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Original Research

Livestock Exclusion Impacts on Oak Savanna Habitats—Differential Responses of Understory and Open Habitats[☆]Karen A. Stahlheber^{a,*}, Carla M. D'Antonio^a, Claudia M. Tyler^b^a Departments of Environmental Studies and Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA^b Earth Research Institute, University of California, Santa Barbara, CA 93106, USA

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ABSTRACT

Large grazing animals can have profound impacts on plant communities and soil properties; however, these impacts are not always uniform across or within regions. The distribution of features such as forage quality, water, or shade within a pasture can change the behavior of grazers and thus, the impact of their grazing. Where managed livestock grazing has been proposed as a conservation tool to enhance or maintain desirable plant communities, understanding how spatial variation between tree and intertree habitats within a savanna landscape affects the response of vegetation and soil properties to grazing will be critical for designing management plans for different sites. In this study, we used a previously established, long-term livestock grazing experiment in California oak [*Quercus* L.] savannas to investigate how the removal of grazing affected plant communities and soil characteristics underneath and outside of isolated tree canopies. In the oak understory, plant community composition shifted in response to livestock removal, largely due to a 68–400% increase in the relative cover of native species. Overall plant community composition in open grassland neighboring trees changed little in response to livestock grazing removal, yet we did see a decrease in species richness and diversity surrounding deciduous oaks as the dominance of the exotic annual *Bromus diandrus* Roth increased. The depth of plant litter increased 1–2 cm in both habitat types when livestock grazing was absent, along with minor changes in soil carbon, nitrogen, and bulk density. These results highlight how different habitat patches within savanna landscape can have varying responses to grazing removal and illustrate how challenging it will be to use grazing as a management tool to enhance the diversity of native species. In the oak understory, native species that are tolerant of herbivory may be absent or unable to coexist with non-native annual grasses. The abundance of understory habitat at a particular site may therefore be an important variable predicting the outcome of livestock grazing.

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Introduction

Livestock grazing is one of the most widespread human land uses globally, with rangelands comprising approximately 51% of the world's land area (Heady and Child 1994). Large grazing animals, whether wild herds or domestic livestock, have significant effects on the ecosystems they occupy (Borer et al. 2014; Milchunas and Lauenroth 1993; Olff and Ritchie 1998). In many grassland and savanna habitats, herbivory by grazing mammals and its associated disturbances alter plant diversity and soil resources, as well as the spread or persistence of exotic species (Dorrough et al. 2007; McSherry and Ritchie 2013; Strum et al. 2015). Livestock grazing tends to reduce dominance by tall, competitive grasses and break up dense litter layers, resulting in positive effects on

overall community diversity by favoring small-stature, broad-leaved plants (Diaz et al. 2007; Pakeman 2004). These effects on plant species are not always similar across local or regional environmental gradients (Cingolani et al. 2005; Koerner et al. 2014; Lunt et al. 2007; Osem et al. 2002). For example, Marty (2015) showed negative, positive, and neutral effects of grazing on native plant richness along a fine-scale moisture gradient in vernal pool grasslands. Understanding how local habitat influences grazing responses will be critical for land managers seeking to use grazing as a conservation tool.

Many local attributes of a rangeland affect the behavior of grazing ungulates within a pasture or rangeland, including the patchiness of forage, water, and shade (Adler et al. 2001; Chapman et al. 2007; Senft et al. 1985). Large, isolated trees in African savannas are important resources for wild and domestic grazing ungulates; understory forage is frequently of higher nutritional quality and dung deposition is higher beneath trees (Belsky 1992; Treydte et al. 2007; Treydte et al. 2010). Yet for many types of grasslands outside of Africa, we lack a clear understanding of how the presence of trees affects the impact of livestock.

Livestock grazing is a dominant land use within California oak [*Quercus* spp.] savannas and woodlands, and it has both directly and

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indirectly impacted the structure of these habitats. In California, > 80% of large properties (> 200 acres) within oak woodland are grazed by livestock (Huntsinger et al. 2010; Spiegel et al. 2016). Although oak trees are an important feature of California landscapes ecologically and socially (Davis et al. 2016; McClaran and Bartolome 1985), they have been extensively cleared and thinned since the arrival of Europeans (Huntsinger et al. 2010; Tyler et al. 2007), and in many cases, thinning took place for rangeland “improvement” (Frost et al. 1997). These losses and the introduction of many new species coincide with reductions in Native American burning across the California foothills (Anderson 2005), undoubtedly also affecting the relative distribution of oaks across the region. Oak recruitment has been episodic or rare over the past 2 centuries, maintaining the widespread decline in oak density across California savannas (McLaughlin and Zavaleta 2013; Zavaleta et al. 2007).

