


RESEARCH ARTICLE

# A decade-long study of repeated prescription burning in California native grassland restoration

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Native bunchgrass communities dominated by *Stipa pulchra* are widely distributed in California but share dominance with non-native annual grasses. Restoration of these grasslands focuses on altering the balance of native to non-native grasses to favor the former. This study investigated the impact of burning on vegetation recovery. In the first postfire year burning showed a 70% reduction in cover of non-native annual grasses (*Bromus diandrus* exhibited the greatest reduction) and minimal impact on *S. pulchra* recovery. In the following 3 years, *S. pulchra* recovered to levels comparable to controls, whereas the annual grasses remained below control levels until the fifth year. Also, in response to reduced annual grass cover on burned sites several species of non-native *Erodium* increased from 10 to 30% relative cover, however, the low growth form of these forbs presented a less competitive threat to bunchgrasses than the non-native annual grasses, and by the third postfire year returned to near control levels. The rare native geophyte *Brodiaea kinkiensis* was present throughout these grasslands and was not inhibited by burning treatments. To document the reliability of these patterns a second prescription burn was conducted on these sites 5 years after the first burn and vegetation recovery followed for the subsequent 4 years. Patterns observed after the first burn were duplicated following the second burn. The cover of *S. pulchra* varied in response to precipitation, with the 95% credible intervals of precipitation parameters overlapping zero, however, the cover of non-native grasses varied greatly with precipitation and had similar trajectories in unburned and burned plots.

**Key words:** Bromus, invasive annuals, native grasslands, *Stipa pulchra*

## Implications for Practice

- Prescription burning is a viable tool for favoring native grasses (*Stipa pulchra*) over non-native invasive grasses (*Avena* spp., *Bromus* spp., *Festuca* spp.).
- Burning is more effective at reducing non-native grasses while not negatively impacting native grasses.
- Burning has no negative impact on a rare native geophyte (*Brodiaea kinkiensis*).
- An important implication is that annual grasslands might be converted to native grasslands when coupling fire with other restoration tactics.

## Introduction

Fire is one of the most widely used tools in efforts to maintain ecosystem processes and structure, control populations of undesirable species, and restore plant communities from dominance by non-native species to higher proportions of native species (Zouhar et al. 2008). The use of fire as a management and restoration tool is complex though, especially in regard to interactions with invasive plants. For example, while fire is regarded as an integral component of many shrubland and forest systems (Keeley et al. 2009), its occurrence can promote the proliferation of invasive plants and result in altered fire regimes and increased threats to human lives and infrastructure (Keeley 2001; Brooks et al. 2004; Syphard et al. 2018). It is widely used in efforts to

control invasive plants but its record of success is mixed, with a greater likelihood of controlling populations of a target species than achieving persistent shifts in community composition (Zouhar et al. 2008). The difficulties in attaining long-term changes in species composition become even greater in systems with multiple invasive species, especially those where transformer species are present (Kuebbing et al. 2013).

Fire is a critically important process in grasslands worldwide and, along with herbivory, was historically responsible for maintaining them as herbaceous-dominated systems (Eldridge et al. 2011; Ratajczak et al. 2014). Grasslands throughout the

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world have also been heavily invaded by non-native plants (Milbau & Nijis 2004). North American grasslands in particular have experienced invasion by numerous herbaceous and woody species (Gaskin et al. 2021). Fire is frequently used to manage grasslands in North America, but its effects vary greatly among prairie, arid, and coastal systems (Brooks & Pyke 2001; Grace et al. 2001; Zouhar et al. 2008). For example, fire tends to favor native over non-native species in the prairies of the central United States (Grace & Zouhar 2008), but in the heavily invaded Mediterranean climate grasslands of California, the opposite is often the case (Klinger et al. 2008).

Prescribed fire in the grasslands of California has usually been applied with two overarching goals: reduction in the abundance of invasive plants and increase in abundance of native species, especially bunchgrasses (Klinger et al. 2018). Historically native grasslands in California comprised perennial grasses with native annual and perennial forbs. Grasses included perennial bunchgrasses *Stipa pulchra*, *Poa scabrella*, *Festuca idahoensis*, *Koeleria cristata*, and forbs were annual species of *Cryptantha*, *Acmispon*, *Amsinckia*, *Daucus*, *Hemizonia*, and perennial monocots such *Brodiaea*, *Calachortus*, *Dichelostemma*, *Sisyrinchium*, and perennial dicots *Tauchsia*, *Trifolium*, and *Sanicula* (nomenclature follows Baldwin et al. 2012). Throughout the state *S. pulchra* is the most characteristic element of native grasslands across a diverse array of habitats (Bartolome & Gemmill 1981), where they exist in a mosaic with shrublands, scrub, and woodlands (Huenneke 1989; Eviner 2016).

European colonists introduced a rich diversity of annual grasses and forbs that rapidly invaded the native grasslands (species of *Avena*, *Bromus*, *Hordeum*, *Festuca (Vulpia)*, *Brassica*, and *Erodium*), which when coupled with extensive livestock grazing transformed both native perennial grasslands and shrublands into the vast extent of non-native annual grasslands present today in the state (Burcham 1957; Keeley 1990; Hamilton 1997; D'Antonio et al. 2007). In southern California the non-native *Bromus diandrus* dominates many native grasslands; dominance is enhanced by its earlier phenology, larger seed size, stature, and biomass production (Holmes & Rice 1996; Molinari & D'Antonio 2014).

Efforts at the restoration of the native perennial *S. pulchra*-dominated grasslands have taken two approaches. One has investigated reintroducing native perennial grasses into entirely annual grasslands, and another has focused on remnant native grasslands, and both attempt to alter the ratio of native to non-native grasses. Long-term studies of annual grasslands show no evidence of colonization by native grasses and fire does not lead to recovery of the native *S. pulchra* unless seeded or planted and even then it has not been highly successful at re-establishing native grasses (Moyes et al. 2005). However, remnant native grasslands can be restored through methods designed to reduce non-native annual grasses.

With both approaches prescribed fire has been used to prepare sites in ways that are expected to favor native bunchgrasses over annual grasses (D'Antonio et al. 2006; Stromberg et al. 2007).

This includes the potential negative impact of fire on seedling recruitment, which creates a major problem for annual grasses, but is a lesser problem for perennial grasses as resprouting is very resilient to fire.

Today remnants of native grasslands occur in various-sized patches throughout the state, on both the mainland and offshore islands, and while they are often distinguished by the dominance of *S. pulchra*, it is extremely rare to find any that are not invaded by non-native annuals, often comprising 50% or more cover (Huenneke 1989). Many efforts have been directed at the restoration of these native grasslands, with the goal of altering the balance between native and non-native grasses to favor the perennial bunchgrasses (Stromberg et al. 2007). Results tend to suggest spring burns have the potential for reducing seed banks, which annual grasses are dependent on, but which are less critical to the recovery of resprouting *S. pulchra* (D'Antonio et al. 2006).

