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Interactive Effects of Nitrogen Deposition and Grazing on Plant Species Composition in a Serpentine Grassland

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Abstract

The interaction of resource availability and disturbance can strongly affect plant species richness and the spread of exotic plants. Several ecological theories posit that disturbance mediates the richness-reducing effects of increased competition as resource levels rise. In the low-nutrient serpentine grasslands of the San Francisco Bay Area, the fertilizing effects of atmospheric nitrogen (N) deposition may threaten native species by promoting nitrophilic exotic grasses. Attempts to mitigate these N deposition effects have focused on cattle grazing as a strategy to reduce exotic grass cover. We simulated realistic N deposition increases with low-level fertilization, manipulated grazing with fencing, and monitored grazing intensity using camera traps in a 4 yr factorial experiment to assess the effects of grazing and N deposition on several measures of native and exotic species dynamics in California's largest serpentine grassland. Our results suggest that native species diversity may increase slightly under low-level N deposition with moderate grazing in this system. However, grazing may not be effective at limiting exotic cover as N accumulates in the future. Examination of treatment trajectories using principal response curves indicated that responses to grazing might be determined more by functional group (forb or grass) than origin (native or exotic). Grazing intensity varied dramatically within the single stocking rate used to manage this ecosystem. Given this variation and the contrasting effects of grazing on different functional groups, more targeted management may be required to improve conservation outcomes.

Key Words: California, camera trap, *Festuca perennis*, grazing intensity, invasive species, principal response curves

INTRODUCTION

Nitrogen (N) enrichment can facilitate plant invasions in a wide range of nutrient-poor ecosystems by allowing previously excluded nitrophilic invasive plants to establish and spread (Scherer-Lorenzen et al. 2007; Fenn et al. 2010; Pasari et al. 2011). Many of the most affected ecosystems are also hot spots of native biodiversity (Phoenix et al. 2006; Bobbink et al. 2010). Grazing is used to manage invasive plants in some N-limited ecosystems receiving atmospheric N deposition because grazing may remove excess N (once grazers are harvested/removed) or reduce the relative cover of invasive species (ten Harkel Matthijs and van der Meulen 1996; Weiss 1999; Plassmann et al. 2009). However, current methods assess grazing intensity at coarse scales with indirect measures that do not correspond well with the scale of plant community measurements. Thus, it is unclear how heterogeneity in grazing intensity affects invasion control and other conservation targets. Furthermore, because of a lack of studies assessing grazing effects under realistic, anticipated increases in N deposition, we do not know if the efficacy of grazing management in N-limited ecosystems will change as N continues to accumulate.

Temperate N-limited ecosystems are particularly prone to invasion by nitrophilic grasses such as *Festuca ovina* L. (Heil and Diemont 1983), *Bromus madritensis* L. (Brooks 2003), and *Festuca perennis* Columbus & J.P. Sm. (Vallano et al. 2012), the most abundant invasive plant in the serpentine grasslands of the San Francisco Bay Area (hereafter Bay Area). In some of these ecosystems, even low levels of N deposition (10 $kg \cdot ha^{-1} \cdot yr^{-1}$) facilitate grass dominance (Bobbink 1991; Bobbink et al. 1998), sometimes irreversibly (Clark and Tilman 2008). Serpentine grasslands are a model system to investigate the effects of nutrient deposition on invasion and invasive species management. These ecosystems have been used as model low-nutrient ecosystems for studying basic ecological and evolutionary questions because of their species diversity, abrupt resource gradients, and patchy distributions within more productive ecosystems (Harrison and Rajakaruna 2011). Resource addition studies have established macronutrient limitation as the most severe limiting factor in many serpentine ecosystems (Proctor 1971; Proctor and Woodell 1975; Roberts and Proctor 1992; Alexander et al. 2007). Likewise, comparisons of disturbances in serpentine and nonserpentine ecosystems have helped improve our understanding of plant ecological strategies and established the strong influence of grazing in many serpentine ecosystems (Safford and Mallek 2011).