Previous evaluations of the effects of livestock grazing have focused mostly on open habitats (i.e., grasslands, or the grass- or herbaceous-dominated portions of savannas) and revealed mostly positive effects on species diversity and richness, particularly among native and non-native forbs (Stahlheber and D’Antonio 2013; Bartolome et al. 2014, but see Bartolome and McClaran 1992). The oak understory, however, is often highly dominated by non-native annual grasses unpalatable to most domestic grazers once they reach anthesis, and thus these plant communities may respond differently (Callaway et al. 1991; Marañón and Bartolome 1993; Marañón et al. 2009; Stahlheber et al. 2015). In this study we took advantage of a long-term livestock grazing experiment established in 1995 (Tyler et al. 2008) to compare the effects of livestock removal on oak understory and open grassland communities. In particular, we asked 1) How does the removal of grazing affect the plant community composition in the oak understory compared with adjacent open grassland habitat, especially the richness and cover of native versus exotic species? and 2) How does the removal of grazing affect soil characteristics and the abundance of plant litter in these two habitat types?

Methods

Study Site

This study was conducted within Sedgwick Ranch (34°41’N, 120°2’W), a 2 388-ha reserve operated by the University of California, Santa Barbara since 1995. The climate is Mediterranean, with hot, dry summers and cool wet winters. The mean annual precipitation at this location is 380 mm, although high interannual variation in rainfall is a defining characteristic of the region. Precipitation for the “water years” (defined as 1 September to 31 August of the following year) during the study (2007–2008, 2008–2009) was 403 and 332 mm, respectively (Table S1; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>). The water year before the survey period began (2006–2007) was particularly dry (167 mm). The study area has not burned since establishment of the reserve.

We gathered data in an area called the “Mesa,” a mostly level, uplifted Pleistocene terrace with fine, sandy loam soils in the Positas series (fine, smectitic, thermic Mollic Palexeralfs). Before creation of the University of California Reserve in 1995, livestock grazing for beef production was the dominant use of this site, and there is no evidence of prior cultivation or plowing (Tyler et al. 2008). Livestock were removed from the majority of the reserve following its establishment, and grazing only continued in fenced pastures in the context of experimental work. Populations of native bunchgrasses such as *Stipa pulchra* Hitchc., *Stipa cernua* Stebbins & Love, and *Poa secunda* J. Presl occur at this site, interspersed within grasslands dominated by the exotic annual grasses including *Bromus diandrus* Roth, *Bromus hordeaceus* L., *Avena barbata* Pott ex Link, and *Avena fatua* L., which originated in the Mediterranean and arrived with European colonists to the region. Similar to many sites in California, several species of oak tree occur throughout the grassland. Here the dominant savanna trees are the evergreen *Quercus agrifolia* Née (coast live oak) and the deciduous *Quercus lobata* Née (valley

oak). The deciduous *Quercus douglasii* Hook. & Arn. (blue oak) is also present, though less common in savanna than the other two oak species.

Vegetation and Soil Survey

In the early spring of 2008 and 2009 (the beginning of the growing season in March–April), we surveyed the surroundings of 10 *Q. lobata* and 11 *Q. agrifolia* divided among grazed and ungrazed locations (5 each for ungrazed locations, 5 grazed *Q. lobata*, and 6 grazed *Q. agrifolia*). The grazing pastures were set up in 1995 as part of a long-term experiment on oak recruitment. Each pasture included one or more 50 × 50 m enclosures, and each enclosure included an adult oak tree at the center (see Tyler et al. 2008 for more information on experimental design). Some of our surveyed ungrazed oaks were inside these enclosures (four *Q. lobata* and two *Q. agrifolia*), while other ungrazed trees were located outside but adjacent to the fenced pastures. Fire and grazing history for these trees is identical to the enclosures within pastures. For both the grazed and ungrazed locations, oaks were haphazardly selected according to the following criteria: 1) located on predominantly flat terrain and 2) isolated from neighboring oaks by > 10 m on at least three sides. At this site, there was no evidence that *Q. agrifolia* and *Q. lobata* occurred on separate substrates or in response to an environmental gradient (discussed in Stahlheber et al. 2015). The stocking rate for the study period was ~45 head each year with paddock size ranging from 10 to 30 acres. Timing and duration of grazing varied depending on grass productivity and height, but typically cattle were introduced into the pastures in January, rotated among pastures, and removed in late May (Tyler et al. 2008).

At each oak tree, we sampled vegetation and soils in 1 × 1 m survey quadrats, equally divided between the understory and surrounding open grassland (defined as > 5 m beyond the canopy drip line). Quadrats were located along transects from the understory to open grassland along azimuths of 0, 90, 180 and 270° relative to true north (Fig. S1; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>) with four plots sampled in understory and four in open grassland in the vicinity of each tree. Survey quadrats were marked in the field and surveyed in both years. Within each quadrat, we recorded the percent cover of all plant species present and the depth of dead plant material on the soil surface 10 cm within each of the four plot corners (including dead annual grass thatch and oak leaf litter). Relative cover (as a proportion of total cover) was used in our subsequent analysis, as we allowed individual plant species cover to total > 100% where there was overlap in canopies. The average total cover of both tree species and pasture types (grazed vs. ungrazed) was close to 100%, however, so using relative cover should not change our interpretation of the data.

