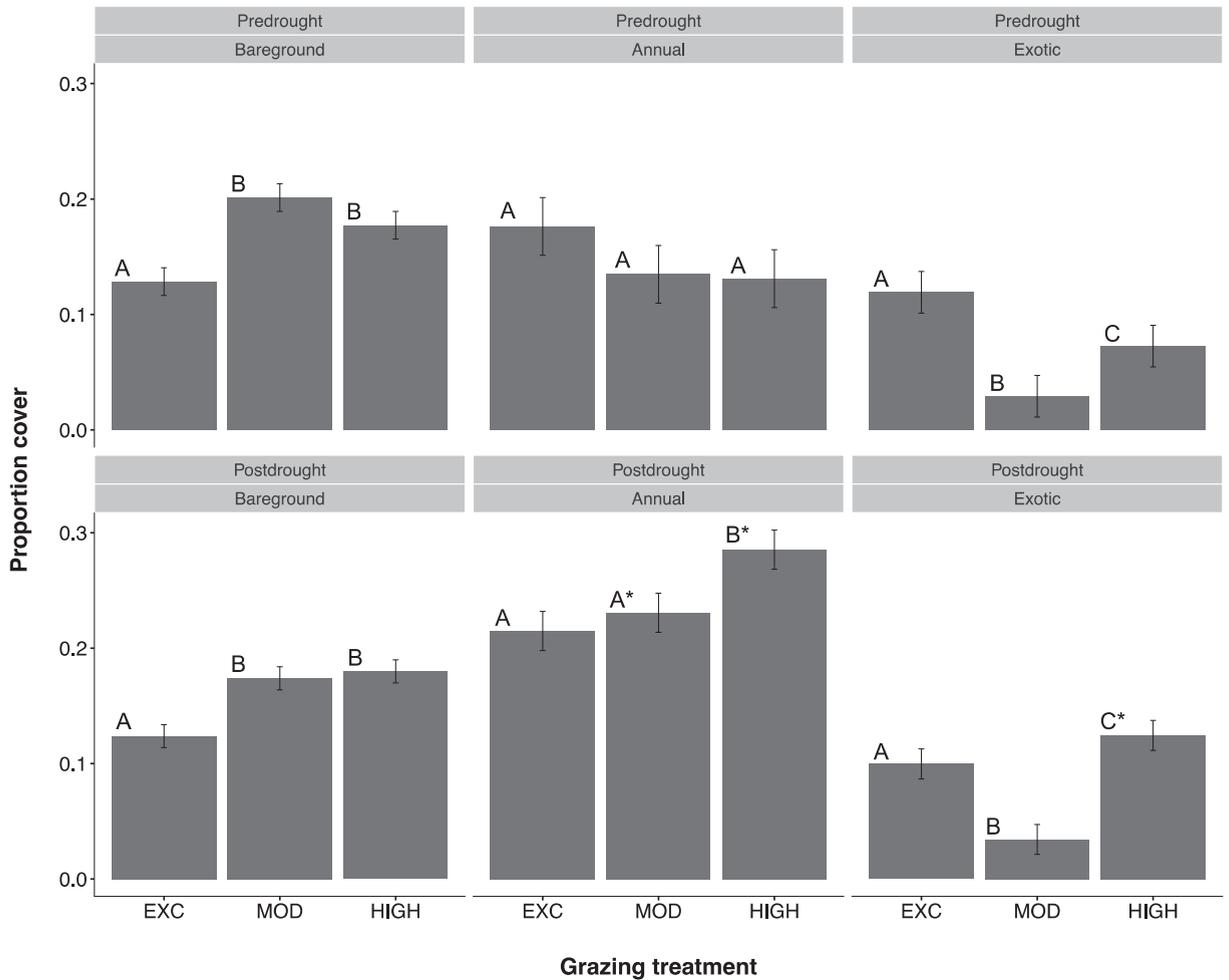
cover in wet years driven primarily by one data point in 2005, an anomalously wet year. In the high intensity grazing treatment, perennial forb cover peaked in drier than average conditions; however, the lowest perennial forb cover occurred in the driest and wettest conditions. There was a trend for climate to explain response of exotic cover in the high intensity grazing treatment, but not for the exclusion or moderate grazing treatments ( $F = 4.7803$ ,  $p = 0.0553$ ;  $F = 2.4117$ ,  $p = 0.1511$ ;  $F = 0.0593$ ,  $p = 0.8126$ , respectively). In the high intensity grazing plots, exotic cover tended to peak when conditions were neither dry or wet. Decreasing sampling frequency in the latter part of the study may have reduced our power to relate vegetation response to climatic conditions, though relationships were not improved by excluding data from the latter half of the study.

