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Grazing maintains native plant diversity and promotes community stability in an annual grassland

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Abstract. Maintaining native biodiversity in grasslands requires management and mitigation of anthropogenic changes that have altered resource availability, grazing regimes, and community composition. In California (USA), high levels of atmospheric nitrogen (N) deposition have facilitated the invasion of exotic grasses, posing a threat to the diverse plant and insect communities endemic to serpentine grasslands. Cattle grazing has been employed to mitigate the consequences of exotic grass invasion, but the ecological effects of grazing in this system are not fully understood. To characterize the effects of realistic N deposition on serpentine plant communities and to evaluate the efficacy of grazing as a management tool, we performed a factorial experiment adding N and excluding large herbivores in California's largest serpentine grassland. Although we observed significant interannual variation in community composition related to climate in our six-year study, exotic cover was consistently and negatively correlated with native plant richness. Sustained low-level N addition did not influence plant community composition, but grazing reduced grass abundance while maintaining greater native forb cover, native plant diversity, and species richness in comparison to plots excluding large herbivores. Furthermore, grazing increased the temporal stability of plant communities by decreasing year-to-year variation in native forb cover, native plant diversity, and native species richness. Taken together, our findings demonstrate that moderate-intensity cattle grazing can be used to restrict the invasive potential of exotic grasses and maintain native plant communities in serpentine grasslands. We hypothesize that the reduced temporal variability in serpentine plant communities managed by grazing may directly benefit populations of the threatened Edith's Bay checkerspot butterfly (*Euphydryas editha bayensis*).

Key words: California, USA; Euphydryas editha bayensis; *grazing; interannual community variation; invasion; native plant richness; nitrogen; precipitation; principal response curve (PRC); serpentine grassland; stability.*

Introduction

Grassland ecosystems have experienced significant ecological changes due to anthropogenic increases in nitrogen (N) deposition (Vitousek et al. 1997, Bobbink et al. 2010), altered grazer assemblages and grazing regimes (Bakker et al. 2006, Fensham et al. 2014), and the invasion of exotic species (Shea and Chesson 2002, Harrison et al. 2006). These shifts in both bottom-up and top-down controls on plant communities have altered ecological interactions in grasslands and compromised the ability of grassland systems to support biodiversity and maintain ecosystem processes (Chapin et al. 2000, Gibson 2009). Thus, the maintenance of native biodiversity in grasslands will depend upon understanding how these systems respond to environmental change over time.

Increased anthropogenic N deposition has been implicated as the primary driver of changing community composition in grassland systems worldwide (Bobbink et al. 2010). Nitrogen enrichment alters the competitive dynamics of grassland communities, usually resulting in increased primary productivity and reduced plant diversity (Suding et al. 2005, Bobbink et al. 2010). Although the magnitude of diversity loss varies among systems and partly depends on system-specific characteristics such as soil properties, the degree of N limitation, and plant traits (Clark et al. 2007), rare species are consistently more vulnerable to local extinction than are abundant species (Suding et al. 2005). Furthermore, increased N availability often favors exotic species and can facilitate exotic plant invasions in systems historically resistant to invasion (Huenneke et al. 1990, Fenn et al. 2003, Suding et al. 2005).

Top-down factors such as grazing also regulate the structure of grassland plant communities. By preferentially consuming certain species, grazers can modify the composition and diversity of plant communities (Milchunas et al. 1988, Collins et al. 1998). In general, grazing is expected to reduce plant diversity in resource-poor environments, but can have positive effects on

diversity as resource availability increases, suggesting that the top-down effects of grazing on plant diversity depend on resource availability (Proulx and Mazumder 1998, Cingolani et al. 2005, Bakker et al. 2006). However, grazing may also interact with other drivers, such as climate and nutrient enrichment, to regulate plant community composition (Collins et al. 1998, Koerner and Collins 2014). Consequently, a better understanding of the interaction between bottom-up and top-down controls is necessary to predict community responses to ecosystem change and develop effective conservation and management strategies (Gruner et al. 2008).

In addition to their effects on community composition, N deposition and altered grazing regimes may affect ecosystem stability. Stability has taken on numerous meanings in the ecological literature, but is defined here as the inverse of temporal system variability (Ives and Carpenter 2007, Hautier et al. 2014). Most previous research has addressed the diversity–stability relationship, providing some evidence that increased diversity decreases ecosystem variability through asynchronous species' responses to changing environmental conditions (Tilman 1996, Isbell et al. 2009; but see Sasaki and Lauenroth 2011, Wilsey et al. 2014). Although environmental perturbations are predicted to drive changes in ecosystem stability by modifying diversity, ecological changes can also influence stability directly (Ives and Carpenter 2007). For example, in a study of 41 natural grasslands across five continents, Hautier et al. (2014) found that N enrichment reduced the stabilizing effects of diversity by decreasing species' asynchrony at high levels of diversity, rather than by reducing diversity of the plant community. Nevertheless, few studies have characterized the direct effects of environmental perturbation on stability. Furthermore, although most previous studies of stability have emphasized variation in ecosystem functions such as biomass production, the concept of community stability (i.e., the stability of species richness and diversity through time) may also be relevant to ecosystem functioning (Yang et al. 2011, Yang et al. 2012). Temporal variation in the diversity and composition of plant communities may shape competitive dynamics among plant species and influence plant interactions with herbivores, pollinators, and pathogens, especially in temporally variable, annual-dominated systems such as annual grasslands (Pake and Venable 1995, Hobbs et al. 2007). Although short-term instabilities in these systems resulting from interannual fluctuations in species abundance are predicted to stabilize long-term community dynamics (Chesson and Huntly 1989), their inherently high species turnover could make temporally variable systems particularly sensitive to environmental perturbation (Zavaleta et al. 2009).

California's annual-dominated serpentine grasslands are characterized by substantial interannual fluctuations in the abundance of plant species (Hobbs et al. 2007).

