



# Using livestock to manage plant composition: A meta-analysis of grazing in California Mediterranean grasslands

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## ABSTRACT

The use of livestock to manage vegetation composition has become a common element of conservation planning in many regions of the world. Similar to many arid and semi-arid grasslands throughout the world, California grasslands have a history of invasion by non-native grasses and forbs. Attempts to restore native plant populations using managed grazing are common, despite the lack of an overarching quantitative basis for assessing livestock effects on different plant groups. Given the wide range of soils, climate and topography over which grasslands are found, it is important to understand the context-dependency of grazing effects across a region. We performed a meta-analysis of livestock grazing within California grasslands to investigate the response of different plant groups to grazing relative to precipitation, grassland type, soil and grazing regime. We found that exotic forbs showed a dramatic, uniform increase in cover with grazing, but no increase in richness. By contrast, native forbs increased in richness yet their cover response was weak and variable depending on grazing regime and precipitation. Exotic grass cover was unaffected while richness was enhanced by grazing. Native grass cover generally increased with grazing, although the high variation among studies was not predicted by the explanatory variables we evaluated. These results lend support to the use of grazing to enhance native forb richness and native grass cover in some settings although this must be weighed against increases in the cover of exotic forbs.

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## 1. Introduction

Large, ungulate herbivores are often primary drivers of plant community structure and dynamics (Bullock et al., 2001; Collins et al., 1998; Díaz et al., 2007; McNaughton et al., 1989; Nuñez et al., 2010; Olff and Ritchie, 1998). At a community level, grazing can influence species richness and diversity, occasionally leading to local extirpation of species or shifts between herbaceous and woody species (e.g. Courtois et al., 2004; Evju et al., 2009; Hunt, 2001; Stohlgren et al., 1999). The specific consequences of grazing, however, are likely to vary across soils and region as well as by type of grazer and grazing regime (Allington and Valone, 2011; Burns et al., 2009; Jones, 2000; Knapp et al., 1999). Over recent decades, the use of livestock has been promoted in many grassland habitats as a means of enhancing the diversity or cover of native species and for control of non-native species (Anderson, 1993; Brunson and Huntsinger, 2008; DiTomaso et al., 2010; Launchbaugh et al., 2006; Lunt et al., 2007; Toombs et al., 2010). In order to effectively utilize livestock grazing to reach a management goal

however, it is important to understand controls over the outcome of grazing.

Across many ecosystems, climate and evolutionary history have been highlighted as important controls over community response to grazing (Díaz et al., 2007; Milchunas and Lauenroth, 1993). In their global meta-analysis of grassland species responses to grazing, Díaz et al. (2007) included several studies from within Mediterranean climate regions. These grasslands were not considered separately despite their differences from other biomes and in particular their high dominance by exotic species and prevalence of annual species. The former, as well as the removal of historic disturbances are among the management concerns faced in many Mediterranean-climate grasslands that are not necessarily significant elsewhere. Despite the growing interest in managing plant diversity via grazing in these areas, a systematic effort to evaluate controls over the outcome of grazing across a region of Mediterranean grasslands has not been done. In these systems, Osem et al. (2002) suggested that the outcome of grazing will depend on site productivity, with impacts switching from a depression of species richness in drier less productive areas to an increase in richness with grazing in more productive areas. A regional approach is therefore important to distinguish between such potentially contrasting influences.

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Grasslands in Mediterranean-climate regions other than the Mediterranean Basin have been invaded by a wide range of non-native, primarily annual, species (Mack, 1989). California grasslands in particular are widely dominated today by non-native species (Bartolome et al., 2007) and grazing has been hypothesized as a management tool for increasing and conserving remaining native species diversity (Menke, 1992; Savory and Butterfield, 1999; Schohr, 2011), which is especially high in comparison to other North American grasslands (Axelrod, 1985; Raven and Axelrod, 1978). Several mechanisms have been proposed through which grazing may sustain or enhance plant diversity in such systems including limiting biomass of undesirable dominant species and allowing the persistence of disturbance-adapted species (Lunt et al., 2007). These ideas have been tested in SE Australian grasslands which although differing in rainfall patterns, share a common suite of exotic winter annual grasses and exotic forbs with California (Prober et al., 2011). The anthropogenic savannas (espinales) of central Chile also share this suite of species, although less is known about shifts in community composition due to grazing in these habitats (del Pozo et al., 2006; Ovalle et al., 1990). In addition to the effects of land use, exotic cover varies with nutrients and across soil types in all of these regions. In Australia and California fertility appears to enhance exotic species dominance (Dorrough et al., 2006; Huenneke et al., 1990; Prober and Wiehl, 2011; Safford and Harrison, 2001), whereas the opposite may be true in Chilean grasslands (Holmgren et al., 2000; Ovalle et al., 2006), highlighting the importance of considering soil variation in an analysis of grazing impacts.

The vast area of California grasslands encompass a significant part of the Mediterranean climate region grasslands in the western hemisphere and include considerable soil and climatic variation (Bartolome et al., 2007; Jackson et al., 2007). Thus, an analysis of controls over variation in the outcome of grazing across this region will contribute to our global understanding of how livestock can be used as a conservation tool. It will also help to generate broad guidelines for managers, particularly for sites where little is known about possible grazing outcomes. In this paper, we therefore use meta-analysis, the formal quantitative summary of independent controlled experiments with a single treatment type, to evaluate the effects of grazing across Californian grasslands. We gathered both published and well-quantified unpublished studies that included grazing treatments with appropriate controls and that included at least some native species. We specifically address the following questions: (1) What is the overall effect of grazing on the cover/dominance and richness of native and exotic grasses, and native versus non-native forbs? and (2) How is the strength and direction of these effects influenced by precipitation, grassland community type, soil type and grazing regime?