Complicating our understanding of the role of fire is that impacts of disturbance are highly contingent on their context, shaped by both historical and contemporary events as well as biotic and abiotic interactions requiring the need for temporal and spatial replication (Young et al. 2014). The competitive impact of invasive annual grasses on native perennial grasses fluctuates greatly, dependent not just on fire but the interaction with annual precipitation levels, and this is confounded by interactions with fluctuations in herb cover (Hallett et al. 2019) as well as grazing (Biggs & Huntsinger 2021). Critically important is that understanding the impact of fire has to consider the longevity of the burning impact over multiple years (Davy & Dykier 2017).

The purpose of this study was to conduct a decade-long investigation of the effects of prescription burns on grasslands on San Clemente Island, California. Prescribed burning with similar goals as our study had been used in grasslands on Santa Cruz Island, California, in the 1990s (Klinger & Messer 2001). Those comprised fall burns applied once to each of three areas (270–490 ha) in successive years (1993–1995). Klinger and Messer (2001) reported shifts in species composition in the 2 years after burning, though these varied considerably by topography; changes in species composition were brief and by the third year postburn the burn areas were similar to composition before burning as well as in unburned control sites. Klinger and Messer (2001) suggested longer-term shifts in species composition could potentially result from repeated burns done earlier in the growing season before the non-native annual species had gone to seed. They cautioned though that it was likely there would be considerable spatial variability because of local environmental conditions (e.g. topography, soils).

Fires in our study were applied in late spring, which has been shown in some cases to result in a greater reduction in alien grass cover than burns done later in the year (Meyer & Schiffman 1999). The length of the study allowed us to evaluate the effect of repeated fire by applying a second prescribed burn halfway through the study. Thus, we were able to compare vegetative changes in the 5 years following the first prescribed burn

(and a wildfire) and then during the subsequent 4 years after the second prescribed burn. In addition, because California grasslands are sensitive to annual fluctuations in precipitation, we assessed changes in response to fire in the context of different levels of annual precipitation. There was a sizeable representation of *S. pulchra* in the grasslands, therefore our main goal was to measure the extent to which fire altered its contribution to total cover, as well as that of the rare native perennial geophyte *Brodiaea kinkiensis* (CNPS 2022), relative to cover of non-native annual grasses and forbs. We addressed five questions: (1) to what degree did the relative cover of *S. pulchra* change after a prescribed fire? (2) to what degree did the relative cover of non-native annual grasses and forbs change after a prescribed fire? (3) to what degree change in the relative cover of *S. pulchra* was a result of changes in its abundance versus changes in the relative cover of non-native annual grasses and forbs? (4) How consistent were the changes in relative cover of *S. pulchra* and non-native annual grasses and forbs at the site and plot scales? and (5) How consistent were the responses of *S. pulchra* and non-native annual grasses and forbs to variation in precipitation?

## Methods

### Study Sites

San Clemente Island is an oceanic island and the southernmost Channel Island off the southern California coast, in the Pacific Ocean near the Mexican border, 100 km west of San Diego; the island is managed by the U.S. Navy. The climate is Mediterranean, with February lows of approximately 4°C and August highs of approximately 35°C (U.S. Navy 2002). Annual rainfall is highly variable (ranging from <50 to >400 mm during the

years of this study; Fig. 1; recorded at two sites in the central (Stone) and northern (NRO) part of the island, MesoWest data; <https://mesowest.utah.edu>). However, additional moisture comes from fog precipitates, which frequently blanket the island in the early warm season (Clemesha et al. 2021). It is one of eight Channel Islands and is intermediate in size and number of plant species. However, with 11 single-island endemic taxa it has more than any of the other Channel Islands (Raven 1965), and one of these frequently found in grasslands, *Brodiaea kinkiensis*, is included in the California Native Rare Plant Inventory (CNPS 2022). Our grasslands were located on the central plateau of San Clemente Island, California. Soils in the grasslands were largely clay derived from volcanic substrates (U.S. Navy 2008).

Non-native European annual plants were accidentally introduced over 200 years ago and now dominate many of the grasslands. Non-native ungulates were introduced to the island over 150 years ago and impacts from pigs, goats, cattle, and sheep continued through the late 20th century. The large non-native grazing animals were removed from the island by 1991 (Keegan et al. 1994), so other than the rodent *Microtus californicus* (introduced sometime in the late 19th to early 20th century by Euro-Americans), San Clemente Island does not have any grazing mammals (U.S. Navy 2002). Being without large grazing animals for several decades is an advantage to working in grasslands on San Clemente Island because this removes a considerable amount of potential confounding between grazing and fire effects.

We identified three study sites that contained a substantial cover of native *Stipa pulchra*. Non-native grasses and forbs comprised a large portion of the remaining cover, but native forbs were present as well. Burn treatments were set up as a randomized block design. Due to logistics associated with

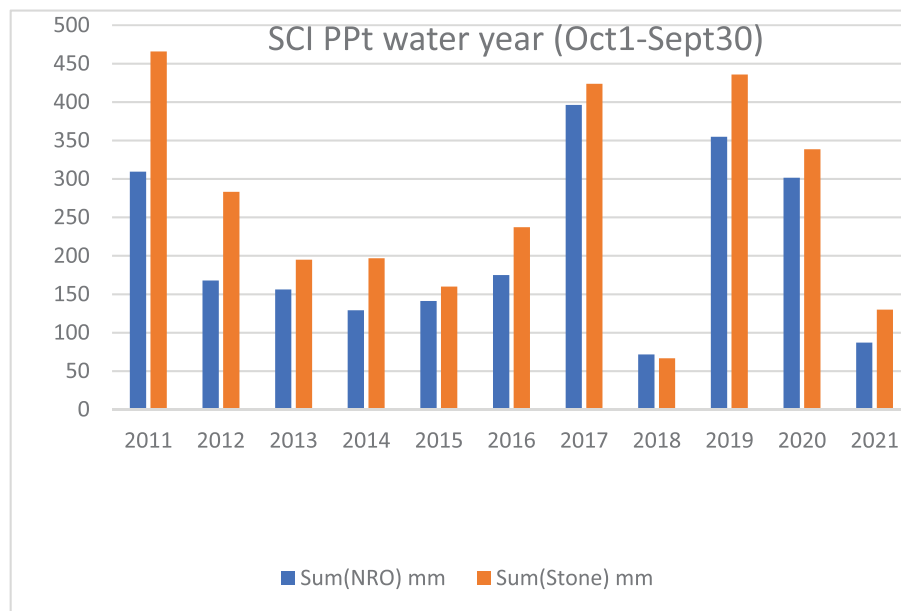


Figure 1. Total precipitation for two sites on San Clemente Island from 2011 to 2021 (NRO and Stone are two sites described in the Methods).