Due to the unique abiotic conditions resulting from low soil nutrient availability, elevated levels of heavy metals such as magnesium and nickel, and poor water retention of serpentine soils (Brady et al. 2005), serpentine grasslands are refuges of regional biodiversity hosting many rare and endemic species, including the federally threatened Edith's Bay checkerspot butterfly (*Euphydryas editha bayensis*; Weiss 1999, Safford et al. 2005). However, high rates of atmospheric N deposition ranging from 4 to 15 kg N·ha^{-1}·yr^{-1} have facilitated the invasion of nitrophilic, exotic grasses that negatively affect native serpentine plants (Huenneke et al. 1990, Fenn et al. 2003, Vallano et al. 2012). Consequently, the conservation of native biodiversity under current and future N loads constitutes a significant management challenge (Fenn et al. 2010).

Although observational studies have suggested that cattle grazing in serpentine grasslands can reduce exotic grass cover, increase native plant diversity, and maintain habitat for threatened species (Weiss 1999, Safford and Harrison 2001, Gelbard and Harrison 2003, Harrison et al. 2003), the continued accumulation of N could reduce the ecological benefits of grazing (Pasari et al. 2014). Furthermore, the ecological effects of grazing and N deposition may vary through time and influence the temporal dynamics of serpentine grassland communities. We examined the interactive effects of N addition and cattle grazing on serpentine plant communities in California's largest serpentine grassland to address two primary questions: (1) What are the individual and interactive effects of N addition and livestock grazing on serpentine plant community composition? (2) How do N addition and grazing affect the temporal stability of serpentine plant communities?

METHODS

Site description and experimental design

Our study was conducted at Coyote Ridge, a 3000-ha serpentine grassland located south of the San Francisco Bay in California (37°11′48.84″ N, 121°40′30.41″ W). The site has a mediterranean climate characterized by cool, wet winters and dry summers, with most precipitation falling as rain between October and April. Annual precipitation at Coyote Ridge averages 519 mm and estimated growing-year precipitation (June–May) ranged from 358 mm to 702 mm between 2008 and 2013 (PRISM Climate Group 2013; Table 1). The portion of Coyote Ridge included in this study is currently grazed at a stocking rate of ~0.25 animal units (AU) per hectare during the winter growing season, and probably has been grazed at this rate for several decades (Pasari et al. 2014).

We conducted two 2 × 2 factorial experiments at 10 locations (blocks) on Coyote Ridge ($n = 5$ blocks in each experiment). Blocks were established on the ridge top and slopes to incorporate the diverse topography present at Coyote Ridge. The first five blocks, hereafter experiment 1, were established in December 2007. In an

attempt to capture additional site heterogeneity, five more blocks, hereafter experiment 2, were established in September 2009. Within each block, we created two 5 × 5 m plots and assigned each plot randomly to a grazing treatment. The ungrazed plot was fenced to exclude cattle and the other plot was left accessible to cattle. Other herbivores, such as tule elk (*Cervus canadensis* spp. *nannodes*), California mule deer (*Odocoileus hemionus californicus*), wild pigs (*Sus scrofa*), and rabbits (Leporidae) are present at the site, but were rarely observed in our plots (Pasari et al. 2014). Plots were subdivided into two 2.5 × 5 m subplots. One subplot was fertilized with NH_4NO_3 dissolved in water and the other subplot was only watered. In September 2008 for experiment 1 and in September 2009 for experiment 2, fertilized subplots received 5 g N/m^2 as dissolved NH_4NO_3 at a concentration of 14.1 g/L. Fertilizer was added one year following the establishment of the grazing treatment in experiment 1, but both grazing and fertilizer treatments were established concurrently in experiment 2. The initial rate of fertilization was intended to mimic a five-year pulse of N at the current deposition rate of 10 kg $N·ha^{-1}·yr^{-1}$ (Fenn et al. 2010). In subsequent years, we applied N annually at a reduced rate of 1 g $N·m^{-2}·yr^{-1}$ (2.8 g/L NH_4NO_3) to simulate realistic levels of N deposition (Pasari et al. 2014). Quantitative estimates of grazing intensity in unfenced subplots (i.e., the number of cow bites·12.5 $m^{-2}·yr^{-1}$) were obtained using motion-detecting, infrared-triggered cameras according to the methods described in Pasari et al. (2014).

We assessed the cover of all plant species annually between 2008 and 2013. Cover was visually estimated within a 0.5 × 0.5 m permanent quadrat in each subplot in late March or early April of each year to coincide with peak biomass. All plant species present in the quadrat as well as bare ground, rocks, and litter/thatch were assigned a cover value of 1, 2, 3, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, or 100%. We also noted whether the plot had been disturbed by gopher activity. Although total cover was constrained to 100%, our use of relatively broad cover classes lead to underestimations of cover in a small number of plots (i.e., the aggregate vegetation cover including bare ground was less than 100%). To ensure that comparisons of functional group cover were conducted on a common scale, we used relative cover rather than absolute cover in our analyses.

Data analysis

We examined the relationship between exotic cover and native species richness in each year of our experiment using analysis of covariance (ANCOVA). In our analyses, we included exotic cover, categorical grazing treatment, and their interaction as explanatory variables. Experiments 1 and 2 were pooled for this analysis, but fertilized and unfertilized subplots were analyzed separately. Native plant richness was log-transformed to improve normality. We also used

TABLE 1. Estimated annual precipitation during the growing year (June–May) and winter precipitation (December and January) at Coyote Ridge, a 3000-ha serpentine grassland south of San Francisco Bay, California, USA, 2007–2013.

	Precipitation (mm)	
Study year	Annual	Winter
2007/2008	424	265
2008/2009	414	105
2009/2010	703	286
2010/2011	672	215
2011/2012	420	92
2012/2013	358	247

Note: Precipitation estimates were obtained from the PRISM Climate Group (2013).

ANCOVA to evaluate the relationship between continuous measures of grazing intensity and plant community composition in grazed plots. Average annual grazing intensity, fertilization treatment, and their interaction were included as explanatory variables in these analyses.

