

# Livestock grazing and topographic site effects on grassland plant communities after long-term grazing cessation

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**Abstract.** Ranchers are increasingly expected to manage grasslands for forage production and native biodiversity enhancement goals. However, longstanding relationships between grazing and plant species are often understudied because elucidating effects of grazing absence and presence often requires experimental opportunities that are difficult to establish, such as the introduction of grazing to long-term ungrazed pastures. Addressing this knowledge gap is critical for heterogeneous landscapes where site-specific properties might interact with grazing effects to ultimately structure plant communities. We conducted vegetation surveys for 3 years after grazing was reintroduced to an annual California grassland that was not grazed for more than 60 years. We investigated how grazing affected plant communities in terms of cover and richness of native and invasive species and how topographic sites of summit, backslope and toeslope altered these relationships. The plant communities were affected by the independent effects of grazing, site and year. Across years, native cover was 39% greater in grazed plots compared with ungrazed plots. Native species richness was slightly lower in ungrazed compared with grazed plots for toeslope sites relative to the other topographic positions. Invasive species cover was 17% lower in grazed plots compared with ungrazed plots and no predictors were found to contribute to significant differences across plots. Although we generally did not find expected relationships between site and plant response to grazing, this work demonstrates how managers can use livestock to quickly modify plant communities in areas with a long history of grazing absence.

**Additional keywords:** grassland, grazing, invasive species, livestock, Mediterranean, plant community.

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## Introduction

Livestock grazing can be an important and practical tool for effectively managing plant communities. Plant communities are expected to change in the presence of grazing both because plants differ in their tolerance to tissue removal as well in their response to changes in competitive dynamics that largely result from altered light conditions (Augustine and McNaughton 1998). For example, in grasslands, the presence of grazing can drive patterns of community assembly (Alberti *et al.* 2017), species richness (Bakker 1998; Rambo and Faeth 1999), rare plant abundances (Pykälä 2003), and invasive species (Davy *et al.* 2015). Although studies demonstrating relationships between grazing and plant communities in working and natural landscapes are well documented, much of this work focuses on desirable forage and invasive species. Much less is known about the effects of grazing reintroduction to long-term ungrazed systems (Gibson *et al.* 1987; Stohlgren *et al.* 1999).

In some grazed habitats of the Western USA, such as California annual grasslands, native plant species do not have a long evolutionary history with grazing animals. In these areas,

native plant species cover and richness might be expected to decline in the presence of grazing (Kimball and Schiffman 2003). However, studies have been equivocal in their assessment of the relationship between native species and grazing. In some cases, grazing produces positive effects on natives (e.g. Gerlach *et al.* 1998; Gennet *et al.* 2017), and in other cases, negative effects (e.g. Huntsinger *et al.* 1996). Moreover, effects can be functional group (Hayes and Holl 2003a) and scale dependent (Landsberg *et al.* 2002). Ranchers and other land managers are increasingly expected to simultaneously manage grasslands for forage production and native biodiversity enhancement goals, and research that elucidates grazing effects on native plants is important for informing management and conservation. However, these relationships are often understudied because elucidating effects of grazing absence and presence often requires experimental opportunities that are difficult to establish (i.e. the introduction of grazing to long-term ungrazed pastures, but see e.g. Pykälä 2003). Addressing this knowledge gap is particularly critical for heterogeneous landscapes where site-specific properties might interact with grazing effects to

ultimately structure plant communities (Fuhlendorf and Engle 2001; Hayes and Holl 2003b; Derner *et al.* 2009; Toombs *et al.* 2010).

Rangelands are characteristically heterogeneous (Bartolome *et al.* 2007), so grazing effects can be largely mediated or simply overshadowed by site-specific factors such as soil type or productivity (Milchunas and Lauenroth 1993). For example, in systems characterised by high nutrient availability, grazing can typically have a positive effect on plant diversity, whereas the opposite is true for systems characterised by low nutrient availability (Bakker *et al.* 2006). Studies have also suggested that plant communities will demonstrate different types of responses to grazing, depending on exposure to drought conditions (e.g. Gornish and Ambrozio dos Santos 2016). In fact, many researchers consider grazing effects on aboveground plant communities as essentially an indirect effect of grazing pressure on belowground (microhabitat) factors (Heyburn *et al.* 2017). Clearly, researchers must account for inherent site heterogeneity across these complex landscapes to improve understanding of real plant–animal interactions.