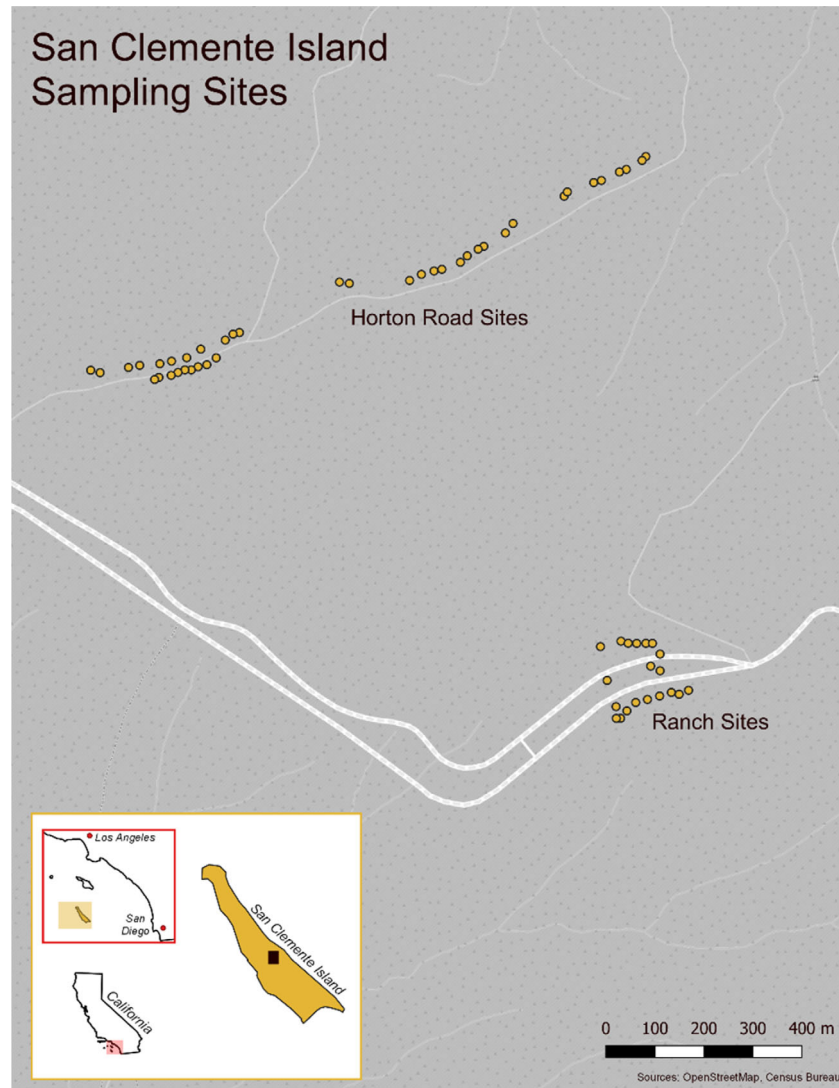


Figure 2. Study site and plot locations on San Clemente Island.

prescribed burning, treatment (burned) and control plots were established within 20–30 m of Horton Road at two sites (Fig. 2). One site was at the eastern end (PGE) and the other at the western end (PGW) of the road. We established a total of 20 plots (10 m × 10 m) per site, then randomly selected 10 plots as burned plots and the remaining 10 as controls. Prescribed burns as described below were conducted in late spring 2012. Ten burned and ten control plots were established at a third site (Ranch Canyon) that was burned by a wildfire on 22 May 2012. Although plot selection occurred after this fire, the locations of the burned and control plots were randomly selected and they were interspersed throughout the site, and thus generally conformed to the protocols as for the Horton Road sites. A second prescribed burn was conducted 5 years after the first (2017) at all three sites. Vegetation sampling was conducted annually in the spring from 2013 to 2021. Other details of these sites are available in Keeley and Brennan (2015).

### Treatments and Sampling

Prescribed burns were conducted in late spring to coincide with grass seed maturation and dispersal. Around the burn plots a 2.5 m wide border was also burned, but not sampled. To the outside of the burned area, a 2 m band was cleared and soaked with phoschek to prevent fire spread beyond the plots (burn prescriptions and fire characteristics are described in Table S1).

Postfire monitoring of vegetation was conducted for 5 years after the first fire (2013–2017) and 4 years after the second (2018–2021). Each 10 × 10 m plot was subdivided into four equal size subplots and a 1 × 1 m quadrat was established in the middle of each subplot. The density and an ocular estimate of cover were recorded for each plant species, as well as if they were present as seedlings or resprouts. Additional species not encountered within the quadrat were recorded in the remaining portion of each subplot. Due to constraints imposed by the Covid pandemic, sampling in 2020 was altered by recording

cover by functional types rather than species. The original sampling protocol was returned to in 2021.

### Analysis

Statistical analyses were partitioned into two groups: (1) comparisons between control and burned plots within and across years; and (2) comparisons between control and burned plots relative to precipitation. Response variables in both groups were the percentage cover of (1) two native species (*S. pulchra*, *B. kinkiensis*) and the non-native annual forb *Centaurea melitensis*; (2) four groups of non-native annual grass, including *Avena* spp. (*A. barbata*, *A. fatua*), *Bromus* spp. (*Bromus diandrus*, *B. hordeaceus*, *B. madritensis*), *Festuca* spp. (*F. bromoides*, *F. myuros*), and all non-native annual grasses (*Avena* spp., *Bromus* spp., *Festuca* spp., *Hordeum* spp., *Lamarkia aurea*, *Phalaris minor*); and (3) the non-native annual forbs *Erodium* spp. (*E. cicutarium*, *E. botrys*, *E. moschatum*). The non-native annual grasses *Hordeum* spp. (*H. marinum*, *H. murinum*), *L. aurea*, and *P. minor* were not analyzed separately because they comprised less than 1% of the cover. Relative cover of each species *i* was calculated as  $\text{cover}_i / \sum \text{cover}_i$ . The relative cover of *Avena* spp., *Bromus* spp., *Festuca* spp., and *Erodium* spp. was the sum of the species' relative cover within each genus.

Cover data are proportions, therefore we specified models in a Bayesian framework with cover assumed to be from a beta distribution (thereby constraining estimates to be in the interval 0–1) and non-informative priors. In group 1, we modeled the relationship between cover (both absolute and relative), burn condition ( $j = \text{unburned}$  and  $\text{burned}$ ), and year ( $k = 2013, \dots, 2019, 2021$ ) as a repeated measure two-way ANOVA with the site and plot effects:

$$\begin{aligned} \text{Cover}_i &\sim \text{Beta}(a_i, b_i), \\ a_i &= \mu_i \times \varphi, \\ b_i &= (1 - \mu_i) \times \varphi, \\ \varphi &\sim \text{Gamma}(0.1, 0.1), \\ \text{logit}(\mu_i) &= \alpha + \beta_{j(i)} \times \text{Burn}_i + \gamma_{k(i)} \times \text{Year}_i + \zeta_{jk(i)} \times \text{Burn}_i \\ &\times \text{Year}_i + \theta_{\text{site}(i)} \times \text{Site}_i + \theta_{\text{plot}(i)} \times \text{Plot}_i, \\ \text{with } \alpha &\sim N(0, \sigma^2), \beta_{jk} \sim N(0, \sigma^2), \gamma \sim N(0, \sigma^2), \zeta \sim N(0, \sigma^2), \\ \theta. &\sim N(0, \sigma^2), \end{aligned}$$

where  $\alpha$  is the overall mean,  $\beta$  is the parameter for burn condition,  $\gamma$  is the parameter for year,  $\zeta$  is the parameter for the burn  $\times$  year interaction,  $\theta.$  are the parameters for the site ( $s = 1 \dots 0.3$ ) and plot ( $p = 1 \dots 60$ ) effects and  $a$  and  $b$  are the shape and rate parameters for the beta distribution.