To characterize the effects of grazing and N addition on serpentine communities, we examined the response of total grass cover, native forb cover, native plant diversity, and native species richness to experimental treatments. We used total grass cover rather than exotic cover because previous studies have demonstrated that exotic and native grasses exhibit functionally similar responses to grazing in serpentine grasslands (Pasari et al. 2014). In general, the exotic cover of experimental plots was closely related to total grass cover, with the exception of several plots in which exotic cover was low but the dominance of an annual native grass (usually *Festuca microstachys*) contributed to high total grass cover in some years. Nevertheless, exotic grasses represented, on average, 76% of total grass cover in our experimental plots. Native plant diversity was quantified using the Shannon-Weaver index (H'), defined as:

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

where p_i is the relative abundance of species i in an experimental subplot, and S is the number of native plant species present in a given plot. In addition to native plant diversity, we also examined native species richness to determine whether changes in plant diversity were influenced by changes in species evenness or richness. We compared the response of each community metric to treatments through time, as well as the directional changes in community composition from the beginning to the end of each experiment (2008–2013 for experiment 1 and 2010–2013 for experiment 2). Directional changes in community composition were characterized using log response ratios (LRRs), which standardize for initial differences in community composition. LRRs were calculated separately for the change in cover (Δcover) of grasses or forbs, change in native

plant diversity (Δdiversity), and change in native species richness (Δrichness) within each subplot using the following equation:

$$\mathrm{LRR}_C = \ln\left(\frac{C_{2013}}{C_{\mathrm{initial}}}\right)$$

where C is one of our four community metrics of interest and C_{initial} represents the value of a community metric in the first year of each experiment. Experiments 1 and 2 were analyzed separately because the experiments were established in different years.

We used principal response curve (PRC) analysis to examine species-level responses to treatments over time. PRC is an extension of redundancy analysis used to examine community response data from experiments sampled repeatedly through time (Van den Brink and ter Braak 1999) and has been used previously in grasslands to examine plant community responses to resource enrichment, disturbance, and grazing (Britton and Fisher 2007, Kardol et al. 2009, Pasari et al. 2014). PRC first attributes variance in community composition to time and then attributes the remaining variance to experimental treatments. Canonical regression coefficients (c_{dt}) from the first component are then plotted against time, yielding a principal response curve for each treatment. The magnitude of c_{dt} indicates the strength of community response to treatments, and the magnitude of species' weights (b_k) reflects the likelihood that species' responses are related to the PRC. Positive species weights indicate those species whose response pattern follows the PRC, while negative b_k values indicate species whose response pattern diverges from the PRC. Species with b_k values near zero are expected to exhibit weak responses or response patterns unrelated to the PRC (van den Brink and ter Braak 1999). We tested the significance of our PRC with Monte Carlo time series permutations. The null hypothesis of this test assumes that there are no significant treatment effects at any point in time. Our PRC analysis was implemented using the vegan package for R, version 2.0-7 (Oksanen et al. 2013).

Finally, we examined treatment effects on the temporal stability of all four community metrics. Stability was defined as the temporal mean divided by the temporal standard deviation of each metric within a subplot over a common time period (Tilman et al. 2006, Sasaki and Lauenroth 2011, Hautier et al. 2014). Because this measure of community stability is standardized by the temporal mean and depends on variation in community composition rather than absolute differences in cover, diversity, or richness over time, we pooled experiments 1 and 2 in our analysis of community stability.

Statistical analyses of time series, directional changes in community composition, and community stability were performed using linear mixed-effects (LME) models. In our analysis of plant community time series, grazing, fertilization, year, and their interactions were modeled as fixed effects, while block, grazing plot, and subplot were treated as random effects to account for site heterogeneity, the split-plot design, and repeated measures, respectively. For our analyses of directional community change (i.e., Δcover, Δdiversity, and Δrichness) and stability, we included grazing, fertilization, and their interaction as fixed effects while block and grazing plot were modeled as random effects. Additionally, experiment (i.e., 1 vs. 2) was treated as a random effect in our stability models. Our LME models were implemented using the lme4 package for R (Bates et al. 2014) and all statistical analyses were performed in R 2.15.0 (R Development Core Team 2013).

RESULTS

Patterns of community composition

We observed substantial variation in community composition among study years (Fig. 1). This interannual variation in community structure (i.e., total grass and forb cover) was consistent between experiments and corresponded with variation in winter precipitation (Table 1). Mean total grass cover (i.e., native and exotic grasses) in experiment 1 was positively correlated with December and January precipitation over the six-year study (Pearson's correlation: $r = 0.97$, $P = 0.007$, excluding 2010). Winters with greater precipitation (2008, 2011, and 2013) had relatively high grass cover and low native forb cover, whereas the driest winters (2009 and 2012) had relatively low total grass cover. In 2010, community composition deviated from this general pattern because relatively high winter precipitation was associated with relatively low grass cover.

Exotic cover was negatively associated with native plant richness in 2010 (ANCOVA: $R^2 = 0.34$, $F_{1,16} = 7.708$, $P = 0.013$), 2011 ($R^2 = 0.39$, $F_{1,16} = 8.936$, $P = 0.009$), and 2013 ($R^2 = 0.27$, $F_{1,15} = 5.468$, $P = 0.034$) in unfertilized subplots; and in 2010 ($R^2 = 0.29$, $F_{1,16} = 6.013$, $P = 0.026$), 2012 ($R^2 = 0.33$, $F_{1,16} = 4.639$, $P = 0.047$), and 2013 ($R^2 = 0.33$, $F_{1,16} = 7.100$, $P = 0.016$) in fertilized subplots. The presence or absence of grazing had no effect on the relationship between exotic cover and native species richness in any year ($P > 0.10$ for all models; Appendix A). Grazing intensity in unfenced subplots ranged from 16 to 147 cow bites·12.5 m^{-2}·yr^{-1} (mean 47.8 cow bites·12.5 m^{-2}·yr^{-1}), but average annual grazing intensity in grazed plots was unrelated to either plant community composition or directional changes in plant communities ($P > 0.10$ for all models; Appendix C).