### 3.2.6. Effects of stochastic drought event

A severe drought occurred in 2002, which interacted with grazing treatments to alter the vegetative community by increasing the post-drought proportion of annual plants in the grazed treatments ( $F = 6.8365$ ,  $p = 0.0011$ ), and the proportion of exotic species in the high intensity grazing plots ( $F = 4.9334$ ,  $p = 0.0074$ ; Fig. 8). Prior to the 2002 drought, the proportion of annual plant cover was similar across all grazing treatments. Following the drought, annual cover increased from ca. 10%–30% of vegetation in the high intensity grazing treatment. While annual cover also increased in the moderately grazed plots following the drought, the proportion annual plant cover in the moderately grazed plots did not differ from the exclusion



**Fig. 7.** Relationships between drought severity and the proportion of annual forb cover in the high intensity grazing treatment, and perennial forb cover in the moderate and high intensity grazing treatments.



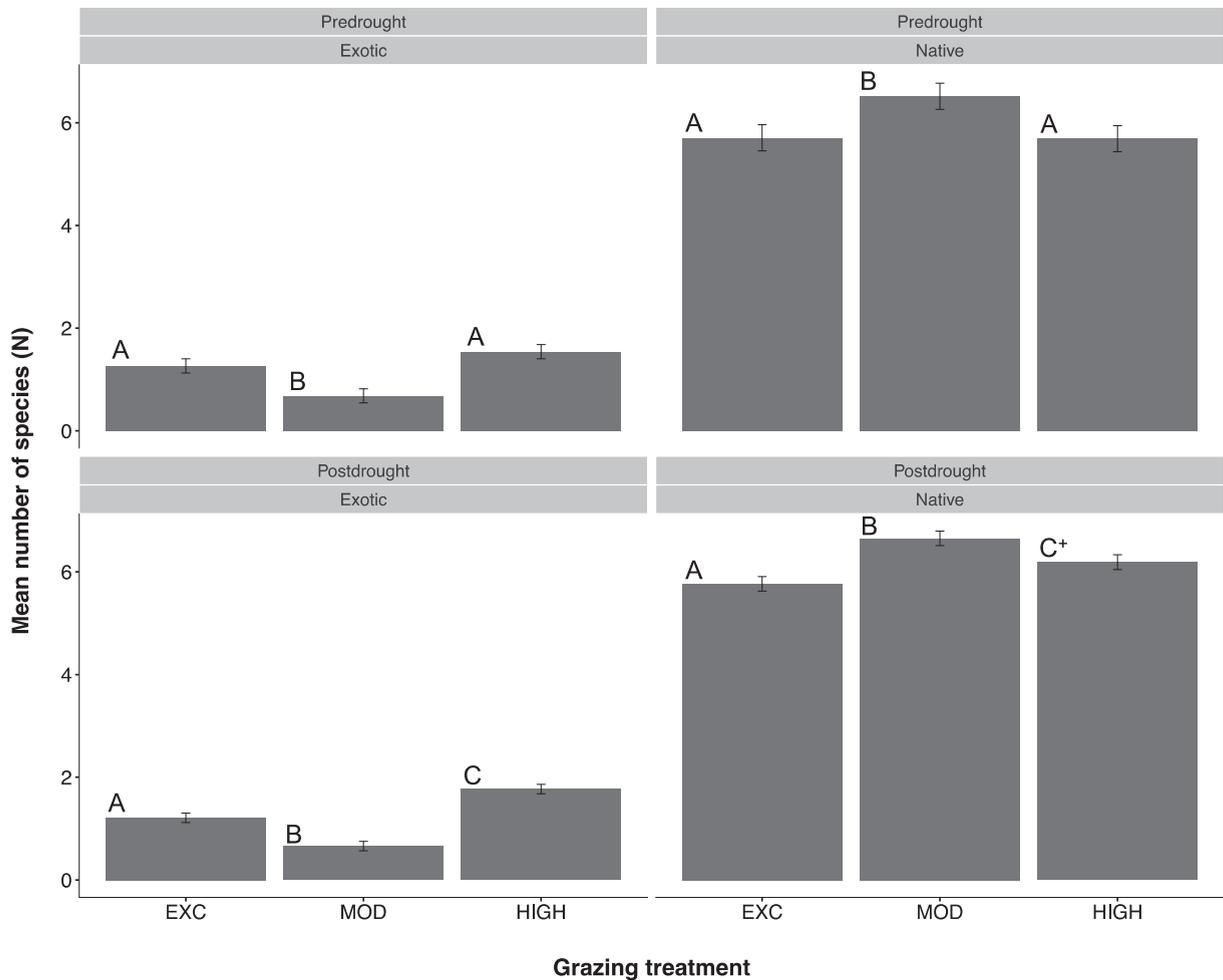
**Fig. 8.** Response of cover types associated with ecosystem services to grazing treatments before and after a drought event. The response variable, bare ground, in the first column of the figure, quantifies the proportion of total ground cover devoid of vegetation, whereas Annual (column 2) and Exotic (column 3) response variables indicate the proportion of vegetative cover comprised by annual and exotic species, respectively. Within each panel, bars connected by the same letter do not significantly differ in value. Asterisks next to letters in post-drought panels indicate a difference between pre- and post-drought means.