The exception to these models was for the absolute cover of non-native grasses, which can be greater than 1 because of the overlap in cover among species. In this case, total cover was assumed to be from a log-normal distribution (thereby constraining estimates to be nonnegative) with non-informative priors:

$$\begin{aligned} \text{Cover}_i &\sim \text{logNormal}(\mu_i, \sigma^2), \\ \sigma^2 &= \text{Uniform}(0, 100), \\ \text{log}(\mu_i) &= \alpha + \beta_{j(i)} \times \text{Burn}_i + \gamma_{k(i)} \times \text{Year}_i + \zeta_{jk(i)} \times \text{Burn}_i \\ &\times \text{Year}_i + \theta_{\text{site}(i)} \times \text{Site}_i + \theta_{\text{plot}(i)} \times \text{Plot}_i, \\ \text{with } \alpha &\sim N(0, \sigma^2), \beta_{jk} \sim N(0, \sigma^2), \gamma \sim N(0, \sigma^2), \zeta \sim N(0, \sigma^2), \\ \theta. &\sim N(0, \sigma^2). \end{aligned}$$

We were primarily interested in the interaction between burning and year and conceptually considered sites and plots as “random effects,” but to gain insight into the magnitude of spatial variation at these scales we calculated effect sizes as derived parameters  $\text{Effect} = \theta. - \text{mean}(\theta.)$ , which propagated error throughout the effect size estimates.

The relationship between absolute cover, burn condition, and precipitation in group 2 was modeled as an ANCOVA with the site and plot effects:

$$\begin{aligned} \text{Cover}_i &\sim \text{Beta}(a_i, b_i), \\ a_i &= \mu_i \times \varphi, \\ b_i &= (1 - \mu_i) \times \varphi, \\ \varphi &\sim \text{Gamma}(0.1, 0.1), \\ \text{logit}(\mu_i) &= \alpha + \beta 1_{j(i)} \times \text{Burn}_i + \beta 2 \times \text{Precipitation}_i + \beta 3_{j(i)} \\ &\times \text{Burn}_{j(i)} \times \text{Precipitation}_i + \theta_{\text{site}(i)} \times \text{Site}_i + \theta_{\text{plot}(i)} \times \text{Plot}_i, \\ \text{with } \alpha &\sim N(0, \sigma^2), \beta 1_j \sim N(0, \sigma^2), \beta 2 \sim N(0, \sigma^2), \\ \beta 3_j &\sim N(0, \sigma^2), \theta. \sim N(0, \sigma^2), \end{aligned}$$

where  $\beta 1$  is the parameter for burn condition,  $\beta 2$  is the parameter for precipitation,  $\beta 3$  is the parameter for the burn  $\times$  precipitation interaction, and  $\alpha$  and  $\theta.$  are as above. We included the variance components for site and plot ( $\sigma^2_{\text{site}}$  and  $\sigma^2_{\text{plot}}$ , respectively) to evaluate the degree to which effect sizes of the burns varied at different spatial scales and among taxa.

Models were implemented in R (R Core Team 2022) with the programming software JAGS and the rjags package (Plummer 2021). For group 1, we used five chains with 20,000 iterations each after a burn-in of 5,000 and an adaptation phase of 5,000. For group 2, we used five chains with 100,000 iterations each after a burn-in of 10,000 and an adaptation phase of 10,000. A thinning rate of 10 was used to reduce autocorrelation of the Markov chain Monte Carlo (MCMC) samples, resulting in 10,000 MCMC samples in group 1 and 50,000 in group 2 for inference. Model performance was evaluated with the inspection of trace plots, effective sample size (ESS), and a scale reduction factor ( $R$ ) proposed by Gelman and Rubin (1992).  $R$  values less than 1.05 were considered to indicate an acceptable level of chain mixing, which was confirmed with the inspection of the trace plots.

### Results

Diagnostics indicated the good performance of all models (Table S2). All  $R$  values were less than 1.03, with 98%  $\leq 1.01$ .

**Table 1.** Absolute cover (%) of the native bunchgrass *Stipa pulchra* and non-native annual grasses in unburned controls and burned treatments on San Clemente Island, California. CIL and CIU are lower and upper 95% credible intervals, respectively.

Year	Unburned (control)				Burned			
	Mean	SE	CIL	CIU	Mean	SE	CIL	CIU
<i>Stipa pulchra</i>								
2013	8.8	1.0	6.9	10.8	9.2	1.1	7.3	11.4
2014	7.9	0.9	6.2	9.7	9.5	1.1	7.5	11.6
2015	7.0	0.8	5.6	8.7	8.7	1.0	6.9	10.8
2016	5.9	0.7	4.6	7.3	5.4	0.7	4.2	6.8
2017	3.5	0.4	2.6	4.4	3.5	0.5	2.7	4.4
2018	3.8	0.5	2.9	4.8	5.4	0.7	4.2	6.8
2019	4.6	0.6	3.5	5.7	6.9	0.8	5.4	8.6
2021	5.0	0.6	3.8	6.2	7.7	0.9	6.1	9.6
Mean	5.5	0.5	4.5	6.5	6.7	0.6	5.5	8.0
Non-native annual grasses								
2013	44.3	2.6	39.1	49.4	13.0	2.6	8.0	18.0
2014	38.0	2.6	32.8	43.1	9.2	2.6	4.1	14.3
2015	26.9	2.6	21.8	32.0	12.6	2.6	7.7	17.7
2016	45.0	2.6	39.9	50.0	20.9	2.6	15.9	25.8
2017	25.2	2.6	20.0	30.3	42.7	2.6	37.5	47.8
2018	12.2	2.6	7.0	17.4	5.6	2.6	0.4	10.6
2019	60.7	2.6	55.6	65.8	41.2	2.6	36.0	46.2
2021	16.3	2.6	11.1	21.5	17.3	2.6	12.2	22.6
Mean	33.5	1.8	30.0	37.1	20.3	1.8	16.9	23.7

ESS ranged from 1,580 to 19,389 in group 1 and 1,700 to 38,709 in group 2.