Grazing and nitrogen effects on community composition

Grazing, but not fertilization, had a significant effect on total grass cover and native forb cover. Beginning in 2010, we observed a divergence in grass cover among grazed and ungrazed plots in experiment 1 (Fig. 1A). Ungrazed plots had greater grass cover than grazed plots and the overall effect of grazing was significant (LME model: $F_{1,4} = 14.398$, $P = 0.019$). There was also a significant grazing × year interaction ($F_{5,80} = 2.926$, $P =$
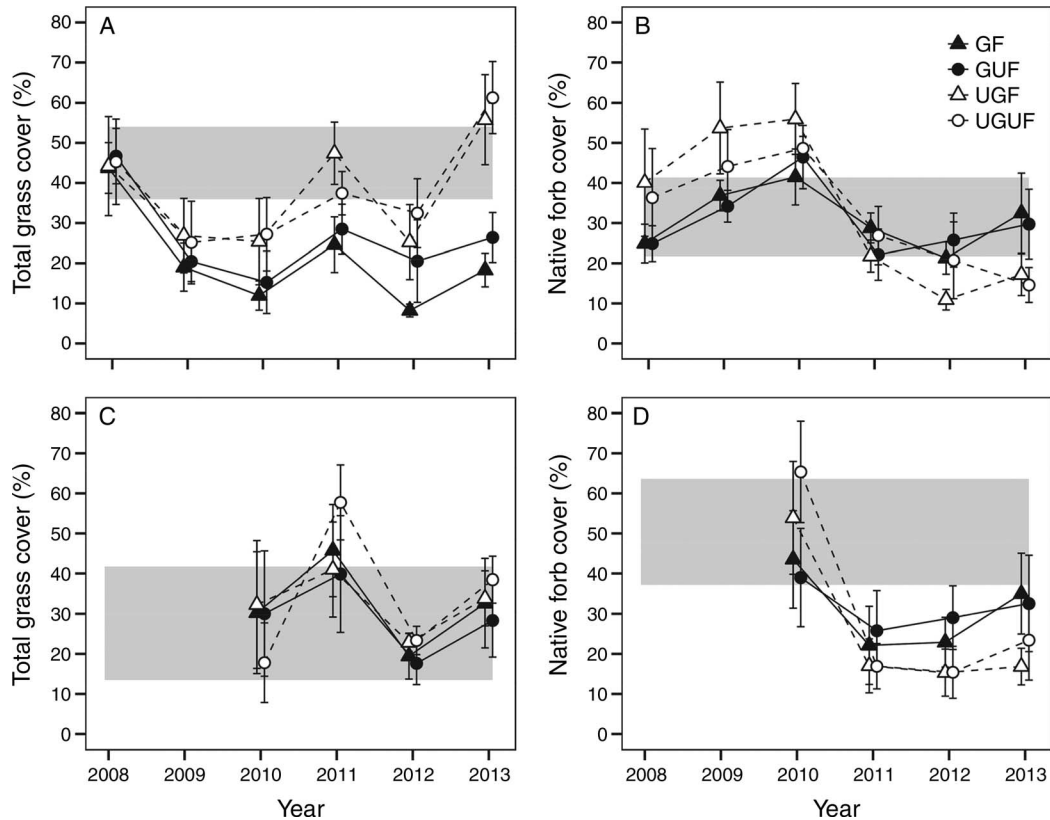
Fɪɢ. 1. Time series of grass percent cover and native forb percent cover in experiment 1 (A, B) and experiment 2 (C, D). Error bars represent one standard error of the mean and the gray bands represent 95% confidence intervals for grass cover and native forb cover in the first year of each 2 × 2 factorial experiment in serpentine grassland blocks on Coyote Ridge, California, USA. Experiment 1, the first five blocks, was established in December 2007. For additional site heterogeneity, five more blocks, hereafter experiment 2, were established in September 2009. Within each block were two 5 × 5 m plots, each randomly assigned a grazing and fertilizer treatment. Treatments were: GF, grazed and fertilized; GUF, grazed and unfertilized; UGF, ungrazed and fertilized; UGUF, ungrazed and unfertilized.

0.018), but we observed no effect of the fertilization treatment ($F_{1,8} = 0.641$, $P = 0.446$; see Appendix B for full model summary). Although grass cover increased by an average of 13.8% ± 11.64% (mean ± SE) in ungrazed subplots and grass cover decreased by 22.9% ± 5.63% in grazed subplots between 2008 and 2013, Δcover of grass did not differ between grazing treatments ($F_{1,4} = 3.963$, $P = 0.117$; Table 2). Four years after the onset of experiment 2, we did not observe grazing or fertilization effects on total grass cover (for grazing, $F_{1,4} = 0.222$, $P = 0.662$; for fertilization, $F_{1,8} = 0.026$, $P = 0.877$; Fig. 1C). Similarly, Δcover of grass between 2010 and 2013 did not differ significantly among grazing treatments ($F_{1,4} = 1.074$, $P = 0.359$).

In experiment 1, we observed substantial interannual variation in native forb cover that was unrelated to our experimental treatments (Fig. 1B). The overall effect of grazing was not significant ($F_{1,4} = 0.106$, $P = 0.761$), but native forb cover tended to be greater in grazed plots as the experiment progressed, resulting in a significant grazing × year interaction ($F_{5,80} = 3.875$, $P = 0.003$). Moreover, the Δcover of native forbs between 2008 to

2013 differed significantly among grazing treatments, with forb cover increasing by an average of 6.2% ± 6.51% S (mean ± SE) in grazed subplots and decreasing by an average of 22.3% ± 8.23% in ungrazed subplots ($F_{1,8} = 12.928$, $P = 0.023$; Table 1). In experiment 2, the overall effect of grazing on native forb cover was not significant ($F_{1,4} = 0.502$, $P = 0.518$), but forb cover tended to be greater within grazed plots in the later years of the experiment, resulting in a significant grazing × year interaction ($F_{3,48} = 5.485$, $P = 0.003$; Fig. 1D). Native forb cover also decreased in ungrazed plots relative to grazed plots between 2010 and 2013, but the effect of grazing on the Δcover of forbs was only marginally significant ($F_{1,4} = 7.115$, $P = 0.056$).

Native plant diversity was consistently greater in grazed plots than in ungrazed plots in experiment 1 ($F_{1,4} = 14.446$, $P = 0.019$). Diversity also tended to be lower in unfertilized subplots than in fertilized subplots ($F_{1,8} = 4.598$, $P = 0.064$). Between 2008 and 2013, Δdiversity was significantly different among grazing treatments as native plant diversity decreased in ungrazed plots relative to grazed plots ($F_{1,4} = 9.156$, $P = 0.039$).