during either time period (Fig. 8). Prior to the drought, exotic plant cover was greatest in the enclosure plots and lowest in the moderately grazed treatment areas (Fig. 8). The proportion of exotic cover did not differ between pre- and post-drought time periods for moderate and enclosure plots, though exotic cover almost doubled in the high intensity treatment, increasing from 7% to 12% of the vegetation. There was a significant grazing treatment effect on exotic cover across time periods, with moderately grazed plots having the lowest exotic cover, and the enclosure and high intensity grazing treatments the highest exotic cover ( $F = 26.6188$ ,  $p < 0.0001$ ). Interestingly, there was not a permanent increase in the proportion of bare ground after the actual drought event ( $F = 2.4990$ ,  $p = 0.1142$ ), though in both pre- and post-drought years, the proportion of bare ground was greatest in the grazed treatments and lowest in the enclosures ( $F = 38.0455$ ,  $p < 0.0001$ ; Fig. 8). While exotic plant cover increased following the drought, post-drought exotic species richness (i.e., the number of exotic species) did not significantly differ from pre-drought numbers ( $F = 0.5476$ ,  $p = 0.4594$ ; Fig. 9). Native species richness differed pre- and post-drought ( $F = 4.3086$ ,  $p = 0.0381$ ); with a tendency for increased native species diversity in the high intensity plots following the drought (Fig. 9). In both time periods, moderate grazing resulted in the highest native diversity and lowest exotic diversity ( $F = 21.1821$ ,  $p < 0.0001$ ). While the enclosure and high-intensity grazing treatments had similar effects on these metrics pre-drought, the high intensity grazing treatment plots exhibited higher levels of native and non-native plant richness post-drought (Fig. 9).

## 4. Discussion

### 4.1. Land cover changes and exotic species

Grazing decreased vegetative cover and increased the proportion of bare ground. The high intensity grazing plots possessed, on average, 5.7% more exposed soil compared to the enclosure plots, which consistently exhibited the highest



**Fig. 9.** Response of exotic and native species richness to grazing treatments before and after an extreme drought event in 2002. Within each panel, bars connected by the same letter do not significantly differ in value. A plus sign next to a letter in post-drought panel indicates a tendency to differ in species richness pre- and post-drought.