Bay Area serpentine grasslands are an important refuge for native insect and plant species, containing 14 federally listed threatened or endangered species and at least 14 others of conservation concern, including many endemics (U.S. Fish and Wildlife Service 1998; Safford et al. 2005; Curtis 2008; Mayall 2008). The most well known of these is the federally listed,

endemic Bay Checkerspot Butterfly (*Euphydryas editha bayensis* Stern.). In the low-nutrient serpentine grasslands of the Bay Area, the fertilizing effects of atmospheric nitrogen (N) deposition (a resource addition) may threaten native species by promoting nitrophilic exotic grasses. Attempts to mitigate these N deposition effects have focused on cattle grazing (a disturbance) as a strategy to reduce exotic grass cover (U.S. Fish and Wildlife Service 1998; Weiss 1999; Fenn et al. 2010). N deposition on Bay Area serpentine grasslands currently ranges from 4 to 15 kg·ha^{-1}·yr^{-1} (Fenn et al. 2010). Nutrient experiments in these grasslands have all shown that exotic grasses respond more favorably to N additions than natives (Hobbs et al. 1988; Huenneke et al. 1990; Vallano et al. 2012). However, all serpentine nutrient addition studies and almost all grassland nutrient addition studies worldwide have added nutrients at rates at least five times greater than current or anticipated deposition loads, and the response of plant communities to realistic increases in N deposition over time is largely unknown.

Observational studies suggest that grazing can reduce adverse N deposition effects in these grasslands (Weiss 1999), though this has yet to be confirmed experimentally. Cattle grazing in California's serpentine grasslands tends to favor native forbs and reduce exotic grasses (Weiss 1999; Safford and Harrison 2001; Gelbard and Harrison 2003; Harrison et al. 2003; Weiss et al. 2007; Safford and Mallek 2011). The grazing levels commonly used to manage these grasslands also increase species richness, which is largely driven by increases in natives since there are fewer exotic species (Safford and Mallek 2011). However, almost all grazing experiments in this and other ecosystems only apply grazing as a categorical treatment, neglecting potential differences in grazing intensity (defined in this paper as the number of bites·m^{-2}) within grazed treatments. Furthermore, existing grazing intensity metrics like stocking rate, residual dry matter, and percentage use coefficients measure grazing indirectly by quantifying the density of grazers or grazed plants, as opposed to the act of grazing.

The individual effects of grazing and N fertilization on serpentine grassland community composition are well established. However, little is known about the interactive effects of this disturbance and this resource addition. Meta-analyses across several ecosystems suggest that intensive herbivory typically decreases producer richness in low-nutrient ecosystems. Conversely, herbivory tends to increase producer richness in nutrient-enriched ecosystems (Proulx and Mazumder 1998; Worm et al. 2002; Hillebrand et al. 2007). The only study that examined the combined effects of nutrient additions and grazing in a California grassland demonstrated important effects of grazing, N, year, and their interactions (Jones and Evans 1960); however, this study was conducted in an exotic-dominated, nonserpentine grassland. Thus, serpentine grasslands present an excellent opportunity to investigate basic ecological questions about the interaction of resources and disturbance, and to improve applied management efforts in a model N-limited ecosystem of conservation concern.

We simulated realistic N deposition increases with low-level fertilization, manipulated grazing with fencing, and monitored grazing intensity directly with camera traps in a 4-yr factorial experiment to assess the effects of disturbance and resource additions on several measures of native and exotic species dynamics in California's largest serpentine grassland. We expected that the removal of grazing would decrease native species richness and that grazing intensity would be negatively correlated with exotic cover. In addition, we hypothesized that N fertilization would also decrease native species richness by increasing dominance of exotics. However, we also hypothesized that grazing intensity and N fertilization may have interactive effects on plant community composition, depending on the relative importance of top-down and bottom-up effects on plant community composition and the variability in grazing intensity within our site. For example, N fertilization may have a stronger effect on plant community composition under low levels of grazing intensity compared to locations experiencing high grazing intensity due to differences in the amount of plant biomass removed by cattle. Thus, we used a continuous measure of grazing intensity in both fertilized and unfertilized treatments to elucidate any interactive effects.