TABLE 2. Summary of LME (linear mixed-effects) model results describing directional changes in total grass cover, native forb cover, native plant diversity, and native species richness in experiments 1 and 2.

Treatment	Experiment 1		Experiment 2	
	F	P	F	P
Change in total grass cover				
Grazing	3.963	0.117	1.074	0.359
Fertilization	0.011	0.918	0.729	0.418
Grazing × Fertilization	0.272	0.616	1.0547	0.335
Change in native forb cover				
Grazing	**12.928**	**0.023**	*7.115*	*0.056*
Fertilization	0.330	0.581	0.085	0.778
Grazing × Fertilization	0.088	0.775	0.050	0.828
Change in native plant diversity				
Grazing	**9.156**	**0.039**	1.752	0.256
Fertilization	**11.889**	**0.009**	0.010	0.924
Grazing × Fertilization	0.319	0.588	0.097	0.764
Change in native species richness				
Grazing	**8.740**	**0.042**	2.702	0.176
Fertilization	1.889	0.207	1.442	0.264
Grazing × Fertilization	0.000	0.995	1.216	0.302

Notes: Changes in community composition were calculated using log response ratios (see *Methods*) between 2008 and 2013 (experiment 1) and between 2010 and 2013 (experiment 2). For Grazing, df = 1, 4; for Fertilization and for Grazing × Fertilization, df = 1, 8. Significant treatment effects ($P < 0.05$) are indicated in boldface; marginally significant effects ($P < 0.10$) are italicized.

Additionally, diversity decreased in unfertilized subplots relative to fertilized subplots ($F_{1,8} = 11.899$, $P = 0.009$). In experiment 2, there was no overall effect of experimental treatments on native plant diversity or the Δdiversity of native species through time.

In experiment 1, the observed patterns of plant diversity were largely driven by changes in species richness. Native plant richness fluctuated substantially through time, but was lower in unfertilized subplots than in fertilized subplots ($F_{1,8} = 11.442$, $P = 0.010$; Fig. 2A). There was no overall effect of grazing on native richness ($F_{1,4} = 2.439$, $P = 0.193$), but native richness was greater in grazed plots in the later years of the experiment, resulting in a significant grazing × year interaction ($F_{5,80} = 3.458$, $P = 0.007$). The Δrichness of native species over the duration of the experiment was affected by grazing ($F_{1,4} = 8.740$, $P = 0.042$), but was not affected by fertilization ($F_{1,8} = 1.889$, $P = 0.207$). Ungrazed subplots lost an average of 4.5 ± 0.78 species (mean ± SE) between 2008 and 2013, whereas grazed subplots gained an average of 0.5 ± 1.32 species. Fluctuations in native plant richness were less pronounced in experiment 2 and unrelated to experimental treatments (Fig. 2B). Between 2010 and 2013, ungrazed subplots lost an average of 2.2 ± 1.09 species, whereas grazed subplots gained an average of 0.5 ± 1.00 species, but there was no significant effect of grazing on Δrichness ($F_{1,4} = 2.702$, $P = 0.176$).

In our PRC analysis of experiment 1, 13.8% of the variance in community composition was attributed to time and 14.8% of the variance was attributed to our experimental treatments and the interaction between time and treatment (Fig. 3). Community responses differed significantly among grazing treatments (PRC, $F = 13.101$, $P = 0.025$). The species whose response to the treatments most closely followed the community pattern in the PRC (i.e., those that were most likely to exhibit increases in abundance in ungrazed plots) were three grasses and one forb species (b_k in parentheses): *Festuca perennis* (3.864), *F. microstachys* (2.122), litter/thatch (1.712), *Microseris douglasii* (1.695), and *Stipa pulchra* (1.015). The species with the most negative weights (i.e., those that were most likely to exhibit decreases in abundance in ungrazed plots) were bare ground (−10.250) and four native forb species: *Plantago erecta* (−1.245), *Eriogonum nudum* (−0.371), *Calystegia subacaulis* (−0.359), and *Hesperavax sparsiflora* (−0.210). Although our PRC analysis of experiment 2 showed similar trends in species' responses to grazing treatments, there were no significant treatment effects ($F = 2.439$, $P = 0.980$; data not shown).