Leveraging a rare opportunity in which grazing was reintroduced to a typical annual California grassland that was not grazed for more than 60 years, we investigated (1) if the presence of grazing affected plant community composition generally as well as cover and richness of native and invasive species; and (2) how landscape positions might alter these relationships.

## Materials and methods

The study was conducted in a previously long-term (60 years) ungrazed area (36.2 ha) on the south-eastern edge of the Pardee Reservoir in Calaveras County (38.241817, -120.824454, WGS 84, Garmin GPS 72, version 2.50). The climate is Mediterranean, consisting of hot, dry summers and cool, wet winters. The Köppen climate classification of the site is Csa. During the tenure of the experiment, average spring temperature and spring precipitation was 17.1°C and 54 mm for 2015; 17.1°C and 165 mm for 2016; and 16.1°C and 136 mm for 2017. Soils are mostly shallow, excessively drained loams (Stonyford series – loamy, mixed, superactive, thermic lithic Mollic Haploxeralfs). The landscape is a typical rolling California foothill grassland, with varying topography (toeslopes, backslopes, summits). Toeslope sites (680 m) exhibit the deepest soils and greatest levels of soil moisture lasting longer into the dry season and are generally the most productive. Backslopes (780 m) have moderate soil depths and moisture regime characteristics. Summit sites (900 m) are characterised by the shallowest soils with the shortest period of available soil moisture, and are generally the least productive. At the initiation of the experiment, toeslope sites were dominated by *Vicia sativa* L. (common vetch); backslope sites were dominated by *Bromus diandrus* Roth (ripgut brome) and *Avena fatua* L. (common wild oat); and summit sites were dominated by *Bromus hordeaceus* L. (soft brome), *Erodium* spp. Aiton (fillaree), and *Trifolium hirtum* All. (rose clover). *Avena barbata* Pott ex Link (slender wild oat) and *Brachypodium sylvaticum* (Huds.) Beauv. (false brome) were common across all sites.

Prior to livestock reintroduction, we installed permanent paired 4-m<sup>2</sup> plots – one cattle grazed plot and one ungrazed

enclosure (control plot) – across three replicates of each site ( $n = 18$ ). Plots within a replicate were separated by at least 10 m. Plant community data were collected from four 1-m<sup>2</sup> subplots within each plot (Supplementary Materials fig. 1 available at journal's website). Grazing occurred, over 3 years, with the following on and off dates and stocking rates of cow calf pairs (animal unit months per hectare): 1 May 2015 to 6 May 2015 at 1.5 AUM ha<sup>-1</sup>, 25 March 2016 to 30 April 2016 at 1.5 AUM ha<sup>-1</sup>, and 1 April 2017 to 31 May 2017 at 1.6 AUM ha<sup>-1</sup>. These are considered light to moderately stocking rates. In the spring of 2015, 2016, and 2017 we estimated percent cover by plant species in each plot via ocular estimation. Data collection in 2015 occurred 1 week after cattle were reintroduced into the pasture. Native status of each species was identified using the Calflora database ([www.calflora.org](http://www.calflora.org), accessed 1 February 2017). Plant community measures at the metre-squared scale were expected to be suitable proxies for habitat level patterns (Pykälä 2003).

## Analyses

To investigate how grazing and site influenced plant community composition, we first conducted ordination analysis on the subplot level community cover data using non-metric multidimensional scaling (Clarke 1993). In the ordination function, the factor specifying the strata for permutation as site and not plot was noted by setting strata equal to site to account for sampling data from multiple plots within each site. Contributions of grazing, site, and year to community composition were tested using a repeated-measures (by year) permutational multivariate analysis of variance, a non-parametric method that operates on Bray–Curtis distance matrices, allowing for multivariate analysis. Community data demonstrated similar multivariate spread among treatments. In instances where any treatment demonstrated significant contributions to community dissimilarity scores, we conducted pairwise contrasts using a Bonferroni correction to identify differences among treatment levels.

To understand whether species richness and cover of native and invasive species changed depending on grazing and site, we used linear mixed effects regression models with site (summit, backslope, and toeslope), grazing (grazed or ungrazed), year (as a categorical factor), and their interactions as fixed effect predictors, and an error term (random effect) for subplot within replicate and replicate within year to account for repeated-measures. For models describing richness, we included a Poisson error structure because the data were counts (Bolker *et al.* 2009) and used the log-link function. We also used a chi-square distribution to test the goodness of fit of our data to a Poisson distribution. We found sufficient evidence to conclude that our data fit a Poisson distribution. Confidence intervals for estimates were identified using the Wald method. Natives and invasives were analysed separately. All analyses were conducted in R version 3.1.1 (R Development Core Team 2014) using the ggplot, vegan, and lme4 packages.