MATERIALS AND METHODS

Study Site and Experimental Design

This study was located in grazed serpentine grasslands at Coyote Ridge in south San Jose, California (37°11′48.84″N, 121°40′30.41″W). These grasslands have a Mediterranean climate, with cool, wet winters and hot summers without significant rainfall or plant growth between June and October. The site is currently cattle-grazed at ~0.25 animal units (AU) ·ha^{-1} and has likely been grazed continuously at a similar stocking rate for several decades (S. B. Weiss, personal communication). In nearby San Jose, the long-term yearly rainfall was 560.8 ± 191.5 mm (mean ± s.d., calculated from 1895 to 2010), and the average daily high and low temperatures are 22.6°C and 9.9°C, respectively (PRISM climate group 2011). However, the timing and quantity of rainfall is highly variable from year to year, which significantly influences species composition (Hobbs et al. 2007). The June through May rain year in 2007/2008, 2008/2009, 2009/2010, and 2010/2011 had annual precipitation of 412 mm, 429 mm, 558 mm, and 569 mm, respectively (PRISM climate group 2011). Hereafter, each growing season will be referred to by the Spring year (e.g., 2007/2008=2008).

We conducted experimental N and grazing manipulations at five locations (blocks) each within a few hundred meters on Coyote Ridge to examine the plant community and ecosystem responses to these treatments. A previous study reported on the effects of grazing and N addition on microbial activity and soil carbon and N mineralization rates in this experiment (Esch et al. 2013).

To capture the topographic heterogeneity at the site, each of the five blocks was located on a unique aspect (ridge top, and north, south, east, and west-facing slopes). Grazers were able to move freely among all blocks within the larger grassland. At each block we established two 5×5 m plots in December 2007 (before the onset of seasonal cattle grazing) and fenced one of them to exclude cattle. Each of the two plots in each block was divided into two 2.5 m×5 m halves: one that received fertilizer, and one that received water as a control. Thus, there are four treatments in each block: grazed/unfertilized (GUF, the

"control" treatment), grazed/fertilized (GF), ungrazed/unfertilized (UGUF), and ungrazed/fertilized (UGF), none of which were replicated within blocks.

In September 2008 we fertilized using watering cans with dissolved NH_4NO_3 at a rate of 5 g $N \cdot m^{-2} \cdot yr^{-1}$ (to pulse the system with the equivalent of 50 kg $N \cdot ha^{-1} \cdot yr^{-1}$) at a concentration of 14.1 g $\cdot L^{-1}$ NH_4NO_3, and the unfertilized treatments were watered without N with an equivalent amount of water. In September 2009, fertilization was reduced to 1 g $N \cdot m^{-2} \cdot yr^{-1}$ (2.8 g $\cdot L^{-1}$ NH_4NO_3) and added annually in September hereafter to mimic a sustained increase of 10 kg $N \cdot ha^{-1} \cdot yr^{-1}$ above background rates of atmospheric deposition. Esch et al. (2013) reported a response by the microbial community to N addition both early and late in the growing season in our experiment, suggesting that the effects of N fertilization were maintained throughout the growing season despite a single annual application of fertilizer.

We used motion-detecting, infrared triggered cameras (Reconyx RM45 camera traps, Reconyx Inc., Holmen, WI) to record grazing intensity as the total number of cow bites that occurred in both 2009 (29 December 2008 to 14 April 2009) and 2010 (21 November 2009 to 5 April 2010) in the fertilized and unfertilized halves of the grazed 5×5 m plot in each block. Thus, grazing intensity is reported as bites $\cdot 12.5$ m^{-2}, reflecting the 2.5×5 m sizes of the fertilized and unfertilized halves of each grazed plot. Cameras were placed at the site once there was both widespread germination and cattle present and were removed at peak biomass once species composition data had been collected. All blocks were grazed for the same period of time, so grazing intensity was calculated as the total number of bites per area over the whole growing season. Our camera traps took one photograph per second when objects emitting a critical level of infrared radiation moved within their field of view. We recorded a cow bite in every photograph in which a cow's mouth was within the boundaries of the plot and in contact with vegetation. To avoid bias, grazing cattle were recorded as being on either the "left" or "right" side of the plot as seen in the image and identification of each side as either "fertilized" or "unfertilized" was later added to the data. Multiple camera failures in 2011 made grazing intensity data unanalyzable for that season. The still shot camera traps used in this study allowed us to measure grazing intensity at the plot scale over long time periods (in the present study a full growing season) at a remote field site experiencing hundreds of thousands of cattle encounters. Other technologies (e.g., radio collars, accelerometers, video cameras) that could be used to directly measure grazing intensity did not meet these criteria.