We collected soil cores (5.4-cm diameter) to 15-cm depth next to each quadrat in late May to early June of 2008. In the laboratory, gravimetric soil moisture was determined for subsamples taken from all soil cores. Whole cores were air-dried and weighed to calculate bulk density. Next, we sieved each core to determine the percent rocks and coarse organic material (> 2 mm) by weight. We measured soil pH using an Orion AquaPro 9156APWP electrode (Thermo Fisher Scientific Inc., Waltham, MA), and electroconductivity (µS/mL) was tested using an ECTestr 11+ (Oakton Instruments, Vernon Hills, IL). Both pH and electroconductivity were determined on a 3:1 (water:dried soil) slurry. Total carbon and nitrogen were measured using an NA 1500 Series 2 analyzer (Fisons Instruments, Beverly, MA). Subsamples of soil were sent to the University of California Davis Analytical Laboratory for measurements of exchangeable K, Na, Ca, and Mg.

Data Analysis

Since the same survey plots were measured in each year, we used repeated-measures models to examine the influence of oak species, grazing, year, and their interactions on various attributes of the plant community. The oak understory and open grassland were considered

separately in these models. Before analysis, we averaged all measurements from the four directional transects at each tree, such that we have one data point per tree. All data analysis was conducted in R 3.2.0, and significance was assigned to *P* values below a threshold of 0.05.

To analyze responses of the vegetation (question 1), we first used nonmetric multidimensional scaling (NMDS) in the “vegan” package (Oksanen et al. 2013) to explore Bray-Curtis dissimilarity between surveyed plots. Dissimilarity was calculated as pairwise differences between all plots within a given habitat category. Significance of differences in dissimilarity was evaluated using permutational analysis of variance (PERMANOVA; Anderson 2001). The *adonis* function in *vegan* does not have a method for repeated-measures designs, so to estimate *P* values for the within-subjects factor (year and its interactions with oak species and grazing), we used a permutation test within trees. For the between-subjects tests (oak species, grazing, and their interaction) we next calculated Bray-Curtis dissimilarities independently for each year and ran three separate PERMANOVA tests. Where there were significant effects in our PERMANOVA (overall or within a given year), we determined what species were responsible for the separation of plots in the ordination space by using the *envfit* function to evaluate linear relationships between individual species abundances and NMDS scores. We also performed indicator species analysis with the *signassoc* function of the “indicpecies” package (De Cáceres and Legendre 2009). These are species that are important in defining a particular group of interest.

To further characterize the vegetation responses to livestock grazing removal (question 1), we calculated species diversity for each plot using the Simpson diversity index $[1 - \sum p_s^2]$ where p_s is the proportional cover of each species in the plot. This index represents the probability of two randomly selected individuals being of different species. We also calculated total species richness and the richness and relative cover of native and exotic species. Evenness was described with Simpson's evenness $[(1/\sum p_s^2)/S]$ where *S* is the number of species found in the plot, a metric independent of species richness (Smith and Wilson 1996). These variables, along with plant litter depth, were each analyzed using repeated-measures ANOVA.

Soil environmental variables were analyzed using standard 2-way ANOVA to address our second question about the impacts of livestock grazing removal on soils, as they were only measured in 1 yr. We checked for normality of residuals using Shapiro-Wilk tests and normal Q-Q plots. Levene's test was used to check for homogeneity of variances. Where necessary, transformations (log or *n*-root) were applied in order to meet these assumptions. In the case of native and exotic cover, we also used a logit transformation (Warton and Hui 2011) in the repeated-measures models discussed in the previous paragraph. When reporting model outputs, all values presented in this manuscript have been back-transformed to the units of measurement for ease of interpretation. Significant results are highlighted later. For complete ANOVA tables, see Supporting Information (Tables S3 and S4; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>).

Results

Effects of Grazing Removal on the Oak Understory Plant Community

Composition of the understory plant community differed between locations with and without livestock (Fig. 1A). Although there was a trend for the livestock grazing effect to vary between years (*P* = 0.07), in each year the grazed and ungrazed plots were significantly different (Table 1). In 2008, there was a trend toward an interaction between the effects of livestock grazing and oak species but not in 2009 (see Table 1). One reason for this pattern is that in 2008, there was significantly more overlap in community composition between grazed and ungrazed *Q. lobata* understory assemblages compared with *Q. agrifolia* (Fig. S3; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>).