## 2. Materials and methods

### 2.1. Study region

California grasslands occur within a Mediterranean climate region where most precipitation falls between November and April and the amount of precipitation varies widely between years and across latitudinal and coast to interior gradients. The vegetation underwent a widespread transition from dominance by native species, commonly believed to have been perennial grasses (Hamilton, 1997), to introduced annuals coincident with the expansion of livestock grazing, which remains the dominant grassland land use and an important agricultural resource in the state (Bartolome et al., 2007). Overall, California rangelands occupy approximately 10 million hectares and many of the species listed in the state's Inventory of Rare and Endangered Species occur within grassland settings

(Skinner and Pavlik, 1994). Conversion to cropland, residential and urban development and exotic species invasions continue to reduce their area, making intact native grasslands a threatened ecosystem (Noss et al., 1995).

Typically, the California grassland has been divided them into two types, the coastal prairie and the interior valley grassland (Bartolome et al., 2007). As a result of their wetter climates, coastal grasslands are distinguished by having a higher abundance of native perennial grasses whereas valley grasslands are more typically annual-dominated (Bartolome et al., 2007; Ford and Hayes, 2007; Schiffman, 2000). Both types, however, share a high dominance of non-native relative to native species. Despite the lack of scientific observations, it is frequently assumed that the pre-contact California grasslands of both types were composed primarily of perennial grasses for both grassland types (but see Hamilton, 1997) and these are the typical targets of grassland restoration projects throughout the state (Stromberg et al., 2007).

### 2.2. Data search and criteria

To locate studies for our analysis, we searched ISI Web of Knowledge (1923–2011) and Google Scholar. Subject keywords used were “California” in combination with each of the following: “grassland”, “prairie”, “grazing” and “livestock”. Additional studies were located from the references of papers located from these searches. Lastly, we personally contacted scientists and requested access to data.

For inclusion in this analysis, studies had to meet the following criteria: (1) performed in the California Floristic Province in a grassland with at least some native species present, (2) domestic livestock were the dominant grazer, (3) more than one replicate paddock per treatment, (4) use of ungrazed control plots for comparison against the grazed plots (fenceline transects are included as long as there were replicate sites), and (5) collection (and availability) of data (i.e. means and variances) on the difference in abundance (as percent cover, frequency or richness) of native plants in grazed and ungrazed plots in order to provide a common metric of outcome. We did not specify a minimum duration of the grazing treatment, nor did we include estimates of grazing intensity due to a lack of replicate studies at varying levels. Therefore, the studies span a range of grazing duration and intensity. Common problems within the literature include the lack of true replication (e.g. one grazed versus one ungrazed area), the lack of data on variance among plots and the absence of controls. In this analysis we excluded studies of simulated grazing through clipping and mowing, as well as studies investigating the effects of native grazers, which may have differing effects on plant communities (Parker et al., 2006) but have rarely been manipulated in the field (but see Johnson and Cushman, 2007). We also excluded feral pigs from this analysis, given that they are not reared as livestock nor used in restoration or management projects.

### 2.3. Data analysis

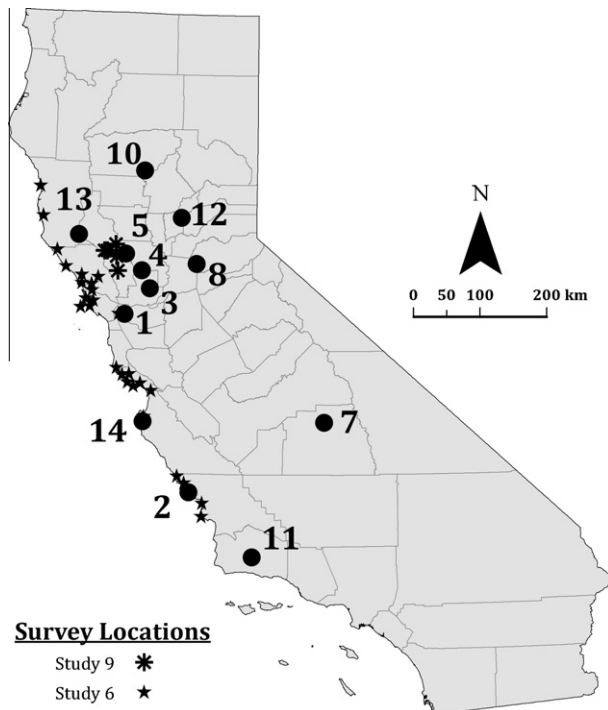
Fifteen studies that met meta-analysis criteria were used to determine the cumulative effect size of grazing on the percent cover of plant functional groups (Table 1). Effect size, or response ratio, is defined as the natural log of the ratio  $[X_{\text{grazed}}/X_{\text{control}}]$  where  $X$  represents percent cover of the plant species or group of interest in a given study. The fifteen studies took place from 1992 to 2009 in thirteen different California counties covering a gradient from 34 to 39.5°N latitude and 118 to 123°W longitude (Fig. 1). We extracted from each study a series of site descriptor variables where available. These included county, soil taxonomic class, soil texture, grassland type, precipitation, and grazing regime. We then extracted the mean percent cover for control and treatment

**Table 1**

Summary information on studies included in the meta-analysis.