## Results

### Community

Across all three study years, 61 species were recorded in the experimental plots, including 34 invasive species and 27 native species. At the start (2015) of the experiment, mean bare ground

for ungrazed and grazed plots were 2% and 1%, respectively, and thatch cover for ungrazed and grazed plots were 65% and 59%, respectively. In the last year (2017) of the study, bare ground for ungrazed and grazed plots were 2% and 11%, respectively, and thatch cover for ungrazed and grazed plots were 74% and 34%, respectively.

A final solution for non-metric multidimensional scaling was reached after 17 iterations at a final stress of  $<0.2$  (Fig. 1). The permutational multivariate analysis of variance demonstrated the independent contribution of each factor resulted in significant differences among community ordination scores: microhabitat ( $F=0.06$ ,  $P=0.001$ ), and year ( $F=0.06$ ,  $P=0.001$ ), and to a lesser extent, grazing ( $F=0.01$ ,  $P=0.02$ ). The significant interaction between site and year ( $F=0.04$ ,  $P=0.001$ ), suggested that, across sites, plant communities shifted over the study period (Supplementary Materials table 1). Pairwise contrasts highlighted that community ordination scores were significantly different across all 3 years and all three sites.

### Cover

Native plant cover was relatively low across all plots (mean = 7.9%, s.e. = 7), although it did increase over the study period (Fig. 2a; Supplementary Materials table 2). *Hemizonia congesta* DC. (hayfield tarweed) was the most common native across all years. In 2016 *Daucus pusillus* Michx. (wild carrot) also demonstrated proportionately high cover. Across years, native cover was 39% greater in grazed plots compared with ungrazed plots (estimate = 8.88 (95% confidence intervals = -6.4 and 24.2), s.e. = 7.8, DF = 1,  $F=4.69$ ,  $P=0.03$ ; Fig. 2a).

Invasive species dominated all sites for the duration of the study, with an overall mean cover of 77% (s.e. = 11). Across

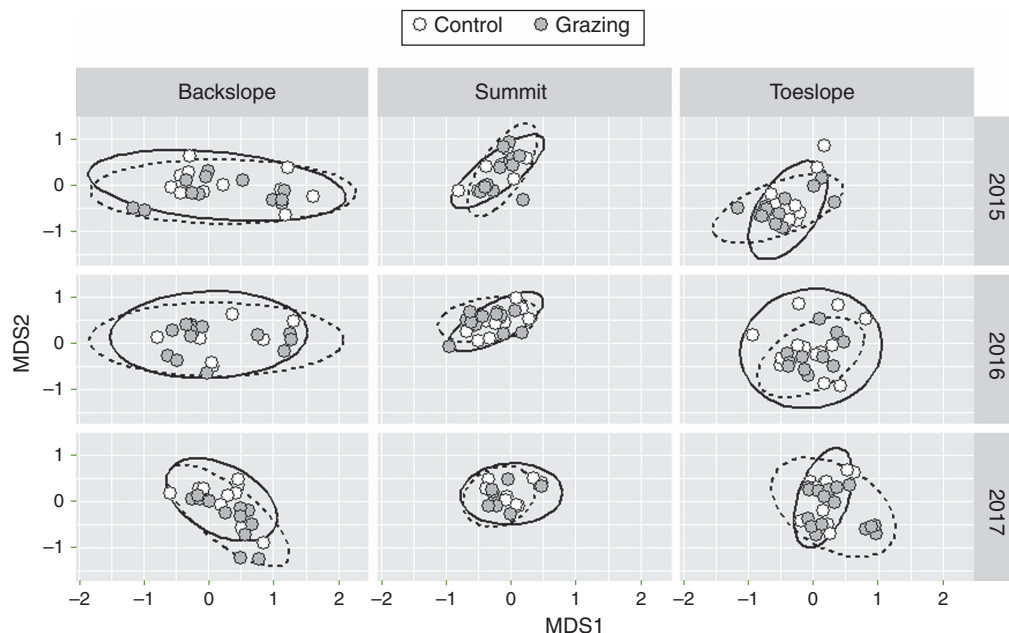
all years, *Avena barbata* was one of the most dominant invasive species in terms of cover. In 2015 and 2017, *Brachypodium sylvaticum* was also a dominant invasive species. In 2016, *Torilis nodosa* (L.) Gaertn. (knotted hedgeparsley) was a dominant invasive and in 2017, *Bromus diandrus* and *Trifolium hirtum* also demonstrate proportionately high cover across plots. Invasive cover was 17% lower in grazed plots compared with ungrazed plots (estimate = -35 (95% confidence intervals = -9.7 and 278), s.e. = 11, DF = 1,  $F=20.49$ ,  $P<0.001$ ; Fig. 2b). We did not find a significant three-way interaction.