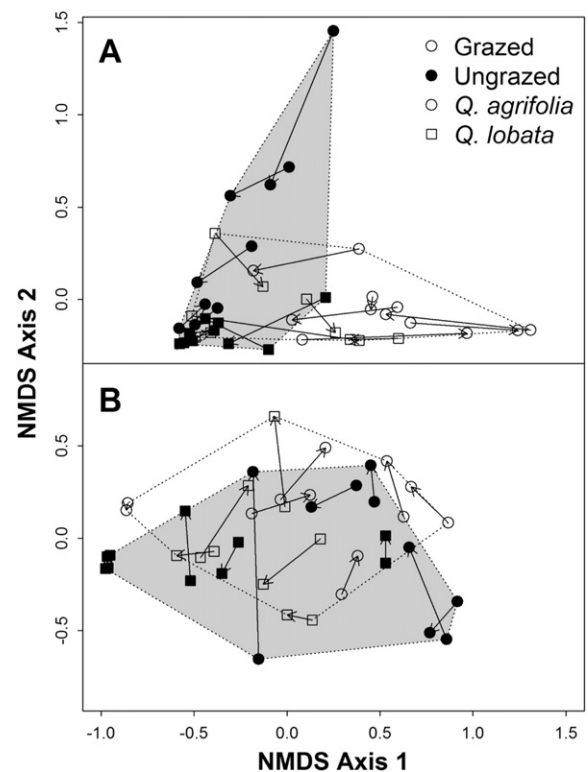


Figure 1. Nonmetric multidimensional scaling analysis of Bray-Curtis dissimilarities in plant community composition in the (A) oak understory and (B) open grassland. Grazed and ungrazed pastures are indicated by symbol color and connected by shaded polygons illustrating the extent of the ordination space they occupy. Symbol shape differentiates the oak species. Arrows illustrate how the community surrounding an individual tree changed between 2008 and 2009. Final stress for the three-dimensional solution was 0.09 after 20 iterations in both oak understory and open grassland. See Figure S2 in online <http://dx.doi.org/10.1016/j.rama.2016.10.003> Supporting Information for corresponding plots of species scores.

By contrast, grazed and ungrazed understory plant communities of both oak species had little overlap in our NMDS analysis in 2009.

Bromus diandrus and *Hordeum murinum* L. percent cover were correlated with NMDS scores in the oak understory in both years, indicating the importance of these species in differentiating plant communities. Grazed understories had higher overall cover of *H. murinum*, while understories without livestock had more *B. diandrus* (Fig. 2). In an indicator species analysis, however, we found that this pattern is affected by the species of oak (Table 2). *Hordeum murinum* was more indicative of grazed *Q. agrifolia*, whereas *B. diandrus* was most indicative of ungrazed *Q. lobata*.

Total species richness (per m²) was not affected by the removal of livestock grazing beneath the tree canopy. Native species richness, however, was one to two species higher per m² in understories of both oak species where livestock were absent ($F_{1,17} = 7.85$, *P* = 0.01, Fig. S4; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>). Indicator species analysis shows several of the native species that were less common when grazing was present, including *Pholistoma auritum* (Lindl.) Lilja, *Viola pedunculata* Torr. & A. Gray, and *Lupinus bicolor* Lindl. The relative cover of native species was likewise higher in *Q. lobata* and *Q. agrifolia* oak understories with grazing removal in both years ($F_{1,17} = 9.40$, *P* < 0.01; Fig. 3A). Species diversity (Simpson's 1-D), evenness (Simpson's Evenness), and the cover of exotic grasses, however, were unaffected by grazing in the understory (Fig. 4A; Table S3).

Effects of Grazing Removal on the Open Grassland Plant Community

Contrary to results in the understory, overall plant community composition in open grassland outside of the oak canopy did not differ between grazed and ungrazed pastures (see Table 1, Fig. 1B). Instead,

Table 1
Permutational analysis of variance (PERMANOVA) results of pairwise Bray-Curtis dissimilarities calculated among survey plots within each habitat type. “Within-subjects” tests examine the effects of year within study plots (individual trees), whereas “Between-subjects” tests address the impacts of grazing treatment and oak tree species.

	Model effect	Oak understory	Open grassland
Within-subjects PERMANOVA	Yr	$F_{1,34} = 0.454, P = 0.468$	$F_{1,34} = 1.983, P < 0.001$
	Yr * Grazing	$F_{1,34} = 1.148, P = 0.073$	$F_{1,34} = 0.355, P = 0.415$
	Yr * Species	$F_{1,34} = 0.040, P = 0.929$	$F_{1,34} = 0.344, P = 0.435$
	Yr * Grazing * Species	$F_{1,34} = 0.724, P = 0.221$	$F_{1,34} = 0.125, P = 0.871$
	Grazing	$F_{1,17} = 3.728, P = 0.006$	$F_{1,17} = 0.755, P = 0.520$
Between-subjects PERMANOVA	Species	$F_{1,17} = 2.817, P = 0.022$	$F_{1,17} = 2.975, P = 0.038$
	Grazing * Species	$F_{1,17} = 2.059, P = 0.077$	$F_{1,17} = 1.406, P = 0.216$
	Grazing	$F_{1,17} = 10.737, P < 0.001$	$F_{1,17} = 0.643, P = 0.662$
	Species	$F_{1,17} = 2.580, P = 0.069$	$F_{1,17} = 3.743, P = 0.009$
	Grazing * Species	$F_{1,17} = 1.526, P = 0.202$	$F_{1,17} = 1.260, P = 0.246$

according to PERMANOVA, year had the largest influence on variation in Bray-Curtis dissimilarities, and this difference did not interact with the presence of livestock grazing or the species of neighboring oak (see Table 1). Plant communities were also differentiated by the species of neighboring oak, despite considerable overlap in our NMDS analysis (see Table 1, Fig. S5; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>). *Bromus diandrus* and *Bromus hordeaceus* were significantly correlated with the primary NMDS axis separating the two oak species; the latter was more associated with *Q. agrifolia* plots, and the former *Q. lobata* (see Fig. S5).