Grazing and nitrogen effects on plant community stability

Grazing increased the temporal stability of native forb cover ($F_{1,4} = 20.451$, $P = 0.001$), native plant diversity ($F_{1,4} = 13.841$, $P = 0.005$), and native species richness ($F_{1,4} = 6.350$, $P = 0.033$; Fig. 4, Table 3). Additionally, the stability of native forb cover was greater in unfertilized subplots than in fertilized subplots ($F_{1,8} = 5.934$, $P = 0.025$). Because temporal stability is a function of both the temporal mean and standard deviation, increased stability could have resulted from increased mean, decreased standard deviation, or both increased mean and decreased standard deviation of cover, diversity, and richness in grazed plots. We did not observe a difference in mean native forb cover between grazed and ungrazed plots ($F_{1,4} = 0.063$, $P = 0.808$) or between fertilized and unfertilized plots ($F_{1,8} = 0.116$, $P = 0.737$). However, the standard deviation of native forb cover was 47% lower in grazed plots ($F_{1,4} = 11.737$, $P = 0.008$). There was no effect of fertilization on the standard deviation of native forb cover ($F_{1,8} = 1.905$, $P = 0.184$). Similarly, neither mean plant diversity ($F_{1,4} = 1.032$, $P = 0.336$) nor mean native richness ($F_{1,4} = 0.250$, $P = 0.629$) differed between grazing treatments, but the standard deviation of native plant diversity was 32% lower in grazed plots ($F_{1,4} = 11.965$, $P = 0.007$) and the standard deviation of native species richness was 24% lower in grazed plots than in ungrazed plots ($F_{1,4} = 5.147$, $P = 0.049$). Both mean grass cover ($F_{1,4} = 4.839$, $P = 0.055$) and the standard deviation of grass cover ($F_{1,4} = 11.775$, $P = 0.007$) were greater in ungrazed plots. Nevertheless, the stability of grass cover was not significantly different among grazing treatments because the concurrent increase in the mean and standard deviation of total grass cover in ungrazed plots did not
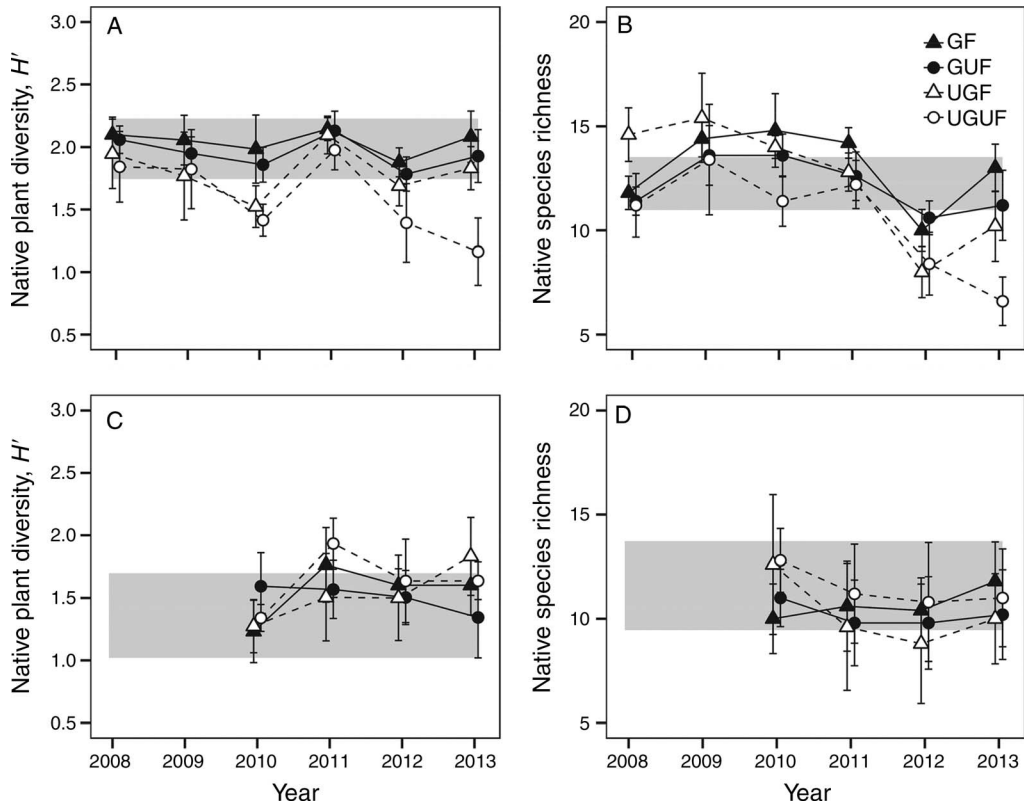
FIG. 2. Time series of native plant diversity and native plant species richness (actual number of species, untransformed) in experiment 1 (A, B) and experiment 2 (C, D). Error bars represent one standard error of the mean and the gray bands represent 95% confidence intervals for native plant richness in the first year of each experiment. Treatments were: GF, grazed and fertilized; GUF, grazed and unfertilized; UGF, ungrazed and fertilized; UGUF, ungrazed and unfertilized.
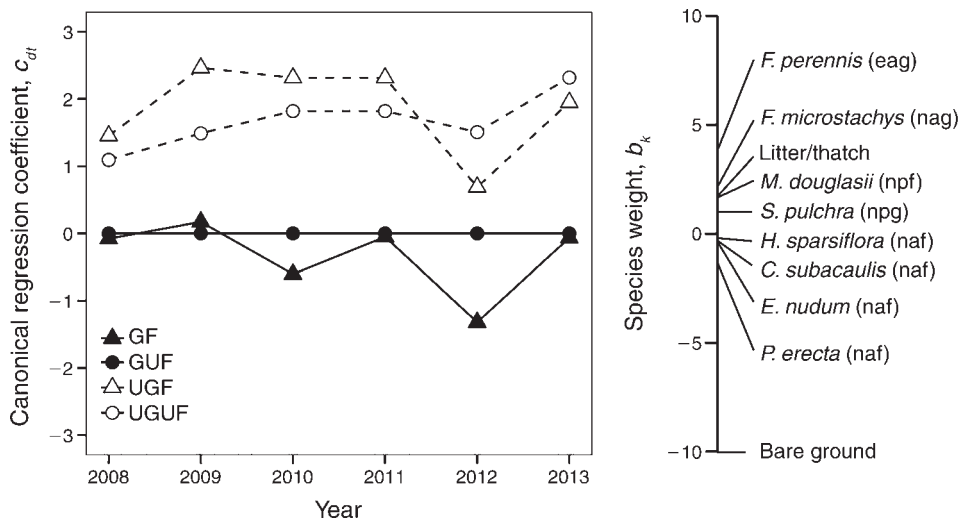

FIG. 3. Principal response curves (PRC) for experiment 1 showing each treatment's canonical regression coefficients over time relative to the control treatment (GUF). Community responses differed significantly between grazing treatments ($F = 13.101$, $P = 0.025$). The five species with the largest and the five species with the smallest weights (b_k) are displayed and functional groups are provided in parentheses for each species: eag, exotic annual grass; naf, native annual forb; nag, native annual grass; npf, native perennial forb; npg, native perennial grass.
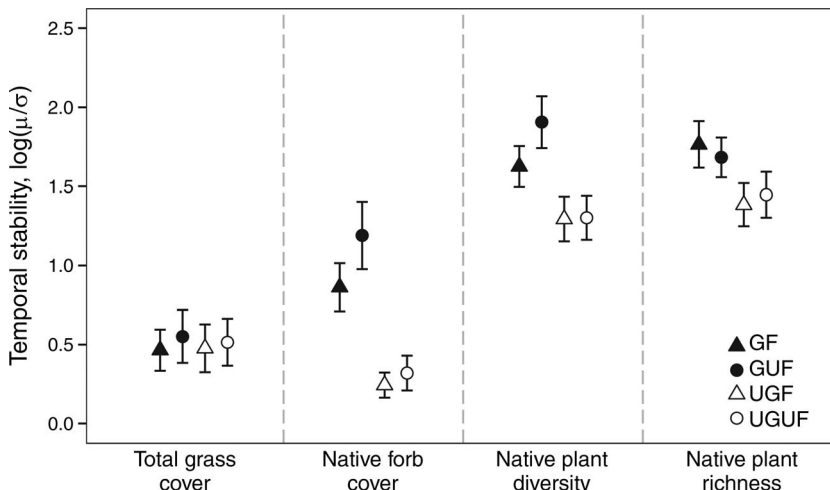
FIG. 4. Temporal stability (mean ± SE) of serpentine plant communities. The temporal stability of total grass cover, native forb cover, native plant diversity, and native plant richness are shown for our four experimental treatments: GF, grazed and fertilized; GUF, grazed and unfertilized; UGF, ungrazed and fertilized; UGUF, ungrazed and unfertilized.