Location/reference	County	Site	Precipitation (mm) <sup>a</sup>	Grassland type	Soil series	Soil texture	Study years	Grazing treatment	N	Grazing regime
(1) Bartolome et al. (2004)	Contra Costa	Sather Canyon (37.933N, –122.244W)	884	Coastal	Los Gatos	Clay loam	1994–1998	Paddock	9–10	Continuous, dry and wet season
(2) D'Antonio and Canestro (unpublished)	San Luis Obispo	Rancho Marino Reserve	382–585	Coastal	Concepcion	Sandy loam	2006, 2009	Paddock	3	Wet season
(3) DiTomaso et al. (2009)	Yolo	Bobcat Ranch	580	Interior	Corning and Positas	Gravelly loam	2004–2006	Paddock	24	March/September, May/September, September, and March/May/September
(4) Dyer and Rice (1997)	Solano	Jepson Prairie Reserve	475	Interior	San Ysidro	Sandy loam	1996	Paddock	3	Continuous
(4) Dyer (pers. comm.)	Solano	Jepson Prairie Reserve	475	Interior	San Ysidro	Sandy loam	1992–1995	Paddock	6	Dry and wet season
(5) Gelbard and Harrison (2003)	Napa, Lake and Colusa	Many	1150	Interior	Many	Gravelly loam and silt loam	2001–2002	Pasture	16–25	Continuous
(6) Hayes and Holl (2003)	Mendocino to San Luis Obispo	Many	505–535	Coastal	Many	Sandy loam	2000–2001	Pasture	17–25	Continuous
(7) Keeley et al. (2003)	Tulare	Sequoia National Park	660	Interior	Cieneba and Vista	Sandy loam	1999	Pasture	10	Continuous
(8) Marty (2005)	Sacramento	(38°38'N, 121°02'W)	560	Interior	Auburn	Silt loam	1999–2003	Paddock	5	Continuous
(8) Marty (unpublished) <sup>b</sup>	Sacramento	(38°38'N, 121°02'W)	560	Interior	Auburn	Silt loam	2004–2009	Paddock	5	Continuous
(9) Safford and Harrison (2001)	Lake and Napa	Many	732	Interior	Many	Gravelly loam and silt loam	1999	Pasture	3–5	Dry season
(10) TNC (2000)	Butte and Tehama	Vina Plains Preserve. (39°53'N, 121°59'W)	Unknown	Interior	Tuscan	Cobbly loam	1997–1999	Pasture	4–8	Wet season
(11) Tyler et al. (unpublished)	Santa Barbara	Sedgwick reserve	167–924	Interior	Botella, Elder and Positas	Sandy loam and clay loam	1998, 2007–2009	Paddock	4–7	Wet season
(12) Seabloom et al. (unpublished a)	Yuba	Sierra Foothill REC	1001	Interior	Auburn and Sobrante	Gravelly loam	2006	Paddock	6	Unknown
(13) Seabloom et al. (unpublished b)	Mendocino	Hopland REC	1147	Coastal	Bearwallow and Hellman	Loam	2006	Paddock	6	Unknown
(14) Skaer et al. (in press)	Monterey	Palo Corona Regional Park (36°29'N, 121°53'W)	378	Coastal	Cieneba and Sheridan	Sandy loam	2007–2009	Paddock	10	Wet season

<sup>a</sup> Precipitation is actual amount during the study years where possible, otherwise mean annual precipitation for the site is used.<sup>b</sup> These data are a continuation of the published project and were treated as part of that study for this analysis.



**Fig. 1.** Map representing the locations of studies included in the meta-analysis. See Table 1 for studies corresponding to numbers. Studies 9 and 6 surveyed multiple locations, shown as asterisks and stars, respectively.

(grazed) plots by year and the standard deviation around the mean, as well as the sample size. For a smaller subset of seven studies where data were available, we also calculated mean species richness and standard deviation.

For studies that spanned more than 1 year, we conservatively estimated a single effect size per study by taking the average mean and standard deviation. Interestingly, the use of multiple effect sizes per study by including different years increased the size of the confidence intervals observed due to the high inter-annual variability inherent in California grassland communities. Where individual studies explicitly described locations with different soil types, these locations were treated as independent points as long as there were replicate plots on each soil type. Studies that evaluated multiple grazing regimes in a single location were treated as independent points only for the comparisons of grazing regime; for all other analyses a single effect size was used for these studies.

We performed the meta-analysis using MetaWin 2.1 (Rosenberg et al., 2000) and the *metafor* (Viechtbauer, 2010) package for R 2.12.2. Since our studies encompassed a significant amount of the geographic range of grasslands in California, and our hypotheses only address the effect of grazing within this region, fixed-effect models were used to estimate effect sizes and evaluate their significance. Using random-effect models did not substantially change any of the major findings reported here, and only altered the confidence interval estimates.