### Burn × Year

**Mean Responses.** The first burn had little effect on the absolute cover of *Stipa pulchra* (Table 1). From 2013 to 2017 the 95% credible intervals (CI) of absolute cover in burned plots overlapped almost entirely with those in control plots, with mean values across the initial 5 years differing by less than 1% (Table S3). There was an indication the second burn had a small but positive effect on the absolute cover of *S. pulchra*, especially in 2019 and 2021 (Table 1); mean values the 4 years after the second burn only differed by 2% but overlap in CIs was minimal (Table S3). Relative cover of *S. pulchra* showed strong interannual fluctuations in both control and burned plots, but there was minimal or no overlap in CIs in 2015, 2018, and 2021 and mean values were 1.5 × to 2 × greater in burned than control plots during those 3 years (Fig. 3).

Absolute and relative cover of non-native annual grasses decreased substantially in response to burning, with the effects on relative cover persisting 3–4 years after both fires (Table 1; Fig. 3). Across years, the absolute cover was 13.3% lower in burned than unburned plots, with the largest proportional decrease occurring in 2013 and 2014 (Table 1). The relative cover of non-native annual grass in unburned plots showed strong interannual variation, but in general, it comprised greater than 50% across years. In contrast, the relative cover of non-native annual grass in burn plots was 22.4% less than in unburned plots across years (Fig. 3).

The overall decrease in cover of non-native annual grasses after burning varied substantially among species. *Bromus* spp., dominated by the very vigorous *Bromus diandrus*, had the greatest drops in absolute and relative cover on burned sites (Table S3; Fig. 3), whereas *Avena* spp. (mainly *Avena barbata*) had more modest decreases (Table S3; Fig. 3) and the diminutive *Festuca* spp. (mostly the former *Vulpia myuros*) increased on burn sites (Table S3; Fig. 3).

The three forbs we focused on responded quite differently to burning. The non-native *Erodium* spp. was heavily favored by burning, exhibiting marked increases in the first and second postfire years after both burns (Table S3; Fig. 3). *Erodium* were the dominant forbs in the grasslands regardless of burning, but across years their relative cover in burned plots was nearly three times that in unburned plots (Fig. 3). Mean absolute and relative cover values of *Centaurea melitensis* were lower on burned plots in most years, but until 2017 the 95% CIs of the burn plots overlapped those of the unburned plots (Table S3; Fig. 3). After the second burn in 2017, mean absolute cover of *C. melitensis* in burned plots was less than 2% and mean relative cover in unburned plots was less than 3% in all years. The relatively rare native geophyte *Brodiaea kinkiense* showed no meaningful differences in absolute (Table 1) or relative cover between the unburned and burned sites. Across years, its relative cover in unburned plots was 2.7% (95% CI: 2.1–3.4) and 3.1% (95% CI: 2.4–4.0) in burned plots.

**Spatial Variation of Responses to Burning.** Across all taxa, variation in relative cover was greatest at the plot level (Table 2). The proportions varied greatly among taxa, but it

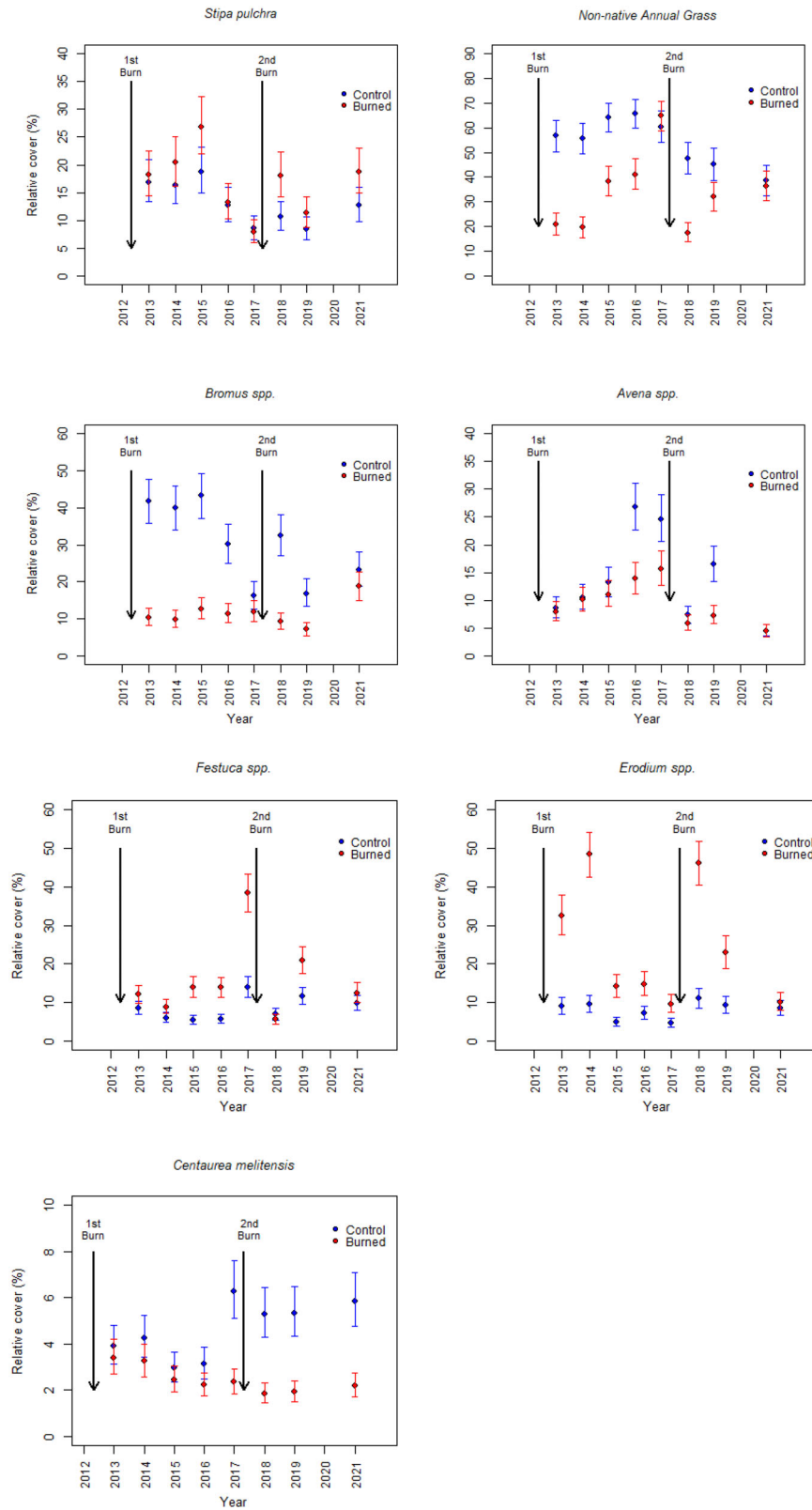


Figure 3. Dynamics in relative cover (mean  $\pm$  95% CI) of: the native perennial bunchgrass *Stipa pulchra*, non-native annual grasses (pooled across species), three non-native annual grass genera (*Bromus spp.*, *Avena spp.*, *Festuca spp.*), a genus of non-native annual forbs (*Erodium spp.*), and the non-native annual forb *Centaurea melitensis* over a 9-year period in unburned (Control) and burned plots on San Clemente Island, California, U.S.A.