vegetative cover of all treatments. The effect of grazing on ground cover was amplified in dry years, when the proportion of bare ground reached as high as 31.1% in the high intensity grazing treatment, and was even more pronounced at smaller spatial scales, where some subplots had as little as 6% vegetative cover. The overall proportion of exposed soil likely varies throughout the year, and thus could be higher immediately following grazing or in the period prior to monsoonal rains. Numerous studies have demonstrated the role of grazing in decreasing vegetative cover, exposing bare soil, or relatedly, increasing the patchiness of vegetative cover in arid and semi-arid grasslands (Adler et al., 2001; Hanke et al., 2014; Jones, 2000). Repeated removal of aboveground biomass decreases the competitive ability of some grazed plants and results in mortality when grazing intensity surpasses tolerance thresholds. Preferential grazing of particularly palatable plants in combination with species-specific and individual variation in ability to avoid or tolerate herbivory often results in a patchy mosaic of ground and vegetation in grazed systems (Adler et al., 2001; Walker et al., 1981). Evaporative loss of water and erosion of nutrients from exposed soil can reinforce spatial patterning of vegetation, as drier, nutrient-poor soils are less likely to support plant establishment and growth (Asner et al., 2004; Belnap et al., 2009; Walker et al., 1981). Indeed, grazed plots in this study system retained less soil moisture and demonstrated higher levels of soil compaction relative to ungrazed plots, likely driven by grazing-mediated changes to vegetative cover and physical soil characteristics (Roberts, 2016).

Small-scale vegetation dynamics may play an important role in structuring plant communities in this grassland, as persistent patches of exposed soil may serve as points of entry for non-native species, which possess life history traits (e.g., reproductive and growth rates) that allow rapid colonization of available habitat and physiological traits (e.g., phenotypic plasticity) that provide tolerance to extreme microsite conditions (e.g., dry, depauperate in nutrients). While microsite vegetation dynamics have not been explicitly studied in this system, other studies have demonstrated that loss of perennial cover increases the likelihood of cheatgrass invasion (Chambers et al., 2014; Condon et al., 2011), and in this study system, exposure of bare ground preceded the dramatic increase in exotic cover following the 2002 drought. This was especially apparent in the high intensity grazing plots, in which vegetative cover was reduced by 50% during the drought, followed by a greater than 4-fold increase in exotic cover the subsequent growing season. In water-limited systems like semiarid grasslands, disturbance frees water and soil nutrient resources allowing competitive release of invasive species (Knapp et al., 2008; Knapp, 1996; Mack, 1986; Olf and Ritchie, 1998; Walker et al., 1981) and favoring the establishment of exotic plant seedlings (Dobrowolski et al., 1990; Jackson et al., 1996). As a counterexample, observed increases in exotic species within the enclosure plots were almost exclusively driven by increases in *Melilotus officinalis* (L.) Pall. (Supplemental Information). Increases in *M. officinalis* occurred in 1998, 2008, 2011, and 2017, and do not appear to correspond with soil exposure, as the enclosure plots had comparatively stable and extensive vegetative cover throughout the study period relative to grazed areas. *Melilotus officinalis* is a preferred forage for livestock (Currie et al., 1977), which likely explains the higher coverage of this species within areas that cattle were excluded, suggesting that, in this instance, grazing reduces exotic abundance.

#### 4.2. Growth form and life history

At most time points, the moderate and enclosure treatments did not significantly differ in functional group composition. Plots exposed to high intensity grazing, however, frequently exhibited lower proportions of perennial forb cover and higher proportions of annual plant cover. In previous studies of cattle forage preference on the Colorado Plateau, cattle primarily consumed perennial grasses, such as *B. gracilis* and *P. smithii*, when forage was not limited. Forb consumption by cattle in these studies was considerably lower than that of grass consumption; forbs comprising less than 10% of the diet (Clary et al., 1978; Reppert, 1960). High stocking rates in the high intensity grazing treatment may have created competition for forage, resulting in the consumption of non-preferential food sources, such as forbs. In fact, this is one of the desired outcomes of high intensity grazing regimes, as it is believed to reduce pressure over the course of the grazing season on the most favored forage plants (Savory and Butterfield, 1999). However, forbs often exhibit lower tolerance to grazing relative to grasses, which in this case, likely underlies the observed decrease in the proportion of forbs in the high grazing treatment plots. The negative impact of high intensity grazing on forbs was exacerbated by the 2002 drought, after which annuals replaced much of the perennial forb cover. Other studies conducted in semi-arid grasslands have documented similar increases in annual species in response to intensive grazing in low precipitation years (Derner et al., 2008; Díaz et al., 2007; O'Connor and Roux, 1995). It is unclear whether reduction in perennial cover indicates plant mortality, dormancy, or simply reduction in size. Regardless of the ultimate fate of individual plants, loss of perennial cover may none-the-less hasten conversion to an annual-dominated system. Differences in periodicity of reproductive output and germination requirements may allow annual species, many of which are exotic, to opportunistically establish when perennial cover is diminished, thus inhibiting future perennial recruitment and eventually displacing perennial species (Humphrey and Schupp, 2004; Lenz and Facelli, 2005; Zimmermann et al., 2008). Relative to annual plants, perennial species have developed root systems that stabilize soil and persistent aboveground parts that trap litter and soil (Belnap et al., 2009). Thus, shifts from perennial-dominated systems to communities richer in annual species could negatively affect soil nutrient and moisture dynamics and related ecosystem services.