One way to describe the variation in the average effect size is to statistically evaluate the values within and among categorical descriptors based on attributes of the studies. The effect sizes can also be explained by continuous variables using weighted least squares regression. For both cases, a *Q* statistic is used to partition the heterogeneity in effect sizes according to these descriptors (Rosenberg et al., 2000). In this analysis we explored the relationships between effect size and several different categorical variables, as well as precipitation. Categorical variables used were location (coastal versus interior), soil texture, and grazing regime.

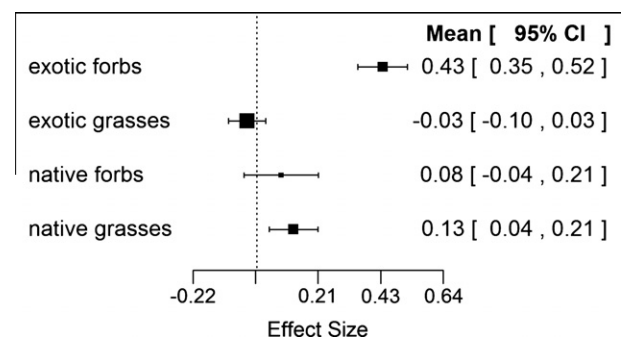
The grazing regime categories used were as follows: continuously grazed (all year), wet-season grazing (typically November–May in California), and dry season (June–October). We also used soil taxonomic classes to divide the many soil types into several categories roughly representing fertility and age. Our groups were as follows: Alfisols and Mollisols, young soils with suffixes of -ept or -ent, older soils such as Palexeralfs or Ultic soils, and serpentine soils (Soil Survey Staff, 1999). Alfisols and Mollisols are fertile, dark-colored and base-rich, whereas serpentine soils are high in heavy metals and low in essential nutrients. In addition to comparing each variable separately, for the native forbs we used the *metafor* package in R to test fixed-effects models including many descriptors with and without an interaction term. We calculated Akaike information criterion (AIC) for each model to determine the best fit. In this model, only studies containing data for all variables were used. Results are presented in online supplemental material (Supporting information, Appendix A).

Although our number of studies is small, we evaluated publication bias using Spearman's rank-order correlation between the effect size and variance. This relationship was not significant (defined as  $p < 0.05$ ) for cover ( $R_s = 0.212$ ,  $p = 0.095$ ) or richness ( $R_s = 0.125$ ,  $p = 0.447$ ), suggesting that publication bias is not overwhelming our estimate of the effect sizes, although it does suggest a trend for percent cover. We also calculated Rosenthal's fail-safe number, or the number of non-significant studies that would need to be added to the meta-analysis to change the results from significance to non-significance (Rosenthal, 1979). The suggested threshold for this number is  $5k + 10$ , with  $k$  being the number of studies.

### 3. Results

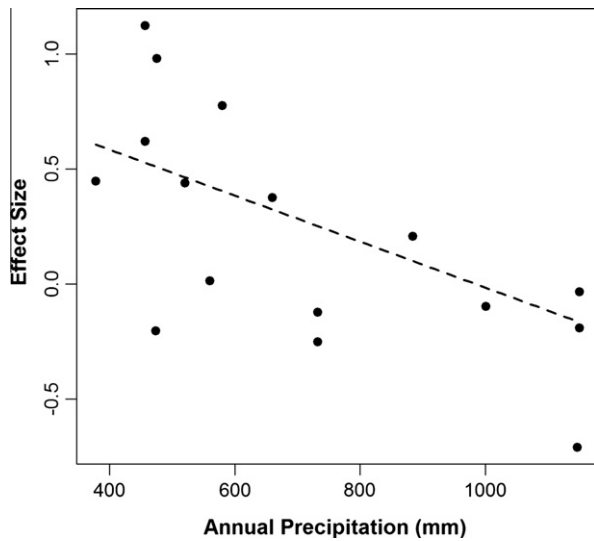
#### 3.1. Species cover

Cover of forbs and grasses showed different responses to grazing. Forbs significantly increased in cover (Effect size =  $0.325 \pm 0.085$ ) with grazing whereas grasses did not differ from zero (Effect size =  $0.025 \pm 0.048$ ), although responses within each varied ( $Q_W = 252.97$ ,  $185.70$  respectively;  $p < 0.00001$ ). Separating native and exotic species explained some of this variability (Fig. 2;  $Q_B = 87.83$ ,  $p < 0.00001$ ). Exotic forb cover was significantly enhanced by grazing (Fig. 2), while the responses of native forbs overlapped with zero. Native and non-native grasses likewise responded differently to grazing. Native grass cover was enhanced by grazing while exotic grass cover was unaffected (Fig. 2). This simple model, however, still left variation within the groups

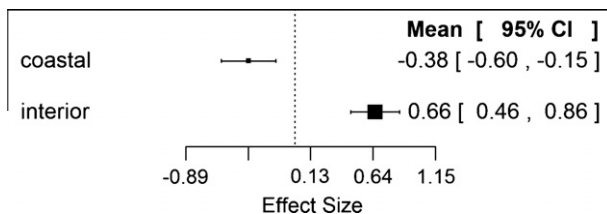


**Fig. 2.** Estimated effect sizes for percent cover by geographic origin and taxonomic group. Error bars indicate the 95% confidence intervals generated via 9999 resampling iterations. Effect sizes with confidence intervals not crossing zero (dotted line) are considered significant.  $Q_W$  significant for each group at  $p < 0.05$ , indicating residual within-group heterogeneity. For exotic forbs and exotic grasses  $n = 16$ , native grasses  $n = 14$ , native forbs  $n = 17$ .