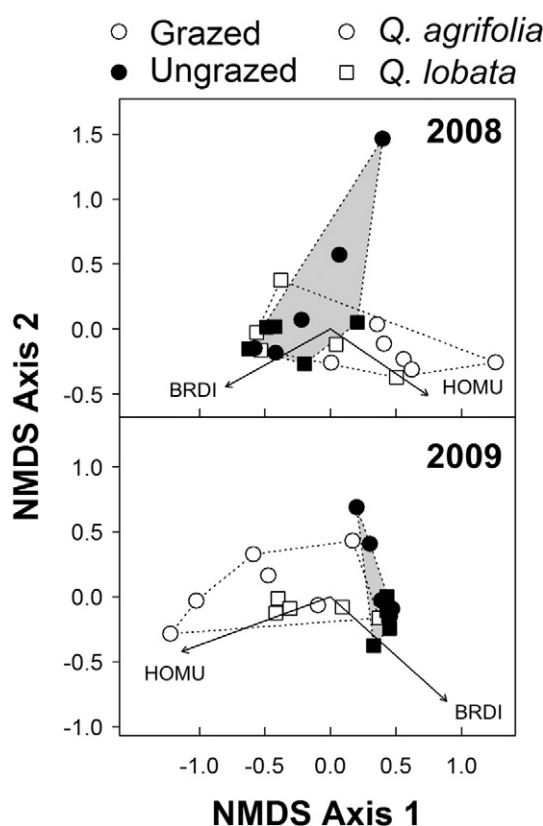


Figure 2. Nonmetric multidimensional scaling (NMDS) analysis of Bray-Curtis dissimilarities in plant community composition of the oak understory. NMDS was performed separately for each year. Grazed and ungrazed pastures are indicated by symbol color and connected by shaded polygons illustrating the extent of the ordination space they occupy. Symbol shape differentiates the oak species. Vectors (black arrows) indicate species that are significantly correlated with the NMDS scores of the sites ($P < \text{Dunn-Sidak threshold value for the number of species tested}$). Species names corresponding to abbreviations can be found in Table S2. Final stress for the three-dimensional solution was 0.06 after 20 iterations in both years.

When grazed, total species richness was similar ($\sim 9 \text{ species m}^{-2}$) in open grasslands surrounding either species of oak; however, the direction of the difference between grazing treatments varied. Ungrazed open grasslands with a neighboring *Q. agrifolia* were more rich ($\sim 12 \text{ species m}^{-2}$) than grazed plots, whereas ungrazed pastures surrounding *Q. lobata* were less rich ($\sim 6 \text{ species m}^{-2}$) compared with grazed plots (oak species * grazing: $F_{1,17} = 5.44, P = 0.03$). The same pattern was true for native species richness (oak species * grazing: $F_{1,17} = 7.89, P = 0.01$). A group of these native species were distinctive of ungrazed grasslands neighboring *Q. agrifolia*, as revealed by indicator species analysis, along with two exotic forbs (see Table 2). In contrast to native species, exotic species richness was not affected by grazing in open grassland plots (see Table S3).

Native species cover in open grasslands had a difference between livestock grazing treatments (at a higher significance threshold of $\alpha = 0.10$), and this effect depended on the species of the neighboring oak (oak species * grazing: $F_{1,17} = 4.08, P = 0.06$). Open grassland associated with *Q. lobata* without livestock had lower native cover than grazed areas, but the converse was true for *Q. agrifolia* (see Fig. 3B). Ungrazed grassland surrounding *Q. lobata* also had significantly higher exotic grass cover than all other locations (82% vs. 58–68%; oak species * grazing: $F_{1,17} = 5.64, P = 0.03$), primarily *Bromus diandrus* (see Fig. S5).

Unlike in the oak understory, we did observe significant effects of livestock grazing on diversity, at least around *Q. lobata* (see Fig. 4B). Grazed open grasslands surrounding *Q. lobata* were 58% more diverse (as measured by Simpson1-D) than ungrazed pastures (oak species * grazing: $F_{1,17} = 5.36, P < 0.01$) though species evenness was not affected by livestock grazing (see Table S3). Year affected both diversity measures. Diversity in open grasslands was significantly lower in 2008 compared with 2009 (0.52 and 0.58; $F_{1,17} = 7.91, P = 0.01$), and species evenness was also lower in 2008 compared with 2009 ($F_{1,17} = 10.03, P < 0.01$).

Effects of Grazing Removal on Environmental Characteristics

Livestock grazing affected only a few of the soil characteristics we measured in either the oak understory or the open grassland (Table 3; Table S4). In the oak understory, C:N ratios were significantly higher in grazed pastures, mostly due to increased carbon. This was true across both oak species, despite background differences in soil C:N beneath them (as discussed in Stahlheber et al. 2015). Exchangeable K^+ was also significantly higher in grazed oak understories and there were trends toward higher percent coarse organic matter and lower bulk density. In the open grassland outside the oak canopy, soil from grazed pastures had higher total carbon, nitrogen, and C:N ratios (see Table 3).