**Table 2.** Variance components from the analysis of a field experiment examining the effect of two prescribed burns (2012 and 2017) on seven taxa in grasslands on San Clemente Island, California. Cover was recorded annually from 2013 to 2021 in four 1 m<sup>2</sup> quadrats within each of 10 plots within each of three sites. CIL and CIU are lower and upper 95% credible intervals, respectively.  $\sigma$  = standard deviation.

	Mean	SE	CIL	CIU	Proportion
<i>Stipa pulchra</i>					
$\sigma$ site	0.1220	0.0275	0.0688	0.1760	0.148
$\sigma$ plot	0.5362	0.0579	0.4352	0.6603	0.650
$\sigma$ residual	0.1668	0.0013	0.1645	0.1694	0.202
Non-native annual grass					
$\sigma$ site	0.2766	0.0268	0.2240	0.3292	0.267
$\sigma$ plot	0.5408	0.0577	0.4399	0.6656	0.522
$\sigma$ residual	0.2185	0.0010	0.2167	0.2205	0.211
<i>Avena</i> spp.					
$\sigma$ site	0.2915	0.0286	0.2359	0.3478	0.344
$\sigma$ plot	0.4059	0.0467	0.3229	0.5057	0.480
$\sigma$ residual	0.1490	0.0012	0.1468	0.1514	0.176
<i>Bromus</i> spp.					
$\sigma$ site	0.1160	0.0262	0.0647	0.1674	0.144
$\sigma$ plot	0.5075	0.0544	0.4119	0.6245	0.631
$\sigma$ residual	0.1811	0.0011	0.1791	0.1834	0.225
<i>Festuca</i> spp.					
$\sigma$ site	0.0544	0.0229	0.0126	0.1017	0.104
$\sigma$ plot	0.3128	0.0403	0.2412	0.3996	0.601
$\sigma$ residual	0.1536	0.0011	0.1514	0.1558	0.295
<i>Erodium</i> spp.					
$\sigma$ site	0.2161	0.0272	0.1625	0.2692	0.259
$\sigma$ plot	0.4673	0.0515	0.3769	0.5791	0.561
$\sigma$ residual	0.1500	0.0010	0.1480	0.1522	0.180
<i>Centaurea melitensis</i>					
$\sigma$ site	0.0717	0.0236	0.0266	0.1194	0.146
$\sigma$ plot	0.3534	0.0416	0.2793	0.4424	0.717
$\sigma$ residual	0.0676	0.0005	0.0666	0.0687	0.137

was 1.5 $\times$  to 6 $\times$  greater than that at site and quadrat (residual) scales. The CIs at the plot level overlapped zero in most instances though, with only a few plots indicating a relatively greater positive or negative response to burning (Fig. 4).

Variation in effect sizes for *S. pulchra* indicated that its responses to burning were generally consistent at the site scale, with the CIs for PGW and RC overlapping zero and a relatively small overall range in values (Fig. 4). In contrast, there were substantial differences in site-level effects among the non-native annual grasses (Fig. 4). They varied widely for *Bromus* and, especially, *Avena*, but were very similar for *Festuca* (Fig. 4). While differing in magnitude, *Bromus* and *Avena* had large positive responses to burning at the PGW site and large negative responses at the RC site. There were strong differences in effect sizes among sites for *Erodium* and *C. melitensis* (Fig. 4), with relatively large positive responses by *Erodium* at the PGW and RC sites and by *C. melitensis* at the PGE and PGW sites (Fig. 4).

#### Burn $\times$ Precipitation

There was no evidence cover of *S. pulchra* varied in response to precipitation (Fig. 5), with the 95% CIs of both precipitation parameters overlapping zero (Table S4). Cover of non-native

grass varied with precipitation and had similar trajectories in unburned and burned plots within each of the three taxa (Fig. 5). There were contrasting directions in trajectories though among the taxa; *Avena* had strong positive trends while *Bromus* and *Festuca* had more moderate negative trends (Fig. 5). The two non-native annual forb taxa also showed markedly different trajectories, with *Erodium* having negative trends, particularly that in the burned plots (Table S4), while *C. melitensis* had very strong positive trends (Fig. 5). The proportion of variation at the plot scale was consistently greater than at the site scale for all six taxa (1.5 $\times$ –6.5 $\times$ ; Table S5).

#### Discussion

This study shows the potential for prescribed burning to alter the non-native composition of remnant stands of California native bunchgrass dominated by *Stipa pulchra*. The small changes in the absolute cover of *S. pulchra* following burning indicated that increases in its relative cover were due to shifts in the cover of non-native grasses and forbs. In our study, the dominant non-native grass was the tall-statured aggressive *Bromus diandrus*, and prescribed burning produced substantial decreases in cover of that species. Particularly convincing is that this pattern was repeatable as seen in a similar reduction after the second prescribed burn.

The reduction in non-native grasses and associated increases in relative cover of the native *S. pulchra* provides evidence that prescribed burning can be an effective tool for altering the balance between native to non-native grasses. While some non-native annual grass species increased with burning, this was likely a result of a lack of suppression by the dominant *B. diandrus*. The fact that cover of the native bunchgrass and *Brodiaea kinkiense* remained stable suggests these other non-natives have much less of an inhibitory effect than *B. diandrus*, which is not surprising considering the substantial size and biomass of that non-native annual grass (Holmes & Rice 1996; Molinari & D'Antonio 2014) relative to non-native annual *Festuca* spp. Besides potentially benefitting *S. pulchra* and other native plant species, reduction in non-native grasses can have broader beneficial effects for native animals. For example, burning often reduces non-native annual grass thatch, which is thought to negatively affect habitats for listed bird species on San Clemente Island (U.S. Navy 2008).

The marked increase in the non-native *Erodium* spp. observed in this study is widely reported where fire reduces non-native grasses (Meyer & Schiffman 1999; Cox & Allen 2011; Davy & Dykier 2017). This represents a fundamental change in functional types due to prescription burning. The low-growing nature of these forbs alters the competitive balance between *S. pulchra* and non-native species and does not represent a major challenge to native grass recovery as *S. pulchra* cover remained stable despite increases in *Erodium* after both prescribed burns.