**Fig. 3.** Weighted least squares regression model showing significant negative relationship between the effect size for exotic forb cover and annual precipitation. Both the intercept and slope of the model were significant at  $p < 0.00001$  and  $p = 0.002$ , respectively, generated from 9999 resampling iterations. Rosenthal's fail safe number for this analysis was 157.9.

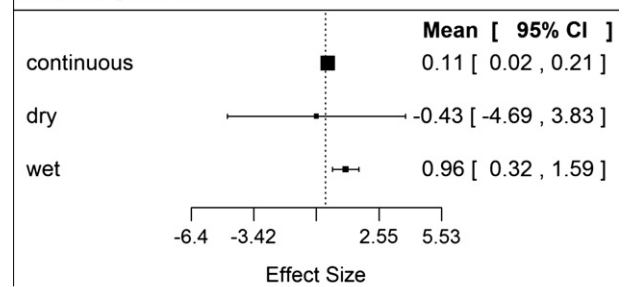


**Fig. 4.** Effect size for native forb percent cover in coastal versus interior grasslands. Error bars indicate the 95% confidence intervals generated via 9999 resampling iterations.  $Q_W$  significant for each group at  $p < 0.00001$ . For coastal grasslands  $n = 5$ , interior  $n = 12$ . Rosenthal's fail-safe number is 105.2.

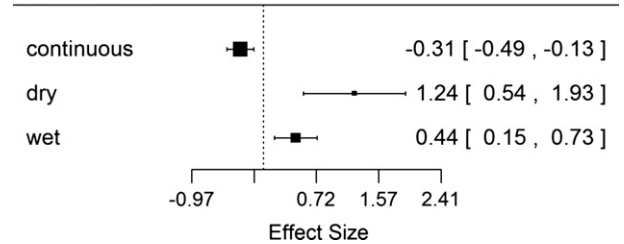
unexplained ( $Q_W = 404.85$ ,  $p < 0.00001$ ). Exotic forbs had the least residual heterogeneity in their response ( $Q_W = 27.15$ ,  $p = 0.027$ ), and native forbs the most ( $Q_W = 202.56$ ,  $p < 0.00001$ ). Rosenthal's fail-safe number for this overall analysis was 904.7, indicating that these results are robust to publication bias despite small sample size.

Precipitation showed a clear negative relationship to effect size for exotic forb cover (Fig. 3,  $Q_M = 9.44$ ,  $p = 0.002$ ). Exotic forbs were enhanced by grazing at some of the more arid sites (e.g. Sedgwick Reserve, Jepson Prairie Reserve) but unaffected or even suppressed by grazing at the wetter sites (e.g. Sierra Foothill, Hopland). This relationship explained the majority of the variability in exotic forb response ( $Q_E = 17.86$ ,  $p = 0.213$ ). The wetness gradient does not covary with grassland type (e.g. coastal versus interior) since the latter categorical variable did not explain a significant amount of the variation for exotic forbs ( $Q_B = 0.096$ ,  $p = 0.76$ ). In contrast to exotic forbs, effect sizes of exotic grass and native forb cover were positively associated with precipitation; however, the slopes were small (0.005 and 0.008, respectively) and the residual heterogeneity was significant. Hence some other unidentified factor is causing heterogeneity among studies. The response of native grasses to grazing showed a slight trend with precipitation whereby effects were more positive at drier sites ( $Q_M = 2.75$ ,  $p = 0.097$ ), however, residual heterogeneity was greater than that explained by the model.

#### A. Native grasses



#### B. Native forbs



**Fig. 5.** Effect sizes for percent cover of both native taxonomic groups in response to different grazing regimes. Descriptions of the grazing regimes presented in Section 2. Error bars indicate the 95% confidence intervals generated via 9999 resampling iterations. For native grasses  $Q_W = 120.35$ ,  $p < 0.00001$  and Rosenthal's Fail-Safe number is 47.0. For native forbs  $Q_W = 130.08$ ,  $p < 0.00001$  and Rosenthal's Fail-Safe number is 30.1. Continuous  $n = 8$  for both native grasses and forbs, dry  $n = 3$  for forbs and  $n = 2$  for grasses, wet  $n = 9$  for forbs and  $n = 7$  for grasses.

Grassland community type (coastal versus interior) was associated with a significant portion of the variation in response among studies for native forb cover (Fig. 4;  $Q_B = 72.96$ ,  $p < 0.00001$ ), although within-group heterogeneity remained high ( $Q_W = 129.61$ ,  $p < 0.00001$ ). Native forb cover in interior sites had a consistent positive response to grazing while native forb responses in coastal sites tended to be negative. Neither native grasses nor exotic grasses showed any variation in response between coastal and interior sites.

Seasonality of grazing (grazing regime) also influenced responses for some of the plant groupings. The response of exotic forbs did not vary with grazing season ( $Q_B = 0.236$ ,  $p = 0.888$ ) but exotic grass cover decreased significantly during wet-season grazing compared to neutral responses to continuous or dry-season grazing ( $Q_B = 26.55$ ,  $p < 0.00001$ ). Native grasses, in contrast, increased dramatically in response to wet season grazing compared to only a modest increase under continuous grazing and a neutral response to dry season grazing (Fig. 5A;  $Q_B = 13.17$ ,  $p < 0.00001$ ). Native forbs had the largest differences in effect size among the grazing regimes; their cover increased in response to both dry and wet-season grazing, but declined strongly in continuously grazed treatments (Fig. 5B;  $Q_B = 86.44$ ,  $p < 0.00001$ ).