The depth of dead plant material (both annual grass thatch and oak leaf litter) tended to be 2 cm thinner when cattle were present in the understory of both oak species ($F_{1,17} = 9.48, P < 0.01$). Similarly, in open grassland the depth of dead litter and thatch was thinner in grazed open grasslands, although the difference was much greater ($\sim 1.5 \text{ cm}$) in 2008 compared with

Table 2

Indicator species for each grazing treatment in understory and open grassland associated with either species of oak. Both years have been averaged together in this analysis. Native species are in bold; nomenclature and origin follow Baldwin et al. (2012).

Oak species	Grazing	Oak understory	Open grassland
<i>Q. agrifolia</i>	Grazed	<i>Hordeum murinum</i> ¹	<i>Erodium moschatum</i> ² <i>Agoseris heterophylla</i> ² <i>Carduus pycnocephalus</i> ³ <i>Dichelostemma capitatum</i> ² <i>Thysanocarpus curvipes</i> ² <i>Torilis arvensis</i> ¹ <i>Uropappus lindleyi</i> ³ <i>Viola pedunculata</i> ¹
	Ungrazed	<i>Pholistoma auritum</i> ² <i>Quercus agrifolia</i> seedling ² <i>Viola pedunculata</i> ²	<i>Avena fatua</i> ³ <i>Croton setigerus</i> ²
<i>Q. lobata</i>	Grazed	<i>Erodium moschatum</i> ² <i>Silybum marianum</i> ³ <i>Sisymbrium officinale</i> ² <i>Amsinckia menziesii</i> ¹ <i>Avena barbata</i> ² <i>Bromus diandrus</i> ¹ <i>Bromus hordeaceus</i> ³ <i>Lupinus bicolor</i> ² <i>Quercus lobata</i> seedling ³	<i>Bromus diandrus</i> ¹ <i>Trifolium ciliolatum</i> ³
	Ungrazed		

¹ $P < 0.01$.

² $P < 0.05$.

³ $P < 0.10$.

2009 (grazing * year: $F_{1,17} = 6.10$, $P = 0.02$; Fig. S6; available online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>).

Discussion

This work highlights the varied impacts that livestock can have on different locations within a landscape, as well as how those impacts differ over time. We found that cattle grazing had a positive effect on species diversity and the cover of native species in open grasslands neighboring (> 5 m beyond the canopy edge) the deciduous *Q. lobata*.

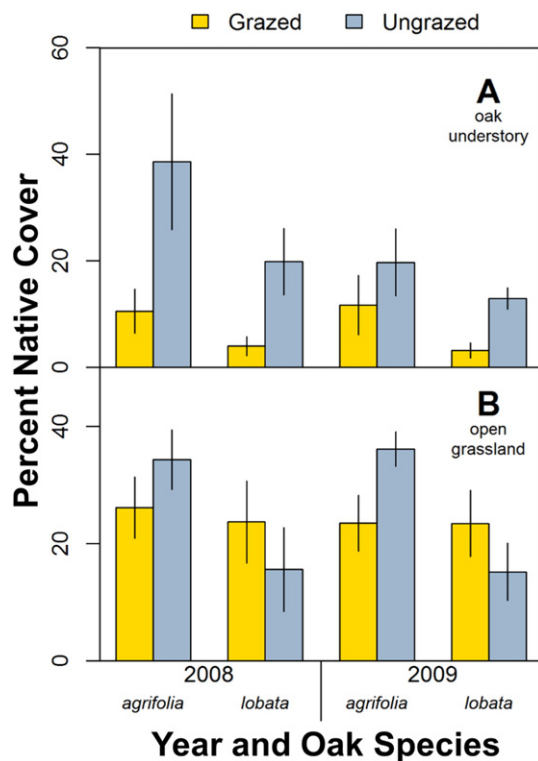


Figure 3. Relative native cover (%) ± 1 standard error in the (A) oak understory and (B) open grassland by year, oak species, and grazing treatment. Native cover (as a percent of total cover) was consistently lower in grazed understories of both oak species, but in open grasslands native species were only reduced by grazing when neighboring *Q. agrifolia*.

When left ungrazed, these locations became highly dominated by exotic annual grasses, with deep layers of dead plant thatch and few native wildflowers. By contrast, grasslands surrounding the evergreen *Q. agrifolia* had higher species richness when left ungrazed, and species diversity was not affected by the presence of livestock. In the understory of both oak species, the richness and cover of native species were positively affected by the removal of livestock grazing. In the more diverse year (2009), livestock grazing had larger effects, whether positive or negative. Some have suggested that the relative abundance of grasses and forbs in California grassland is dependent on fluctuations in precipitation (Hobbs et al. 2007; Pitt and Heady 1978), as it is