#### 4.3. Grazing mediated changes in other plant functional groups

By chance, moderately grazed plots initially contained a greater proportion of C4 grasses relative to other treatments. This difference disappeared following the 2002 drought, and treatments exhibited a similar proportion of C4 to C3 plants until 2008 and 2017, when moderately grazed and enclosure treatments diverged; the proportion of C3:C4 plants decreasing in the

grazed plots and increasing in the enclosure plots. This pattern could reflect differential grazing impacts on C3 and C4 grasses due to dissimilarities in phenology (growing season for C3 grasses is skewed towards winter, and C4 grasses skewed towards summer), physiological effects of climate, cattle grazing preferences (Caswell et al., 1973; Ehleringer et al., 2002; Craine et al., 2010), and/or time delays in the response to urine deposition between C3 and C4 grasses (Jaramillo & Detling 1992). The relatively low abundance and variation through time of C4 grasses in this system limits interpretation of response of these species to grazing and climate.

Observed increases in N-fixing species within the enclosure plots were driven primarily by increases in *Melilotus officinalis* (SI. Fig. 1). As a nitrogen-fixing species, *Melilotus officinalis* has been shown to alter nitrogen cycles in ecosystems and serve as a nurse species for both native and exotic species in semiarid regions (Van Riper & Larson 2009; Van Riper et al., 2010). *Melilotus officinalis* is also a nectar source for pollinators, including honeybees (Cane, 2005; Tepedino et al., 2008). The ecological effects of *M. officinalis* in this system remains unclear, though expansion of this species could provide an unexpected benefit to insect-pollinated species and alter plant composition by changing soil nitrogen levels.

## 5. Climatic determinants of vegetative response to grazing

When response of vegetative cover was related to climate, few consistent patterns emerged. The proportion of bare ground, exotic cover, and grass cover were not predicted by drought conditions. Forb cover was, however, explained by climatic variation, though the response varied among grazing treatments and depended on habit (i.e., annual vs. perennial species). In the high intensity grazing treatment only, annual forb cover decreased with drought severity, supporting other studies, which have demonstrated greater drought sensitivity of forbs relatively to grasses (Hoover et al., 2014). Interestingly, this pattern only emerged in the high intensity grazing treatment, suggesting that grazing reinforces the negative relationship between drought and forb cover. Dry conditions may drive cattle to consume forbs, a non-preferential food source in this system, while forbs more frequently escape herbivory in years with more total aboveground biomass. Perennial forb response to climate was more complex. In the moderate grazing treatment, forb cover was lowest in climatically average years, while the opposite was observed in the high intensity grazing treatment. Adaptation to the local environment, which maximizes performance at typical site conditions, is common in plant species, and could explain the parabolic response of perennial cover in the high intensity grazing treatment, in which cover is maximized when climate shows little deviation from mean conditions (Kawecky and Ebert, 2004; Linhart and Grant, 1996; Souther and McGraw, 2011). The response of vegetation within moderately grazed plots at first glance appears counterintuitive, since it does not reflect home-site advantage nor the pattern that you would expect if cattle consume non-preferred forage, as was observed for annual forb response to climate under dry conditions. However, this pattern could emerge indirectly due to grazing and climatic impacts to perennial grasses, the dominant species in this system. Due to lower stocking rates, cattle in the moderate grazing plots may selectively graze grasses, even under drought conditions; however, the combined pressure of grazing and drought, may inhibit performance of grasses allowing the competitive release of forbs. Given lack of forage choice in the high intensity plots, the relationship between grazing and perennial forb cover may more directly reflect the physiological tolerances of the forbs, since higher stocking densities would lead to forbs being consumed at similar rates across years. The complexity of these relationships, unsurprising given that interactions between individual plant physiology, grazing tolerance, competitive relationships among plant species, and grazer behavior coalesce to shape grassland community composition, underscores the difficulty predicting deterministic responses of rangelands to climate change.