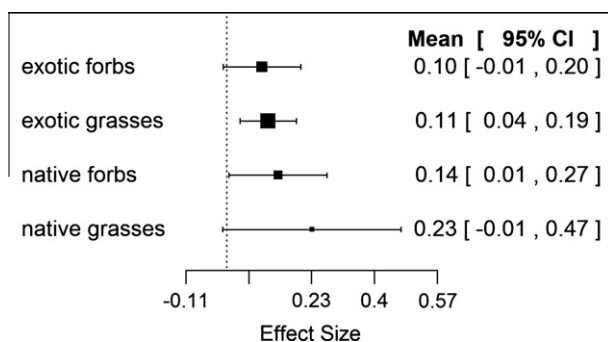
Dividing studies based on soil texture or taxonomy resulted in groups with very small sample sizes, leading to large confidence intervals around the estimated effect sizes. In general, very few of the categories had enough samples to generate confidence intervals that did not overlap zero. Differences in soil texture did not explain meaningful variation in the responses of any of the vegetation groups. Estimated effect sizes for studies with soils in the Alfisol–Mollisol category overlapped zero for all vegetation types despite having the largest sample size ( $n = 4–5$ ) indicating perhaps that this classification was too broad. Serpentine and “young” soils had only 2 studies each and their effect sizes also did not differ from zero for all vegetation types. By contrast, effect sizes for “old” soils (mostly Palexeralfs) mirrored the overall trend for each vegetation type. On these soils, effect sizes for exotic forbs,

native forbs, and native grasses were positive ( $0.790 \pm 0.404$ ,  $1.090 \pm 0.379$ ,  $0.279 \pm 0.229$  respectively) and negative for exotic grasses ( $-0.199 \pm 0.174$ ).

Due to the large amount of heterogeneity in the effect sizes of the native forbs relative to the other vegetation groups, and the number of descriptor variables that significantly influenced their response, we used hierarchical, fixed-effects linear models to investigate the potential for interactions between variables. Interactions between precipitation and location and precipitation and grazing regime were significant at  $p < 0.0001$ , and the best fit models always included the interaction between precipitation and grazing regime (Table A1). When continuously grazed, native forbs increase in the wettest sites, and decrease in the most arid. Under wet-season grazing, the opposite was the case; native forb cover increased most in the driest sites (Fig. A1).

### 3.2. Species richness

Species richness of both grasses and forbs increased similarly in response to grazing ( $0.123 \pm 0.067$  and  $0.112 \pm 0.076$ , respectively); however, as with percent cover there were differences between native and exotic species (Fig. 6). The increase in forb species richness was due to native species while exotic forbs did not significantly increase in richness with grazing. Therefore, the large increase observed in the cover of exotic forbs is not due to an increase in species richness, but rather to changes in the abundance of species that are already present. For example, most of the increase in cover of exotic forbs at Sedgwick Reserve in response to grazing was due to the cosmopolitan weed *Erodium cicutarium* (Tyler et al., unpublished data) whereas many native forbs appeared only in grazed pastures (e.g. several *Trifolium*) but in low abundance so they had little influence on cover. At Bobcat Ranch, the large increases in exotic forb cover with grazing observed by DiTomaso et al. (2009) were made up mostly of *Hypochaeris* spp. and *Erodium botrys*. D'Antonio and Canestro (unpublished data) also found that *Erodium botrys* tended to increase in cover following grazing, whereas *Plantago lanceolata* declined at the Rancho Marino site in the central coast. Increases in native forb richness were due to a wide range of different forb species rather than responses by a few common species. For example, eight of the eleven native *Trifolium* species surveyed by Safford and Harrison (2001) were more common in grazed plots than ungrazed. The response of native grass richness did not significantly differ from zero, whereas exotic grass richness increased with grazing (Fig. 6). Changes in species richness did not vary with any category, although we often had too few studies to reliably detect differences.



**Fig. 6.** Estimated effect sizes for species richness by geographic origin and taxonomic group. Error bars indicate the 95% confidence intervals generated via 9999 resampling iterations.  $Q_W$  significant for native grasses at  $p < 0.05$ , indicating residual within-group heterogeneity. Between group heterogeneity was not significant ( $Q_B = 1.57$ ,  $p = 0.67$ ). For exotic forbs, exotic grasses and native forbs  $n = 10$ , for native grasses  $n = 9$ . Rosenthal's Fail-Safe number = 477.5.

## 4. Discussion

Contrary to expectations based on the use of livestock to enhance native forb abundance, we found that it was exotic forbs and not native forb dominance that were consistently enhanced by grazing in terms of landscape cover. The observed dramatic increase is due to species already present at a site, given that there was no significant increase in exotic forb richness with grazing. By contrast, native forb cover was only weakly enhanced by grazing due to large differences among sites yet richness increased. The effect of grazing on the abundance of grasses also varied between the exotic and native species. Unlike exotic forbs, exotic grass cover did not increase with grazing, although richness did increase. Our results also give some support to the use of grazing to enhance the cover of native grasses although the responses were variable and poorly explained by the descriptor variables we tested. The species richness response of native grasses was also highly variable and did not differ significantly from zero.