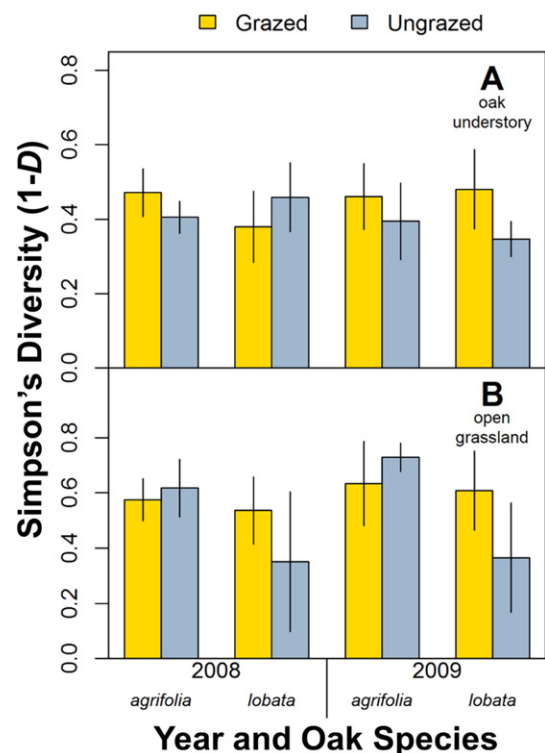


Figure 4. Mean Simpson's diversity ± 1 standard error in the (A) oak understory and (B) open grassland, separated by oak species, year, and grazing treatment. Diversity was unaffected by grazing in the understory but was enhanced by grazing in open grasslands surrounding *Q. lobata*.

Table 3

Soil characteristics showing least square means from analysis of variance and significance of the grazing effect. Only variables with significant pasture differences in at least one location type are shown.

Soil characteristic	Location	Grazed mean	Ungrazed mean	Grazing main effect from analysis of variance
% Coarse organic matter (> 2 mm)	Oak understory	2.24	1.27	$F_{1,17} = 3.49, P = 0.079$
	Open grassland	0.15	0.11	$F_{1,17} = 1.92, P = 0.184$
Bulk density (g/cm ³)	Oak understory	1.23	1.38	$F_{1,17} = 3.70, P = 0.071$
	Open grassland	1.53	1.60	$F_{1,17} = 0.94, P = 0.346$
% Carbon	Oak understory	4.45	3.49	$F_{1,17} = 3.26, P = 0.089$
	Open grassland	2.43	1.94	$F_{1,17} = 10.00, P = 0.006$
% Nitrogen	Oak understory	0.39	0.35	$F_{1,17} = 1.19, P = 0.291$
	Open grassland	0.28	0.24	$F_{1,17} = 6.89, P = 0.018$
C:N ratio	Oak understory	11.13	9.81	$F_{1,17} = 8.21, P = 0.011$
	Open grassland	8.67	8.04	$F_{1,17} = 4.98, P = 0.039$
K ⁺ (meq/100 g)	Oak understory	2.07	1.54	$F_{1,17} = 7.69, P = 0.013$
	Open grassland	0.76	0.67	$F_{1,17} = 1.24, P = 0.280$

elsewhere in the world (Oosterheld et al. 2001; Sala et al. 1988). We expect, therefore, that interactions among weather, season of grazing, and resident plant community will affect the ability to use grazing to achieve management goals.

Our results in open grassland support previous studies that report mostly neutral to positive impacts of livestock grazing on species diversity and richness in upland grasslands of California (as reviewed in Stahlheber and D'Antonio 2013). Although removing grazing did not lead to large changes in overall plant community composition as measured with multivariate analysis, it did affect community metrics such as species diversity, richness, and the cover of native plants. Interestingly, this effect differed depending on the species of the nearest neighboring oak. This is despite the fact that most major environmental differences (e.g., soil nutrient availability, light levels) between the evergreen *Q. agrifolia* and deciduous *Q. lobata* occur in the understory (Stahlheber et al. 2015). Greater investment in fine surface roots by *Q. agrifolia* compared with *Q. lobata* could be responsible for differences in community composition and the response to livestock grazing beyond the tree canopy boundary, especially if the presence of oak roots is detrimental to dominant annual grasses (Callaway 1990; Callaway et al. 1991; Mahall et al. 2009). Additionally, fine-scale variation in the germination and habitat preferences among oak trees could also result in different plant communities outside the canopy. At this particular site, we have no evidence to date suggesting *Q. agrifolia* and *Q. lobata* are partitioning the environment (Stahlheber et al. 2015), yet there could be unmeasured gradients driving this response.

In the oak understory, we found predominantly negative effects of livestock grazing on native species richness and cover regardless of the species of canopy tree and in spite of consistently lower light levels underneath the evergreen *Q. agrifolia* compared with its deciduous congener. Additionally, indicator species of grazed oak understories were all exotic species such as the annual grass *Hordeum murinum* and the forb *Silybum marianum*. Thus, grazing may disproportionately reduce native plants compared with exotic grasses and forbs in the high-nutrient, reduced-light understory environment. One possibility for the negative effects on native plants in the understory could be due to cattle congregating in shade for either forage or relief from hot weather typical for California's Mediterranean climate (Ittner et al. 1958; Wagon 1963).