change the mean to variance ratio of ungrazed plots relative to grazed plots.

DISCUSSION

Ecological determinants of serpentine community structure

Our findings suggest that both top-down and bottom-up controls influence the plant community composition of a serpentine grassland in a mediterranean climate. Climate, the most important bottom-up control in this study, was responsible for substantial interannual variation in plant community composition observed at Coyote

Ridge between 2008 and 2013. Previous research has shown that precipitation strongly influences serpentine community structure (Hobbs and Mooney 1991, Hobbs et al. 2007). Both the timing and amount of precipitation were associated with plant community composition in our study. Total grass cover increased with winter precipitation, ranging from an average of 23% in the driest year to 45% in the wettest year, whereas native forb cover tended to decrease as grass cover increased.

Cattle grazing influenced both directional changes in plant community composition and the temporal community variability in this system. Within the interannual community patterns driven by climatic variability, we

TABLE 3. Summary of LME model analysis of plant community stability, in which stability values were ln-transformed to improve normality.

Treatment	Stability (μ/σ)		Temporal mean (μ)		Standard deviation (σ)	
	F	P	F	P	F	P
Total grass cover						
Grazing	0.009	0.927	*4.839*	*0.055*	**11.775**	**0.007**
Fertilization	0.364	0.554	0.278	0.605	0.365	0.553
Grazing × Fertilization	0.055	0.817	0.006	0.981	0.177	0.679
Native forb cover						
Grazing	**20.451**	**0.001**	0.063	0.808	**11.737**	**0.008**
Fertilization	**5.934**	**0.025**	0.116	0.737	1.905	0.184
Grazing × Fertilization	2.327	0.145	0.210	0.653	0.579	0.457
Native plant diversity						
Grazing	**13.841**	**0.005**	1.032	0.336	**11.965**	**0.007**
Fertilization	1.316	0.266	1.355	0.260	0.584	0.455
Grazing × Fertilization	1.181	0.291	0.038	0.848	1.817	0.194
Native species richness						
Grazing	**6.350**	**0.033**	0.250	0.629	**5.147**	**0.049**
Fertilization	0.006	0.938	1.279	0.273	0.032	0.861
Grazing × Fertilization	0.354	0.560	0.101	0.754	0.019	0.892

Notes: For Grazing, df = 1, 9; for Fertilization and for Grazing × Fertilization, df = 1, 18. Significant treatment effects ($P < 0.05$) are indicated in boldface; marginally significant effects ($P < 0.10$) are italicized.

observed a divergence in community composition between grazed and ungrazed plots, beginning in the fourth year of experiment 1. Consistent with previous observational studies (Weiss 1999, Safford and Harrison 2001, Harrison et al. 2003), we found that grazed communities had reduced grass cover, greater native species richness, and greater native forb cover compared to ungrazed communities, indicating that grazing is an effective management strategy to maintain native richness on Coyote Ridge. Although grazing effects were less pronounced in experiment 2, there appeared to be a trend toward community divergence between grazed and ungrazed treatments.

Ecological theory predicts that top-down controls should have a stronger influence on community composition in resource-poor environments than in high-resource systems (Milchunas et al. 1988, Proulx and Mazumder 1998). Although large herbivores generally exert a negative influence on plant diversity in low-productivity systems (Bakker et al. 2006; but see Fensham et al. 2014), we found that the presence of large herbivores had a positive effect on plant diversity and richness. Positive effects of grazing on plant diversity are most commonly observed in mesic grasslands with a long evolutionary history of grazing (Collins et al. 1998, Koerner and Collins 2014). In these systems, grazers preferentially consume the large-statured, dominant grasses that often suppress small-statured species. Similarly, it has been proposed that grazing in serpentine grasslands reduces the biomass of the dominant species (exotic annual grasses), resulting in competitive release for a host of native forbs and enhanced plant richness (Weiss 1999, Safford and Harrison 2001, Harrison et al. 2003). Commensurate with this mechanism, we observed a negative correlation between exotic cover and native plant richness in multiple years. Moreover, grazing did not influence the relationship between exotic cover and plant richness, suggesting that grazing maintains plant richness indirectly by reducing grass biomass. Although the relationship between exotic species abundance and native plant richness in serpentine grasslands may depend on scale (Shea and Chesson 2002, Harrison et al. 2006), our analysis was conducted at an appropriate spatial scale to evaluate direct competitive interactions among native plants and exotic invaders (Davies et al. 2005, Melbourne et al. 2007).

Although the categorical grazing treatments had significant effects on community composition, we predicted that, similar to previous findings (Pasari et al. 2014), continuous measures of grazing intensity would provide a better metric for quantifying the effects of grazing on serpentine plant communities. In contrast, we found no relationship between mean annual grazing intensity and community composition over the full duration of the experiment. Variation in precipitation could have produced these disparate results, but patterns of winter precipitation, which we found to be most strongly associated with community composition, were unrelated to the patterns in the community response to grazing intensity. Instead, we hypothesize that continuous measures of grazing intensity are better predictors of short-term community change (i.e., within or between years) rather than changes over longer time periods. Two previous studies at this site found that continuous measures of grazing intensity were associated with changes in community composition (Pasari et al. 2014) as well as rates of microbial N mineralization and extracellular enzyme activity (Esch et al. 2013), suggesting that measures of grazing intensity may be useful for characterizing short-term ecosystem responses to grazing. In the present study, we were unable to examine community responses to grazing intensity over short time periods because of numerous camera failures between 2011 and 2013, but the categorical effects of grazing strongly influenced community composition over time.