### 4.1. Controls over response of native versus non-native species

Unlike the native and exotic grasses, which differ dramatically from each other in life history (natives = perennials, exotics = annuals) and water use (Holmes and Rice, 1996), the cause of variation in the response of native versus exotic forbs is unclear. The exotic forbs responsible for the majority of the increases in cover at Sedgwick Reserve and Bobcat Ranch were generally prostrate plants with basal rosettes appearing early in the growing season (*Erodium* and *Hypochaeris* spp.), supporting the idea that grazing favors shorter-statured species (Bullock et al., 2001; Díaz et al., 2007; Evju et al., 2009). Indeed Rice (1987) has shown that *Erodium* species are nearly eliminated in ungrazed sites and need disturbances to remain in grassland systems.

Exotic and native forb species may also differ in leaf traits, although this has not been quantified for California grassland communities as a whole. Smith and Knapp (2001) found that in tall-grass prairie in the USA, exotic species tended to have approximately 30% greater specific leaf area (SLA) compared to natives. Exotic species in low-fertility communities in southeastern Australia also appear to have larger leaf area than natives (Lake and Leishman, 2004) and Ordonez et al. (2010) documented a global pattern of 15% greater specific leaf area for exotic species in various community types. Additionally, both grazing and fertilization result in the replacement of low SLA plants by those with higher SLA in a variety of Australian grasslands (McIntyre, 2008; McIntyre and Lavorel, 2007). Larger leaf area per unit mass could allow exotic species to compensate (and eventually overcompensate) for herbivory more quickly or efficiently. Kimball and Schiffman (2003), for example, have shown *Erodium* plants quickly recover from clipping relative to native forb species. Alternatively, successful exotic forb species in California grassland may not occupy as broad a range of life histories as native forbs and therefore respond more uniformly to grazing. Exotic forbs able to naturalize in California grasslands may have possessed adaptations to tolerate grazing from their native range. Native forbs are more taxonomically diverse, and therefore might be expected to vary more in response to grazing, perhaps leading to the high heterogeneity found in this meta-analysis.

Differences between the responses of native forb cover in interior versus coastal grasslands could be related to the presence of native perennial species on the coast and their absence from interior sites. Indeed Hayes and Holl (2003) found an increase in native annual forbs on the coast with grazing but a decrease in native perennial forbs (although not significant). Likewise, Skaer et al. (in press) saw a decrease in native perennial forbs on the coast

with grazing. Thus, forb cover response may depend on whether they are perennial or annual, which appears to vary with grassland type. In Australian temperate grasslands, where many of the exotic grasses and forbs are shared with California, [Dorrough et al. \(2004\)](#) found that annual species tended to increase following grazing whereas perennial species declined. This same pattern has also been documented in sandy semi-arid grasslands in Mongolia ([Zhang, 1998](#)) and the succulent Karoo of South Africa ([Todd and Hoffman, 1999](#)).

Season of grazing was also an important influence of the response of native forb cover; however, the lack of studies with dry-season grazing hampers adequate comparisons with continuous or wet-season grazing. Based on our findings, continuous grazing may only be beneficial to native forbs in more mesic grasslands. Wet-season grazing produced variable effects on the drier end of the precipitation range, but on average the response of native forbs and grasses were positive (for percent cover). Reductions of exotic grasses were likewise highest in the wet-season grazing treatments, suggesting that this may be the most appropriate type of grazing for improving reducing exotic annual grasses and increasing native plant cover. These results may relate to the seasonal growth patterns for native versus exotic grasses and forbs. Exotic annual grasses in California germinate following the onset of the rainy season (October–November) and grow actively until late winter/early spring when they reach peak flowering ([Bartolome, 1979](#); [Hobbs and Mooney, 1985](#)). Therefore their biomass may be best controlled by grazing before the initiation of flowering. By contrast native grasses typically have a later or more flexible phenology although this varies by species ([Smith, 2012](#)). Exotic and native forb species present in the included studies have widely varying seasonal growth patterns; some complete their lifecycle by early to late spring similar to exotic grasses whereas others grow throughout the dry summers ([Mooney et al., 1986](#)).

#### 4.2. Knowledge gaps

Despite widespread belief that grazing can be used to restore grasslands towards native species, we found several knowledge and research gaps that limit such a conclusion. First, there is still a paucity of grazing studies in California grassland that have at least two replicates and ungrazed ‘controls’, allowing for estimation of the variation in response. Additionally, very few studies have been done comparing grazing responses across soil types. Soil variation within California is high, yet the frequency of studies on even broad categories is too low to attempt a meaningful comparison. Broad soil classifications such as those used in mapping may also not be appropriate for making predictions about the impacts of grazing. Other meta-analyses of species from many locations worldwide have suggested that monocot and dicot herbs respond differently to herbivory at high versus low resources ([Hawkes and Sullivan, 2001](#)), and in California grasslands on serpentine soils frequently respond differently to grazing than those on more fertile soils ([Gelbard and Harrison, 2003](#); [Safford and Harrison, 2001](#)). More studies explicitly comparing different soil types are needed to examine the role of soil fertility using a meta-analysis.