## 6. Stochastic events shape of vegetative communities in grazed systems

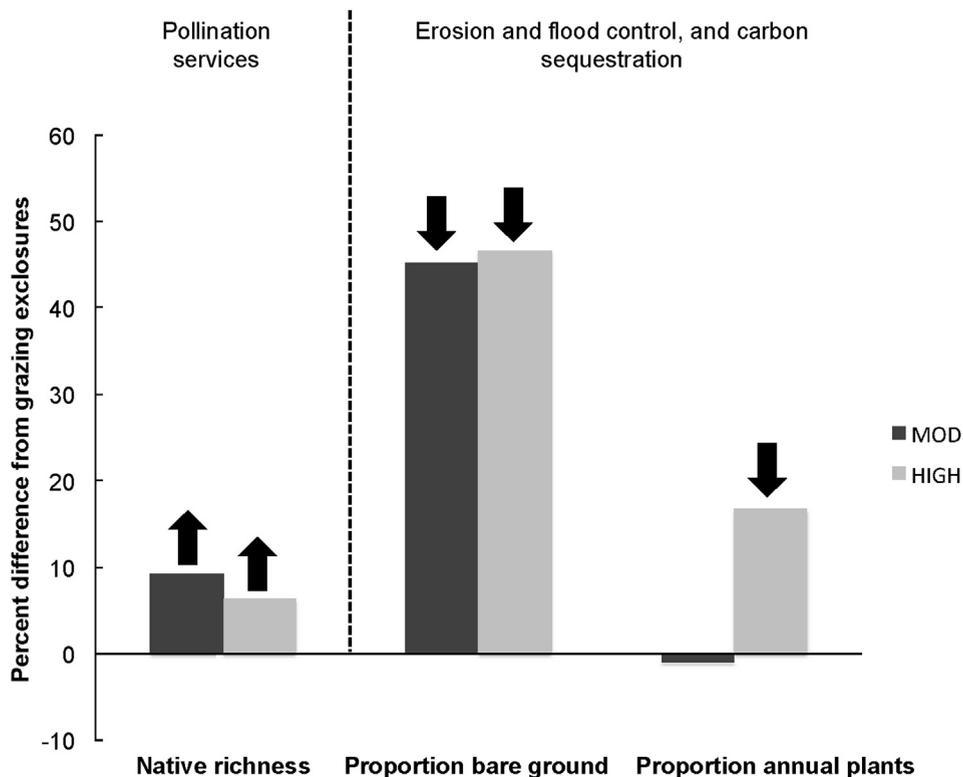
An extreme drought event interacted with grazing to shape vegetative communities. Following the 2002 drought, grazed treatments had significantly more annual plant cover. Grazing has been shown to increase annual plant cover, since the short lifespan and high seed production that accompanies annual habit allows annual species to establish in vegetative gaps created by grazing (Díaz et al., 2007; Pakeman, 2004; Papanikolaou et al., 2011; Strahan et al., 2015). This phenomenon was likely exacerbated by the drought, which significantly decreased vegetative cover in 2002, allowing expansion of annual species and exotic plant cover in the high intensity grazing treatment. Generally, this grassland system has demonstrated remarkable resiliency to invasion by exotic plants; exotic cover returning to predrought conditions within 3 years. However, in the high intensity grazing treatment, annual and exotic plant cover remained significantly greater post-drought, with exotic cover expanding dramatically when conditions were amenable. Similarly, a co-occurring study in this rangeland found that the 2002 drought altered plant community composition and diversity in the high intensity treatment, with differences persisting until the final sample event in 2017 (Souther et al., 2019). Other studies have demonstrated conversion of semiarid grasslands to desert, shrub, or annual grass-invaded systems, using a state and transition modeling framework (Allen-Diaz and Bartolome, 1998; Bestelmeyer et al., 2009, 2004; D'Odorico et al., 2012; D'Odorico et al., 2013; Westoby et al., 1989). State and transition models posit that multiple alternative stable states or regimes exist for a given ecosystem. When disturbance or change in environmental factors (e.g., climate, fire intensity) cross a threshold, the ecosystem may rapidly transition to an alternative stable state, reversal from which is difficult, even when precipitating environmental changes are alleviated (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Feedback loops both maintain stability within states and accelerate state transitions, such that regime shifts may occur rapidly even when causal environmental change is gradual (Scheffer et al., 2012). Here, the combined stressors of high intensity grazing and drought altered the vegetative cover in ways that persist

today, shifting communities towards compositions enriched in annual and exotic species. In this way, extreme events could be as important at predicting grassland response to climate change, as the cumulative effect of multiple stressors may elicit a state change to a system characterized by novel climate-vegetation relationships (Hoover et al., 2014; Jentsch et al., n.d.; Kreyling et al., 2008).