We collected data on percentage cover of all species in 0.5×0.5 m quadrats in each of the four treatments at peak biomass in late March or early April 2008, 2009, 2010, and 2011. Percentage cover of each species, litter, and bare ground was assessed visually as 1%, 2%, 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, or 100% cover. Total cover (including bare ground and litter) was constrained to 100%, and total plant cover values were typically well below 100% in this low-productivity ecosystem.

Data Analysis

In order to improve detection and interpretability of treatment effects given the high interannual variability of serpentine grasslands (Hobbs et al. 2007), we assessed grazing and fertilization effects on the change in native richness, change in native cover, and change in exotic cover from 2008 to 2011 using ANOVA. We used a split-plot ANOVA with block, grazing treatment, fertilization treatment, and their interactions as fixed effects, and subplots nested within grazing treatments as a random effect.

We did not analyze treatment and year effects on raw cover and richness because dependent variables within treatments were likely correlated with respect to year. We did not use repeated measures ANOVA because binary treatment levels and lack of treatment replication within blocks produce linear dependencies that bias estimates in a repeated measures model.

Treatments are categorical in this experiment, however we also measured continuous levels of grazing intensity in each treatment to complement our categorical, ANOVA-based analysis. We used ANCOVA to analyze the effects of grazing intensity (continuous), fertilization treatment (categorical), and block on the change in native richness, change in native cover, and change in exotic cover from 2008 to 2010. We used graphs of ordinary least squares (OLS) regressions between continuous dependent and independent variables within each categorical treatment to display treatment and interaction effects from ANCOVA. Dependent variables in this analysis (change from 2008 to 2010) differ from those in the ANOVA analyses (change from 2008 to 2011) because grazing intensity was measured only in 2009 and 2010.

We expected that fertilization would increase grazing intensity by increasing productivity and/or plant tissue N. To examine variability in grazing intensity between and within treatments, we compared it using one-tailed paired t tests because of the expectation of increases due to fertilization.

We also used OLS regression to investigate the effects of exotic cover on native richness, litter cover on exotic cover, litter cover on native cover, litter cover on native richness, exotic cover on next year's litter cover, and exotic cover on next year's native richness. For data collected for more than 1 yr, we also analyzed the change in each independent variable on the change in each dependent variable. We log transformed data as necessary to improve normality, but all figures use raw data to improve interpretability. All means are reported with their associated standard errors.

We analyzed treatment trajectories and effects on individual species using principal response curves analysis (PRC). PRC is a special case of redundancy analysis that was developed for analysis of community response data from designed experiments sampled repeatedly through time (Van den Brink and Ter Braak 1999). PRC provides clear visualization of community composition trajectories in comparison to a control treatment and has been used in other grasslands to track community response to resource enrichment or disturbance (Britton and Fisher 2007; Pavlů et al. 2007; Kardol et al. 2009). Specifically, PRC measures species composition variance due to time and then attributes remaining variance to experimental treatments. The significance of the PRC was tested by performing Monte Carlo time series permutations of the quadrats in the partial redundancy analysis from which the PRCs were obtained using
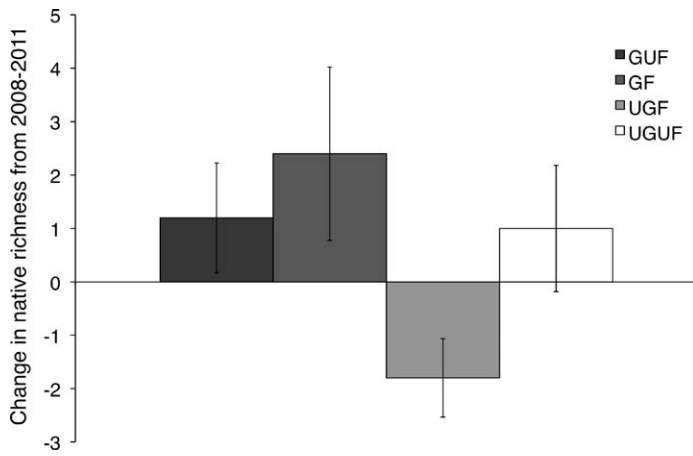
Figure 1. Change in native species richness from 2008 to 2011 (mean ± standard error). GF indicates grazed/fertilized; GUF, grazed/unfertilized; UGF, ungrazed/fertilized; and UGUF, ungrazed/unfertilized. Treatments are listed in the order shown in the key. The ungrazed treatments began before the 2008 season and the fertilization treatments began before the 2009 season. There was a significant interaction between grazing and fertilization treatments ($P=0.05$).