Grazing intensity and seasonality are often difficult or impractical to manipulate in extensive field projects. A few studies from outside California have investigated the relationship between precipitation and forage production under different grazing intensities, but the forb and grass or native and exotic components are rarely separated ([Fuhlendorf and Engle, 2001](#); [Milchunas et al., 1994](#); [Patton et al., 2007](#)). A few studies in this meta-analysis ([Bartolome et al., 2004](#); [DiTomaso et al., 2009](#); [Marty, 2005](#)) have comprehensively manipulated grazing season; however, the sample sizes in each group were generally small. Most of the studies

we evaluated used continuous or wet-season grazing, thus future studies investigating dry season grazing would be particularly informative. More studies manipulating grazing intensity would also be instructive although this is extremely hard to control due to the lack of predictability of rainfall in California ([Perica et al., 2011](#)).

#### 4.3. Comparisons to other regions of the world

There is a substantive literature documenting a decrease in grasses and an increase in forbs in response to increasing levels of a variety of disturbances in grassland around the world (e.g. [Ash and McIvor, 1998](#); [Burns et al., 2009](#); [Collins et al., 1998](#); [Fensham et al., 1999](#); [Ruthven, 2007](#)). Although our study was restricted to California, the response of forbs (particularly exotic forbs) to grazing may be generalized to other grassland communities, especially those with low productivity and strongly seasonal climates. Many temperate Australian grasslands, for example, are invaded by a similar suite of annual grasses and forbs and these plants tend to increase dramatically in response to grazing in contrast to native perennial species ([Dorrough et al., 2004](#); [Pettit et al., 1995](#); [Yates et al., 2000](#)). This is typically due to increases in exotic species; both cover and richness of native annual and perennial forbs respond negatively to grazing in these communities ([Prober et al., 2011](#)). Thus the positive response of native forbs to grazing in our study suggests different controls may be operating in California grasslands despite overlap in composition of exotics. This potentially could be due to fertilization legacies and invasion by exotic legumes in many Australian grasslands ([Dorrough et al., 2006](#)). More similar to our study, native species richness in Chilean Mediterranean espinales increases with increasing grazing intensity, although the cover of exotic species remains high relative to natives ([del Pozo et al., 2006](#)).

The global meta-analysis by [Díaz et al. \(2007\)](#) found species that allocate a large portion of their resources to aboveground biomass and height typically decrease in response to herbivory, favoring shorter-statured species, which is similar to many other studies ([Belsky, 1992](#); [Bullock et al., 2001](#); [Evju et al., 2009](#); [Milchunas and Lauenroth, 1993](#)). In California grasslands, the exotic grasses are taller and allocate more to shoot biomass than most forbs, perhaps leading to the enhancement of forbs in the presence of grazing. Likewise, in Mediterranean Israeli grasslands as well as those in temperate Argentina, plant height was important in determining response to grazing with tall plants declining and short plants – including many forbs – increasing with grazing ([Díaz et al., 2001](#); [Noy-Meir et al., 1989](#)). Plant height, however, may not be an important trait in grasslands with extremely low productivity, as [Vesk et al. \(2004\)](#) found in arid Australian communities.

#### 4.4. Implications for using livestock in plant community management

Like many grasslands in other parts of the world, the group responding the most strongly in dominance to grazing appears to be forbs, particularly non-native ones ([Fensham et al., 1999](#); [Heady, 1966](#); [Sala et al., 1986](#)). Grazing also enhances the richness of native forb species and native grasses show a significant, if small increase in cover following grazing. This suggests that in many locations, the presence of grazing is compatible with the success or restoration of native grass and wildflower populations as has been suggested by [Savory and Butterfield \(1999\)](#) and the California Rangeland Conservation Coalition ([Schohr, 2011](#)). Similar approaches have been advocated and implemented with some success in low-fertility grasslands in Europe ([Dolek and Geyer, 2002](#); [Hampicke and Plachter, 2010](#)) and the Mediterranean ([Verdú et al., 2000](#)).



Land use history may also be a strong determinant of the community-level response to grazing, as it influences the size and nature of the local species pool (Foster et al., 2003). Prior cultivation reduces the local species pool in many grasslands worldwide and is a strong determinant of the community composition, even decades after the cessation of tillage (Bekker et al., 1997; Stromberg and Griffin, 1996). It is not clear whether the limited recovery of tilled fields towards native species dominance is a function of decreased propagule sources or degraded soil structure (Bakker and Berendse, 1999). Soil fertility can also influence the size of the species pool and the performance of N responsive exotic species (Harpole and Tilman, 2007). It is likely an important factor in the difference between serpentine and non-serpentine sites in grazing response (Harrison, 1999). Therefore, a choice to implement grazing management should consider the species pool able to respond to treatments as well as the soil conditions. If few native species remain at a site due to prior cultivation, for example, grazing is unlikely to achieve desired increases in native diversity.

#### 4.5. Conclusions

Overall, although grazing may be a successful tool in the management of plant composition in the right context, it does not consistently lead to enhancement of the target groups in all areas, particularly if the metric of effect is percent native cover. The potential for large increases in cover of exotic forbs must be weighed against other desired outcomes (such as an increase native forb richness) when implementing a grazing plan. This may have particular importance in the driest grasslands, given the strong negative relationship between the effect on exotic forb cover and annual precipitation. Additionally, grazing during the winter and early spring wet season showed the most consistent benefits for richness and cover of native species, especially in the interior grasslands.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.09.008>. These data include Google maps of the most important areas described in this article.

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