### Richness

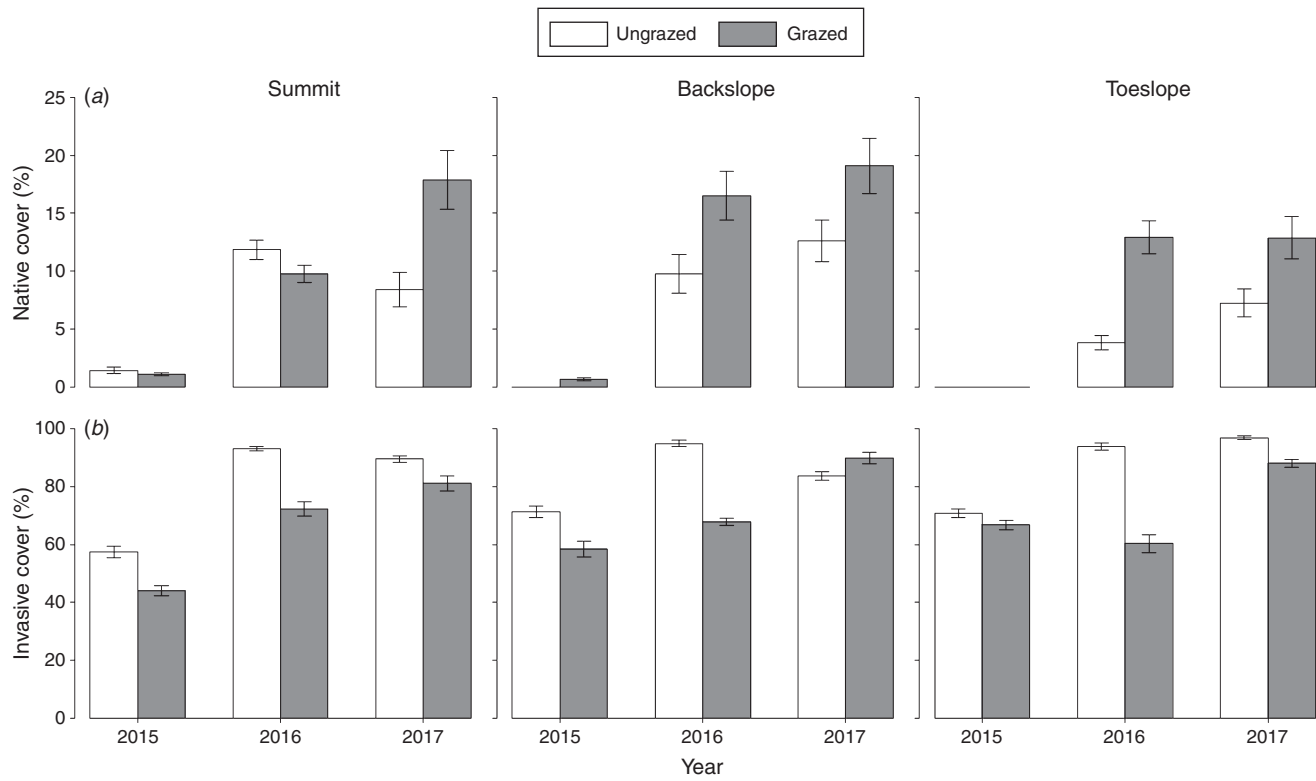
Native species richness was slightly lower in ungrazed (mean = 0.8, s.e. = 0.5), compared with grazed plots (mean = 1.0, s.e. = 0.5) for toeslope sites relative to the other topographic positions (estimate = -1.05 (95% confidence intervals = -8.7 and 8.7), s.e. = 0.38,  $P=0.006$ ; Fig. 3a). However, no other predictor singularly or in combination demonstrated significant contributions to differences in native richness. Invasive richness was also relatively low for an annual grassland across plots (mean = 6.5, s.e. = 1.2) and no predictors were found to contribute to significant differences across plots (Fig. 3b).