Many studies evaluating the responses of plants to grazing have indicated that across a broad range of habitats, annual, short-statured, rosette-forming plants consistently benefit from livestock grazing (Díaz et al. 2007; Pakeman 2004). Outside of the tree canopy, livestock grazing may enhance diversity and species richness because the traits of species favored by livestock grazing are those that are also least likely to coexist with the typically dense, tall exotic annual grasses (Molinari and D'Antonio 2014). Potentially, the traits that would allow coexistence with exotic grasses in the low light environment of the understory are different and unfavorable when livestock grazing is present, particularly if the plants are palatable and readily eaten by congregating cattle. A comparison of plant traits between understory and open habitats in

California has not been attempted and could reveal important differences among native and exotic species in these habitats. Factors such as light and resource levels that are strongly altered by the oak canopy will also likely affect tolerance to herbivory, and most studies have found that sensitivity to herbivory decreases with increasing light availability (Hawkes and Sullivan 2001). Thus, even species that tolerate light grazing in the open grassland may not be able to compensate in the highly shaded understory.

Most previous examinations of livestock grazing responses in Mediterranean savanna or open woodland habitats haven't separated understory and inter-tree habitats but rather consider the plant community response at the pasture scale. More detailed approaches with regard to the spatial variation created by trees within pastures could be informative for future studies in these habitats and illuminate causes for differences between regions or studies. For example, many species originating in the Mediterranean have naturalized and become widespread in *Eucalyptus* open woodlands of Australia and the *espinas* of Chile, largely overlapping with the exotic species dominant in California oak savannas. In Australia, researchers frequently document negative impacts of livestock grazing for native herbaceous plants, especially native perennials (Dorrough et al. 2004; Pettit et al. 1995; Prober and Wiehl 2011; Yates et al. 2000). Native perennials in *espinas* are also considered more sensitive than exotic annual species to domestic livestock (Holmgren et al. 2000; Ovalle et al. 2006), although some studies have found positive relationships between grazing intensity and native species richness (del Pozo et al. 2006). Higher tree densities at some sites relative to each other—and therefore greater proportional representation of understory habitat and an abundance of understory-adapted native plants—could contribute to these differences in the conclusions of these studies, although this idea would have to be addressed with a different study design than we used in this project. Our study is limited by the number of trees we were able to include and the fact that we only assessed impacts of individual trees in a savanna with a given tree density. Sample size limitations may be especially important in interpreting our results for open grassland, where a failure to detect differences could result from a low sample size as opposed to a lack of grazing removal effects.

As in other studies, we found relatively minor effects of livestock grazing on soil properties, particularly compared with differences between the oak understory and open grassland (Camping et al. 2002; Dahlgren et al. 1997). This is consistent with the conclusion of Milchunas and Lauenroth (1993), who found no consistent worldwide signal of livestock grazing on soil properties. Grazing did reduce the depth of thatch and oak litter in understory and open grassland alike, which could in turn be an important structuring force on plant diversity in grasslands (Loydi et al. 2013). Trampling and compaction of the litter layer could accelerate decomposition rates, as has been found in other grasslands (Facelli and Pickett 1991; Shariff et al. 1994), but this is not always the case (Biondini and Manske 1996; Lindsay and Cunningham 2009; Risch et al. 2007). Breakdown of the thatch layer and

decomposition of the exotic annual grasses in California grasslands is typically very slow (Stahlheber et al. unpublished data); thus, physical disturbances reducing thatch may have cascading effects on other soil resources, plant diversity, and arthropod food webs (Molinari 2014; Wolkovich et al. 2009). Changes in species composition and total root biomass resulting from livestock grazing can also affect soil carbon and speed up nitrogen cycling (Frank et al. 1995; Johnson and Matchett 2001). We did not measure N turnover in this study; however, previous reports have found that oak trees accelerate nitrogen cycling similarly on watersheds with and without cattle grazing (Herman et al. 2003; Jackson et al. 1990).

Implications

Our work suggests that past livestock grazing has been more detrimental to the abundance of native species in the understory than in adjacent open grassland. Thus, despite reducing thatch depth and occasionally increasing the presence of exotic forbs, introducing managed grazing in oak understories is unlikely to have positive impacts on natives. Although our study does not directly address this possibility, if the seed bank of native species adapted to the understory has been depleted due to a long history of continuous livestock grazing—or perhaps the dramatic declines in tree density that have occurred over the past century—even the most targeted grazing management will be unable to produce benefits in the oak understory. The traits of species well adapted to the understory may also be those most sensitive to livestock, although this comparison has not been attempted. This potential cost for diversity in understory habitats must be weighed against possible species richness and diversity benefits of livestock in adjacent open grasslands. At the scale of an entire pasture or landscape, tree density or cover within a savanna pasture may therefore influence whether the overall outcome of livestock removal is positive or negative for species richness and diversity. Performing such an optimization exercise would require a more detailed knowledge of the capacity for both habitat types for supporting livestock (to determine grazing intensity), as well as how species richness is affected by grazing across landscapes rather than small plots. Unfortunately, such data are underrepresented in the scientific literature due to the challenge of manipulating grazing at these scales.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2016.10.003>.

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