an F statistic based on the eigenvalue of the component. Canonical regression coefficients (c_{dt}) and species weights (b_k) are used to indicate the strength of treatment trajectories and species responses, where $1-\exp(b_k \times c_{dt})$ is the proportional change of species k in treatment d and year t relative to its percentage cover in the control. Since this grassland has been grazed for a long period, the grazed/unfertilized (GUF) treatment was used as the control in all PRC analyses. To avoid problems associated with zero counts for some species in some treatments, arbitrarily small values were added to such counts before analysis (Van den Brink and Ter Braak 1999). Linear regression was conducted in Microsoft Excel (Microsoft Corporation 2004), ANOVA and ANCOVA were conducted in SAS JMP (SAS Institute 2007), and PRC was analyzed using R (R Development Core Team 2011).

RESULTS

Grazing Intensity

In 2009, grazing intensity (no. cow bites · 12.5 m^{-2}) in grazed treatments ranged from 11 to 146 bites · 12.5 m^{-2}, and there were significantly more bites in fertilized (71.2 ± 24) than unfertilized (43.2 ± 11.6) treatments ($P=0.05$, $t=2.175$, df=4). In 2010, grazing intensity ranged from 33 to 175 bites · 12.5 m^{-2} with no overall difference between fertilized (107.8 ± 27.6) and unfertilized (95.6 ± 23.3) treatments ($P=0.171$, $t=1.079$, df=4). This variability occurred within a single overall stocking rate of ~0.25 AU · ha^{-1}. Variation in grazing intensity appeared random except for the flat, ridge-top block, which consistently and clearly received higher grazing pressure.

Other herbivores that were detected using the camera traps included tule elk (*Cervus canadensis* spp. *nannodes*), California mule deer (*Odocoileus hemionus californicus*), wild pigs (*Sus scrofa*), and rabbits (Leporidae), although the presence of these
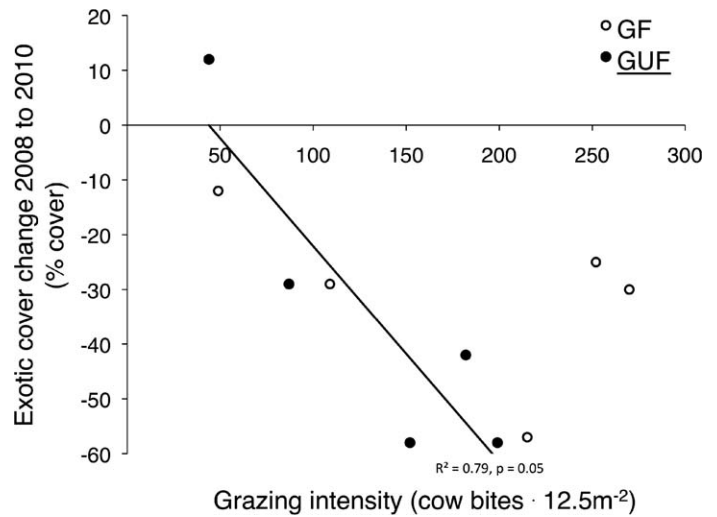