### Discussion

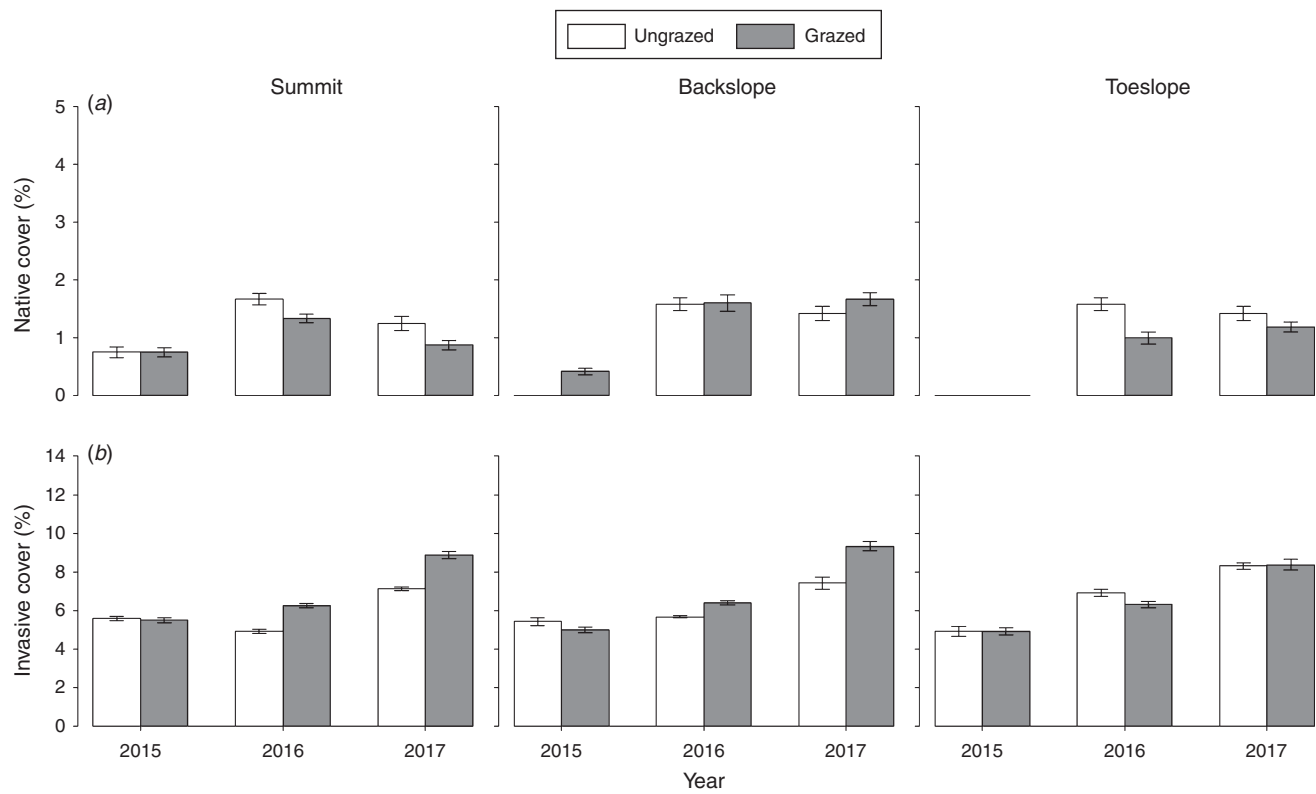
Singular, hierarchical, and interactive effects of site-level characteristics and management activities across heterogeneous grassland systems (e.g. Hayes and Holl 2003a) make disentangling these relationships between these factors difficult. We capitalised on an opportunity in which livestock were reintroduced to an annual grassland that had been ungrazed for



**Fig. 1.** Non-metric multidimensional scaling (MDS1 and MDS2) ordination plot of plant community assemblages across the 3 years of the experiment (2015–2017) and microsites (backslope, summit, and toeslope). Each point represents the species composition in a given subplot. Lines represent the confidence ellipse at the 0.95 level (solid line for ungrazed enclosure plots, dotted lines for grazed plots). Grazed plots experienced between 1.5 and 1.6 AUM ha<sup>-1</sup>.



**Fig. 2.** Cover of (a) native plants and (b) invasive plants across microsites (summit, backslope and toeslope) in ungrazed (exclosed) and grazed plots. Note differences in axes. Grazed plots experienced between 1.5 and 1.6 AUM ha<sup>-1</sup>.