One of the confounding factors in an ecological field study is that species respond to climatic conditions as strongly as to disturbances such as fire. Individual responses are complicated (Pitt & Heady 1978; Endress et al. 2020) and responses can vary



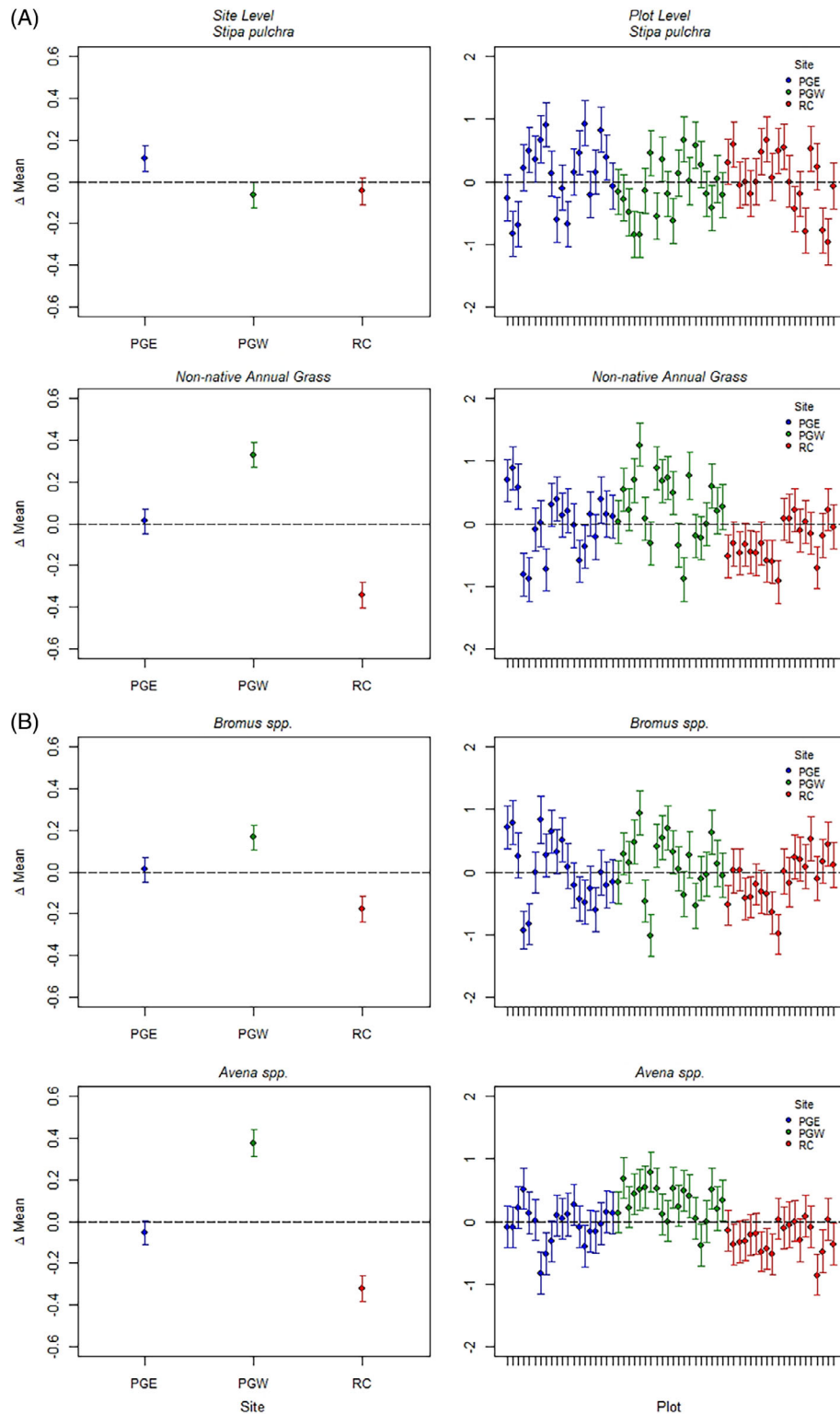


Figure 4. Plot and site effects (mean  $\pm$  95% CI) from a 9-year field experiment (2013–2021) testing the effect of fire on the relative cover of grasses and forbs in grasslands on San Clemente Island, California, U.S.A. There were 10 unburned (control) and 10 burned plots (10 m  $\times$  10 m) within each of three sites (PGE, PGW, RC;  $N = 20$  plots per site, 60 plots total). An initial prescribed burn was conducted in the spring of 2012 at the PGE and PGW sites; a wildfire occurred at approximately the same time in the RC site. A second prescribed burn was conducted in the spring of 2017 at all three sites. Tick marks on the x-axis for the plot-level effects represent the individual plots (numbers not shown).

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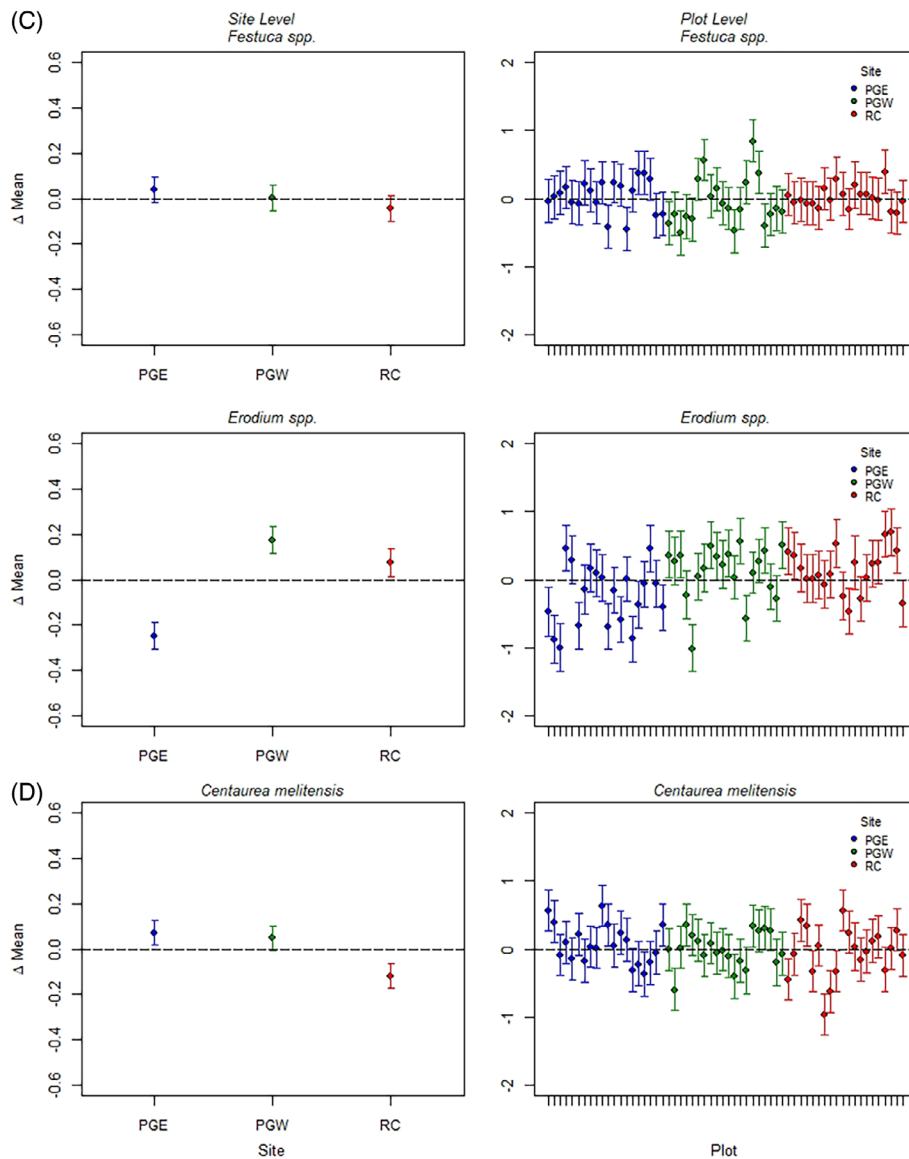


Figure 4 (Continued)

with community composition (Carmona et al. 2015). Further complicating predictions is that modeling how future climates will impact competitive interactions is always dependent on the initial field studies used to parameterize the models and this varies markedly (D’Antonio et al. 2014).