Figure 2. Change in exotic species cover from 2008 to 2010 in grazed treatments as a function of total grazing intensity in 2009 and 2010. Change in exotic cover in unfertilized treatments = $-0.39 \times$ (Cow bites · 12.5 m^{-2} in 2009 + 2010) + 17.30 ($R^2=0.79$, $P=0.05$, $N=5$, solid line). There was no significant effect in fertilized treatments ($R^2=0.23$, $P=0.41$, $N=5$, no line shown) and a marginally significant effect when plots from both treatments were combined ($R^2=0.32$, $P=0.09$, $N=10$, no line shown). This figure represents the significant fertilization treatment × grazing intensity interaction indicated by ANCOVA.

species was rare ($< 0.1\%$ of all photos) and was not included in our analysis.

Native Richness and Cover

Native richness increased by an average of one to two species in all but one treatment (UGF) during the 3 yr of the study, and there was a significant interaction between grazing and fertilization treatments on the change in native richness ($P=0.05$, $F=5.6$, df=1; Fig. 1). There were no significant treatment effects on change in native cover, which changed little during the study: GUF=$-2.8 \pm 5.1\%$, GF=$4.8 \pm 7.0\%$, UGUF=$-3.4 \pm 8.3\%$, UGF=$-8 \pm 5.4\%$. Grazing *intensity* (no. cow bites · 12.5 m^{-2}) did not significantly affect the change in native richness or cover in either fertilization treatment (ANCOVA).

Exotic Cover

There were marginal but insignificant effects of grazing and fertilization treatment on the change in exotic cover (ANOVA). However, ANCOVA revealed a significant interaction between grazing *intensity* and fertilization treatment ($P=0.05$, $F=16.2$, df=1), with higher grazing intensities reducing exotic cover in the unfertilized but not the fertilized treatments (Fig. 2).

Native–Exotic Interactions

Exotic cover had little relationship to native richness in the same year and both positive and negative correlations with the following year's native richness. In all but the first year, exotic cover, litter cover, and the following year's litter cover all increased together (see Supplemental Material, available online at http://dx.doi.org/10.2111/REM-D-13-00116.s1).
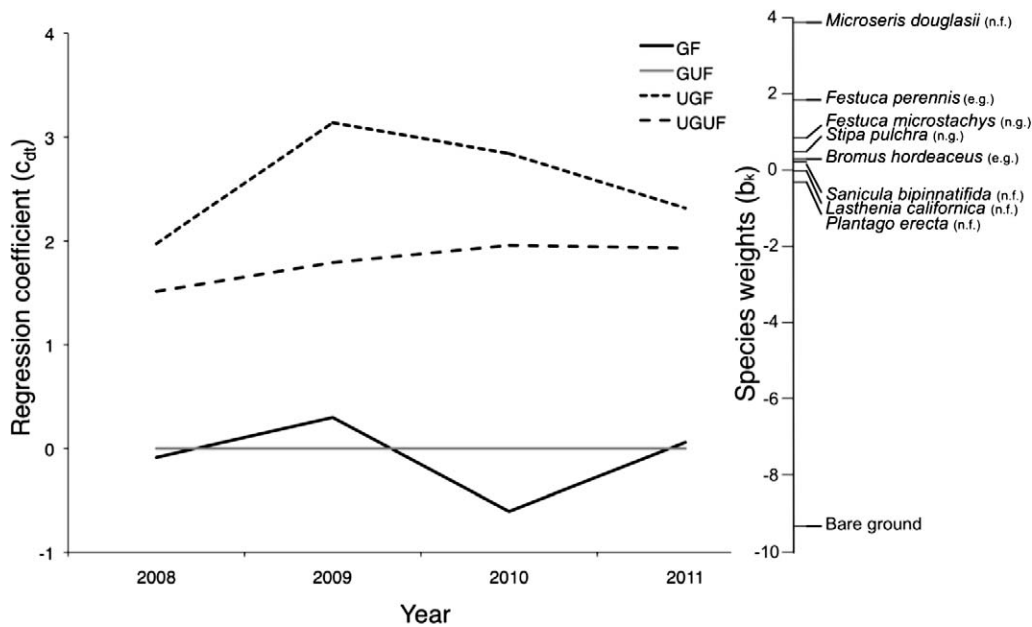
Figure 3. Principal response curves (PRC) showing each treatment's regression coefficients (canonical coefficients) relative to the control treatment (GUF) over time (first ordination axis significant at $P = 0.005$ based on 2000 Monte Carlo simulations). Higher species weights indicate a greater likelihood that a species is following the PRC pattern, while lower weights indicate species likely to follow the opposite pattern. Species close to zero show no response, or a response that is unrelated to the PRC pattern. For clarity, only relatively common species with the best fit to the first ordination axes are shown. Native forbs are abbreviated as (n.f.), native grasses as (n.g.), and exotic grasses as (e.g.). GF indicates grazed/fertilized; GUF, grazed/unfertilized; UGF, ungrazed/fertilized; and UGUF, ungrazed/unfertilized. The ungrazed treatments began before the 2008 season and the fertilization treatments began before the 2009 season.