## 7. Conclusions

During this 20-year study, the effect of cattle grazing on this semi-arid grassland varied through time, presumably in response to climate. High intensity grazing was associated with increases in exposed soil and shifts in community composition toward a greater proportion of annual and exotic species, particularly following a severe drought event that occurred in 2002. If, as predicted by numerous climate models, precipitation becomes less abundant and more variable in the south-western United States (IPCC, 2013), grasslands that experience high grazing intensity may shift, perhaps permanently, towards communities characterized by higher abundance of annual and exotic species. Pre-emptive adjustments in grazing practices to account for changing climatic conditions could prevent degradation of grasslands communities under warmer, drier climate regimes.

While grazing cessation has been widely debated as a means to restore or conserve semiarid rangelands (Fleischner, 1994), our study indicates that this approach may be overly simplistic. Here, moderately grazed areas consistently exhibited plant communities with lower proportions of exotic species relative to enclosure plots, and did not differ from areas where cattle were excluded in relative abundance of plant functional groups. Simultaneously, however, grazing exposed a greater proportion of the soil surface relative to cattle enclosures, which, particularly in dryland systems, can increase erosion rates, deplete soil nutrients, and reduce water infiltration (Belnap, 2006; Frank and Evans, 1997; Schlesinger et al., 1990; Yong-Zhong et al., 2005). These findings suggest that grazing could both benefit aspects of ecosystem function, like pollinator services, that are positively related to native plant diversity, while compromising hydrological systems or nutrient cycling by disturbing and exposing soil (Fig. 10) (Jerrentrup et al., 2014; Kammerer et al., 2016; Lázaro et al., 2016; Sjödin et al., 2007; Yoshihara et al., 2008). Such differing and potentially antagonistic effects of grazing on ecological services indicate that, unsurprisingly, no single management recommendation should be uniformly applied to semi-arid grasslands, if observed



**Fig. 10.** Percent difference from grazing enclosure plots in native species richness, proportion of total ground cover that lacks vegetation, and proportion of total vegetative cover comprised by annual plants of moderate and high-intensity grazing plots across all study years. Arrows above bars indicate hypothesized effects on corresponding ecosystem services (listed at top of figure) relative to enclosure plots based on extant literature. Grazing likely has a positive effect on ecosystem services positively related to diversity, but a negative effect on services related to edaphic processes that are diminished due to soil exposure and shifts to a plant community composition enriched in annual species.

effects on plant community cover and composition indeed affect ecosystem services as suggested by research. Instead, grazing management decisions could be based on specific objectives and landscape features. For example, a manager could restrict grazing near roadways in order to reduce flooding, while at the same time grazing pastureland near agricultural fields in order to encourage a diverse and robust pollinator community. Such mosaic-strategies of grazing management already occur, since managers routinely adjust herd density and grazing time to reflect variation in productivity across pastures (York et al., 2019).

Explicit management for multiple ecosystem services could improve traditional management by strategically maximizing benefits derived from grassland systems, depending on ecological and land-use context. Valuing ecosystem services creates an incentive for ranchers to manage in ways that optimize the ecological function and sustainability of grasslands, even when trade-offs exist between maximizing ecosystem services and livestock production (Boyd and Svejcar, 2009; Eastburn et al., 2017; Goldstein et al., 2011). This may be particularly critical in southwestern ranges, where climate change is expected to decrease in annual net primary productivity over the next century (Havstad et al., 2018; Reeves et al., 2014). If available forage biomass decreases, contemporary moderate stocking rates may exert much greater pressure on grassland resources, and, in combination with droughts of increased severity and duration (IPCC, 2013), could result in degradation of southwestern perennial grasslands and shifts towards annual and exotic-dominated systems (Briske et al., 2005; Illius et al., 2014; Scheffer et al., 2012).

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00770>.

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