Contrary to our expectations, N addition did not drive changes in plant community composition in either experiment. Unfertilized subplots tended to have lower native plant diversity and richness than fertilized subplots in experiment 1, but this pattern was associated with a spike in exotic grass cover within several ungrazed–unfertilized plots in 2013 and may not be attributable to our experimental treatment. The negative effects of N deposition on plant diversity are well documented (Vitousek et al. 1997, Fenn et al. 2003, Clark et al. 2007, Bobbink et al. 2010). Even moderate levels of N enrichment can reduce biodiversity over extended time periods (Clark and Tilman 2008). Previous nutrient enrichment studies in serpentine grasslands have shown that N addition alters the competitive dynamics of plant communities in favor of nitrophilic exotic grasses, which negatively affect native forbs adapted to nutrient-poor serpentine soils (Huenneke et al. 1990, Vallano et al. 2012). Given our relatively broad cover classes, experimental N addition could have increased grass productivity without detectably increasing grass cover, but we did not observe the reduction in forb abundance or diversity expected to accompany an increase in grass biomass production. Alternatively, the lack of a community response to experimental N addition in this study could be ascribed to historically high rates of background N deposition at Coyote Ridge (upward of 15 kg N ha^{-1} yr^{-1}; Weiss 1999), exceeding the estimated critical load for exotic species invasion of 6 kg N ha^{-1} yr^{-1} (Fenn et al. 2010). Yet, in a previous study using the same experimental plots, low-level N addition increased rates of N-mineralization, microbial respiration, and microbial enzyme activity, suggesting that the ecosystem is not N-saturated with respect to microbial processes (Esch et al. 2013). Thus, although low-level N fertilization in addition to background rates of N deposition may be sufficient to impact microbial processes in the soil, it is possible that the accumulation of N in our study has not

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yet reached sufficient levels to induce additional changes in plant community composition beyond those that have already occurred in this system as a result of elevated N deposition over the past several decades (Bobbink et al. 2010, Fenn et al. 2010).

Grazing effects on the temporal stability of plant communities

In addition to reducing the dominance of exotic grasses and maintaining native species richness, grazing increased the temporal stability of native forb cover, native plant diversity, and species richness. This increased stability resulted from decreased interannual community variation with grazing, rather than from a difference in the temporal mean of species richness, suggesting that the observed grazing effects on community stability are independent of diversity (Ives and Carpenter 2007). We hypothesize that grazing decreased variation in native plant communities by restricting the abundance of dominant grasses and weakening the response of grass cover to interannual variation in precipitation. In contrast to previous research demonstrating that dominant species can increase or maintain community stability (Sasaki and Lauenroth 2011, Yang et al. 2011, Wilsey et al. 2014), our hypothesized mechanism suggests that dominant species can decrease community stability in some systems, particularly those in which the invasion of exotic species is mediated by changes in the abiotic conditions of a system.

Temporal stability has been recognized as an important property of ecosystems relevant for the reliable provisioning of ecosystem functions (Tilman et al. 2006, Ives and Carpenter 2007). Although increased stability is often considered beneficial, serpentine grasslands are inherently dynamic systems and decreased system variability could have undesirable consequences. For instance, the fluctuation of species in response to climatic variability can promote coexistence between exotic grasses and native plants in serpentine grasslands by allowing forbs to escape direct competition with the dominant invaders (Levine and Rees 2004). However, it is important to distinguish between the stability of populations and the stability of communities and to recognize that short-term, population-level instability can produce long-term, community-level stability (Chesson and Huntly 1989, Tilman 1996).

The temporal stability of native plant communities in serpentine grasslands could have important ecological consequences for insect pollinators, a group of particular conservation concern on Coyote Ridge because the site hosts the only remaining population of the threatened Edith's Bay checkerspot butterfly. Decreased variation in floral diversity and abundance may increase pollinator diversity and stabilize insect populations (Potts et al. 2003, Ebeling et al. 2008), especially for specialist pollinators in fragmented landscapes (Steffan-Dewenter and Tscharntke 1999, Tscharntke and Brandl 2004). The limited dispersal ability of the Bay check-

erspot butterfly makes it vulnerable to fluctuations in the abundance of its annual host plants (Harrison et al. 1988, Murphy and Weiss 1988, Harrison 1989). The increased stability of native plant communities with grazing could reduce the risk of local extinction in naturally fragmented serpentine outcrops (Weiss 1999, Wolf and Thorp 2011).

Management implications

In this study, we show that grazing can be used to reduce exotic grass abundance, maintain native plant cover, mitigate the loss of native species, and promote community stability in serpentine grasslands at both ambient and moderately elevated levels of N deposition. Although grazing might not be an effective management strategy in all California grasslands (Kimball and Schiffman 2003), our results support the efficacy of grazing as a management tool in serpentine grasslands. Additionally, our findings have direct implications for the conservation of the federally threatened Bay checkerspot butterfly. In combination with its narrow range, limited dispersal ability, fragmented habitat, and annual life cycle, this butterfly's dependence on specific host plants leaves the species vulnerable to local extinction (Murphy and Weiss 1988, Harrison 1989, Weiss 1999, Zavaleta et al. 2009). Thus, increased plant community stability under grazing could maintain host plant abundance and nectar availability in this inherently variable ecosystem. Although the Bay checkerspot butterfly represents the best-studied insect species in serpentine grasslands, numerous other insects of conservation concern are present in the region (Connor et al. 2002) and might also benefit from the increased native plant abundance, diversity, and stability provided by grazing. Consequently, grazing may be necessary to maintain both diverse native plant communities and the insect communities endemic to California's serpentine grasslands (Weiss 1999, Connor et al. 2002, Safford et al. 2005). More generally, our study demonstrates how an understanding of top-down and bottom-up ecological controls can inform management strategies and mitigate the adverse ecological consequences of global change (Bobbink et al. 2010, Fenn et al. 2010).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-1093.1.sm