Treatment Trajectories and Individual Species Responses

PRC identified one significant axis ($P = 0.005$ based on 2000 Monte Carlo simulations; Fig. 3). In 2008, after one growing season without grazing but not yet having been subjected to added N, the ungrazed treatments were already separated from the grazed treatments and remained separated from them after N additions from 2009 through 2011. Also of note is the abrupt increase and gradual return of the UGF regression coefficient relative to the UGUF coefficient following the initial pulse of high N levels in 2009 (Fig. 3).

The strengths of the relationships of individual species to the significant axis varied largely according to broad functional groupings. Aside from *Microseris douglasii* (DC.) Shultz-Bip., native forbs had small or negative species weights, indicating that they did not respond to treatments or that their responses did not follow the patterns in the PRC. The dominant invasive grass *Festuca perennis*, two native grasses *Stipa pulchra* Hitch. and *Festuca microstachys* Nutt., and litter all had higher species weights, indicating that they responded according to the patterns in the PRC.

DISCUSSION

Effects of N and Grazing on Community Composition

By many measures, top-down grazing effects influenced species composition more than bottom-up effects of N enrichment. Grazing altered native species richness (Fig. 1) and overall plant community composition (Fig. 3) more than the low-level N fertilization used here. However, there were also important interactions between grazing and N additions. Native species richness declined slightly in fertilized plots removed from grazing, but native species richness may be increasing slightly in grazed, fertilized plots (Fig. 1). Furthermore, exotic cover declined as grazing intensity increased under current N deposition loads, but not under future, anticipated N deposition loads (Fig. 2).

Assuming fertilization treatments are making this grassland more productive, the trend of native richness increases under grazing observed here supports predictions of Proulx and Mazumder's (1998) grazer reversal hypothesis and Huston's (1994) dynamic equilibrium model, which suggest that disturbance moderates the ability of competitive species to reduce diversity as resource levels rise (Grime 1977; Huston 1979). In support of these hypotheses, we observed a greater decline in native species richness in fertilized plots removed from grazing than in those with grazers present (Fig. 1). In addition, PRC demonstrated the ability of grazing to maintain common species abundance patterns under a heavy dose of fertilization during the first year of the study (Fig. 3). Though PRC does not measure species richness directly, this analysis provides further evidence that disturbance may impart resistance to resource enrichment (Grime 1977; Huston 1979).

Native–Exotic Interactions

We observed few direct relationships between native richness and exotic cover when both were measured in the same year. Given the positive and negative relationships theorized and observed elsewhere (Elton 1958; Grime 1973; Knops et al. 1999; Tilman 1997, 1999; Stachowicz et al. 1999; Lyons and Schwartz 2001; Levine et al. 2004; Zavaleta and Hulvey 2004),