Besides climate, heterogeneity in environmental conditions can also modify fire effects and lead to considerable spatial variability in postfire community composition (Klinger & Messer 2001). We were able to account for this spatial heterogeneity by partitioning the variance at plot and site scales. Variation was greatest at the plot level, but this was due to many different responses in just a few plots compared to the others within a given treatment combination. In a relatively small-scale

field experiment such as ours, where the conditions among the three study sites were similar, it is not surprising that most of the variation occurred at smaller scales. But when prescribed burns are implemented on a larger, more meaningful management scale it is likely variations in factors such as topography, fuel load, fire behavior, and soils will interact and have a much greater influence on species responses. This was evident in our study, where site-level differences among responses were quite evident for most of the taxa. So, while the outcomes of our experiment were generally encouraging, we think it is important to be cautious about extrapolating them to larger scales. Overall mean responses by the taxa could be similar to our findings, but we expect there to be considerable variability around the means.

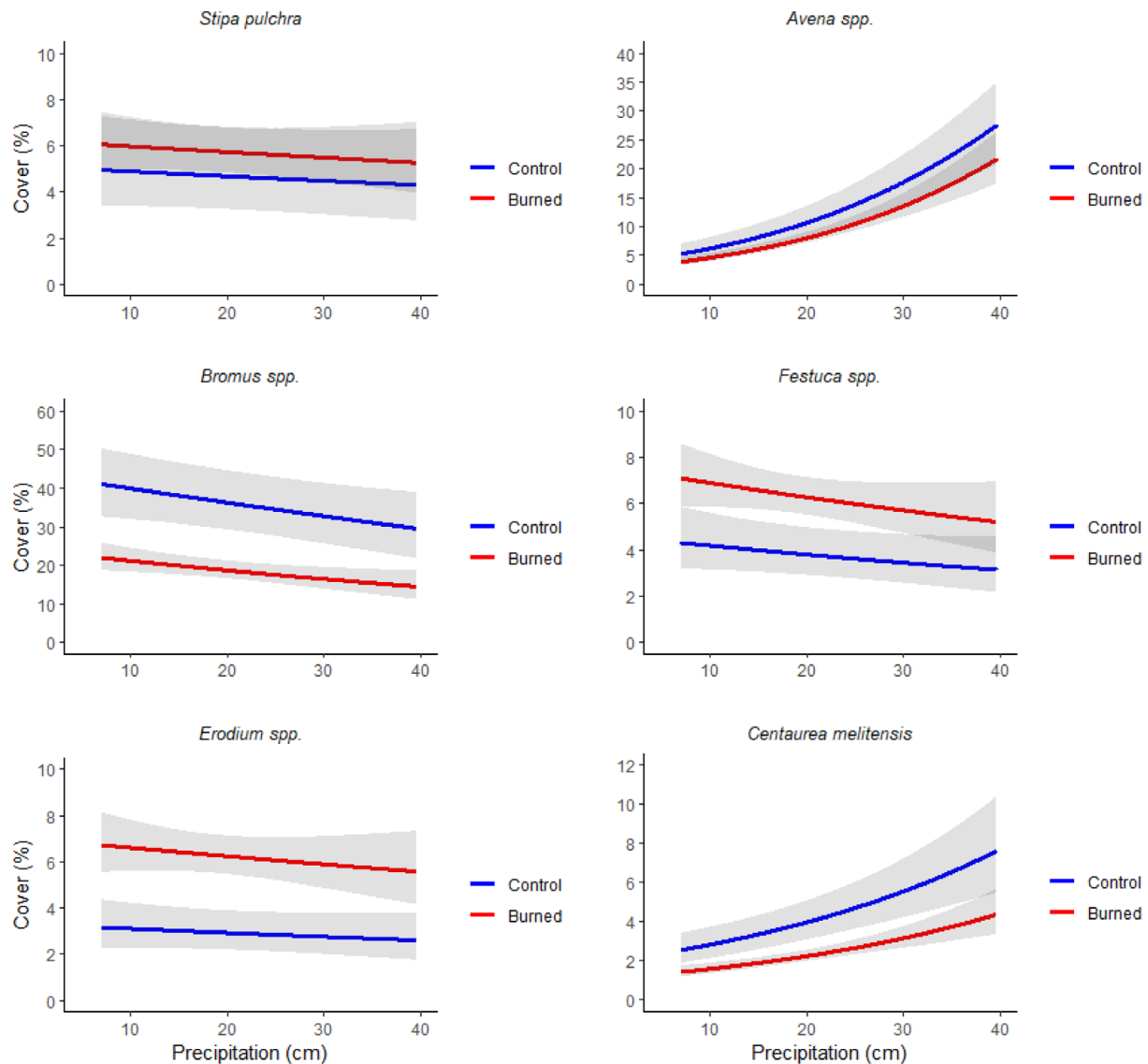


Figure 5. The relationship between prescribed fire treatments, precipitation and cover of six taxa of plants ( $\pm 95\%$  CI) between 2013 and 2021 on San Clemente Island, California, U.S.A. Taxa included the native perennial bunchgrass *Stipa pulchra*, three genera of non-native annual grasses (*Avena* spp., *Bromus* spp., *Festuca* spp.), one genera of non-native annual forbs (*Erodium* spp.), and the non-native annual forb *Centaurea melitensis*.

These remnant native grasslands on San Clemente Island are largely indistinguishable from others on the mainland and thus prescribed burning in California native grasslands should be considered as a potential management approach to native grassland restoration. In all likelihood, though this will require more than single burns and a structured program of repeated burning at approximately 5-year intervals, conducted as early in the year as feasible when vegetation is dry enough to carry fire, but before the non-natives have dropped seed, will have the greatest chance of improving habitat conditions for native plant species.

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## Supporting Information

The following information may be found in the online version of this article:

**Table S1.** Prescription burn measurements during the (A) first and (B) second burns conducted between 11 am and 3 pm.

**Table S2.** Diagnostic statistics for Bayesian models of the response by eight taxa to prescribed burn treatments on San Clemente Island, California, USA.

**Table S3.** Estimates of absolute cover (%) of eight taxa in unburned and burned plots on San Clemente Island, California, USA.

**Table S4.** Parameter estimates for the response in absolute cover by six taxa to the additive and interactive effects of prescribed burning (unburned, burned) and precipitation on San Clemente Island, California, USA.

**Table S5.** Variance components estimates from the response in absolute cover by six taxa to the effects of prescribed burning (unburned, burned) and precipitation on San Clemente Island, California, USA.

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