**Fig. 3.** Species richness of (a) native plants and (b) invasive plants across microsites (summit, backslope and toeslope) in ungrazed (exclosed) and grazed plots. Note differences in axes. Grazed plots experienced between 1.5 and 1.6 AUM ha<sup>-1</sup>.

more than 60 years. We found that plant communities responded to the reintroduction of grazing. In addition to directly affecting plant communities by browsing of grazing intolerant species, livestock likely imposed community-scale changes through indirect effects. For example, increasing small-scale heterogeneity enhances the number of areas that could provide suitable sites for the germination and establishment of particular suites of plant species (e.g. Fowler 1986; Eriksson and Ehrlén 1992). This facilitates the entrance of new plant species and provides opportunities for shifts in competitive dynamics among existing members of the community. Grazing can increase habitat heterogeneity through both disturbance (hoof action and plant defoliation) and nutrient redistribution (faecal and urine deposition).

Although native plant cover generally increased across all plots through the duration of the experiment, it increased proportionately more on grazed plots compared with plots that were protected from grazing. Grazing is expected to enhance native species cover largely through modifications of competitive interactions. For example, grazing reduces aboveground biomass, subsequently increasing light penetration of the herbaceous canopy as well as soil moisture availability (Menke 1992; Eskelinen and Virtanen 2005). Many of California's native plants germinate and establish later than non-natives, and ultimately are outcompeted for soil moisture and light early in the growing season. In the final year of our study, grazed plots had 54% less thatch than ungrazed plots, which might have encourage germination of natives (Bartolome *et al.* 2007). Grazing can also change the identity of dominant invasive species (e.g. Gornish and Ambrozio dos Santos 2016), which can modify competitive interactions between natives and non-natives. Considering that native cover was relatively low across all plots, and tends to be low in California annual rangelands in general, our findings (Supplementary Materials table 1) highlight an important quality of low to moderate intensity grazing for maintaining and potentially enhancing grassland diversity.

Many studies that have found positive relationships between grazing and native biodiversity have done so in systems that have an evolutionary history shaped by the presence of grazing animals (e.g. Collins *et al.* 1998). Because this is not the case for California grasslands, these systems are not expected to harbour native species that respond positively to grazing disturbances. Native plant species richness was low across plots, however, we found it to be higher in grazed versus ungrazed plots within the toeslope site (significant grazing  $\times$  site type interaction) where soil moisture is likely highest (Brubaker *et al.* 1993). Effects of grazing are expected to be greatest in the most fertile microhabitat (e.g. Harrison *et al.* 2003) because in these areas, aboveground biomass and invasive plant dominance tends to be higher than in lower fertility environments (Grime 1979; Milchunas *et al.* 1988). As a result, the disturbance that accompanies grazing (a reduction of aboveground biomass through defoliation) leads to a marked physical change in vegetation structure and plant response above and below ground.

The way in which invasive plants responded to grazing was distinct from the way native plants responded. Invasive plant cover was reduced by almost 20% in grazed plots, compared

with ungrazed plots. Grazing has been shown to be effective for reducing exotic plant species for a variety of reasons (e.g. Sala *et al.* 1986), although this can be dependent on grazing timing and environmental conditions (Davy *et al.* 2015). Most of the non-native plants found dominating our study plots are typical of California grasslands and do not necessarily reflect a community-wide shift in response to a 60-year-long absence of grazing. However, it is possible that extant invasives were less tolerant to grazing as a result of the absence of livestock (Müller-Schärer *et al.* 2004). In this case, the presence of grazing not only provided opportunities for natives by removing physical barriers for establishment (e.g. Wilsey and Martin 2015), but it also provided indirect opportunities for natives by reducing the competitive ability of invasives (Davy *et al.* 2015).

## Conclusions

We did not find much support for our expectations of site effects on the relationship between grazing and native and invasive plants. Data for this study were collected following the driest period in California's history. These drought conditions could have obscured the major soil moisture differences across sites; and moisture availability has been shown to be particularly important for modifying grazing–plant relationships in Mediterranean regions (de Bello *et al.* 2007). Ultimately this work suggests that grazing approaches deployed across heterogeneous landscapes during periods of drought might provide similar plant community outcomes across sites. Additionally, despite the long-time lags that can accompany plant response to grazing cessation in arid landscape (e.g. Valone *et al.* 2002), we found that both native and invasive plants can respond very quickly to grazing reintroduction after long-term absence.

## Conflicts of interest

The authors declare no conflicts of interest.

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