this result was not expected. In addition, it has been previously hypothesized that grazing at our study site maintains native richness by decreasing competition with exotic grasses (Weiss 1999). Several mechanisms could explain the lack of relationship. First, study duration and sample size preclude the types of analyses (e.g., path analysis) that could improve the assessment of indirect and total exotic cover effects on native richness mediated through litter (Huenneke et al. 1990; Foster and Gross 1998; Jackson and Bartolome 2002; Lamb 2008). Second, the 0.5×0.5 m species composition quadrats may not be small enough to capture the scale of species interactions or to reduce the coexistence-promoting effects of resource heterogeneity, thus preventing the detection of the expected negative relationship between native richness and exotic cover (Lonsdale 1999; Stohlgren et al. 1999; Levine 2000; Shea and Chesson 2002; Davies et al. 2005; Melbourne et al. 2007). Third, it is possible that this study used the correct spatial and temporal scales to capture species interactions, but treatment effects were not mediated through species interactions detectable in this study. For example, while grazing may reduce exotic cover, its main benefit to natives could be mediated through reduction in exotic grass height allowing increased light penetration, which was not measured here. Fourth, competition within functional groups has been shown to exert much stronger effects on invasion and community structure in Bay Area serpentine grasslands than competition between functional groups (Hooper and Dukes 2010). Since there was only one native annual grass species detected in this study (*Festuca microstachys*), it is possible that the exotic annual grasses invading serpentine grasslands are filling empty niches without affecting the forb and perennial grass-dominated native community.

Plot-Level Variation in Grazing Intensity

Our results suggest that direct, plot-level quantification of grazing intensity is useful for determining the effects of grazing at scales relevant to community dynamics, and may capture responses that are not apparent when considering grazing as a categorical variable. In our study, grazing intensity varied by more than an order of magnitude within a single cattle stocking rate, and this variation had an effect on exotic cover that provided more information than the use of grazing as a categorical variable alone. The analysis of grazing intensity also elucidated effects on microbial processes such as N mineralization rates and enzyme activity reported previously by Esch et al. (2013). Since camera traps measure grazing intensity directly, they could be used to assess the link between grazing intensity and grazing impacts in any grazed ecosystem. This method may be particularly effective in systems with cattle grazing that also include significant populations of native herbivores with unknown population densities. This direct measure of grazing intensity may also be useful because indirect measures like stocking rate (Cao et al. 2004) are inappropriate for quantifying differences within single stocking rates, and measures based on residual biomass (Biondini et al. 1998; Allen-Diaz and Jackson 2000), residual dry matter (Bartolome et al. 1980, 2002), or percentage use coefficients (Holechek and Galt 2000) may be confounded by environmental factors other than grazing.

Management Implications

Our management recommendations are most directly informed by exotic cover responses to grazing intensity and N fertilization. While grazing reduced exotic cover under current levels of N deposition, it is not clear that grazing at any intensity will significantly mitigate possible exotic cover increases under future N accumulation (Fig. 2). Our findings also highlight the variability of grazing intensity and its effects even within a single cattle stocking rate (Fig. 2), and suggest that more targeted management might be required to ensure that any conservation benefits of grazing are distributed more evenly throughout this site (Bailey 2004; Finnoff et al. 2008). In addition, our analysis of treatment trajectories (PRC) revealed community responses not apparent by looking at native richness and exotic cover alone. Specifically, some native grasses (e.g., *Festuca microstachys* and *Stipa pulchra*) and even select native forbs (e.g., *Microseris douglasii*) may respond to grazing differently than the majority of native species overall (Fig. 3). Future studies are urgently needed to determine if more targeted grazing management might improve conservation outcomes for all native species. Lastly, it is important to remember that this grassland received significant amounts of N deposition for decades prior to this study due to its location near a major urban area. The effects of increasing N deposition at more pristine serpentine grasslands may be quite different.

While grazing may not effectively control invasive plants in all California grasslands (Kimball and Schiffman 2003), there is much evidence suggesting that it is effective in California's serpentine grasslands (Weiss 1999; Safford and Harrison 2001; Gelbard and Harrison 2003; Harrison et al. 2003; Weiss et al. 2007; Safford and Mallek 2011). Our results support the use of grazing as an effective management tool, but also suggest that grazing may become less effective as N accumulates through atmospheric deposition over time at this site. We also suggest that more targeted grazing management might improve conservation outcomes at this site. Thus, in the absence of policy changes to reduce N emissions, a reevaluation of the most effective means of controlling exotic species in this serpentine grassland may be needed.

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