Manipulating disturbance regimes and seeding to restore mesic Mediterranean grasslands

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Abstract

Question: Can managing disturbance regimes alone or in combination with seeding native species serve to shift the balance from exotic towards native species?

Location: Central coast of California, USA.

Methods: We measured vegetation composition for 10 yr in a manipulative experiment replicated at three sites. Treatments included no disturbance, grazing and clipping at three frequencies with and without litter removal. We seeded eight native species into clipped plots and compared cover in comparable plots with no seeding.

Results: Regardless of frequency, clipping generally shifted community dominance from exotic annual grasses to exotic annual forbs, rather than consistently favoring native species. At one site, perennial grass cover decreased in no-disturbance plots, but only after 4 yr. Litter removal had minimal impact on litter depth and plant community composition. Grazing had a highly variable effect on the abundance of different plant guilds across sites and years. Seeding increased abundance of only two of eight native species.

Conclusions: Managing disturbance regimes alone is insufficient to restore native species guilds in highly-invaded grasslands and seeding native species has highly variable success.

Introduction

Many grassland types are affected by exotic plant invasions. Mediterranean grasslands were the first to gain recognition, but exotic species are increasingly abundant in temperate (Skorka et al. 2010), desert (Anable et al. 1992), and sub-humid (Alejandro et al. 2010) grasslands, and invasion of new species continues. Land managers face dilemmas of managing these novel ecosystems to restore native species where disturbances necessary to maintain them (Collins et al. 1998; Schultz & Crone 1998) frequently also facilitate invasion (Hobbs & Huenneke 1992; Alejandro et al. 2010). Disturbances, such as fire and grazing, are used to restore native species richness and cover in these degraded ecosystems (Uys et al. 2004). In contrast to clearing a site and seeding desired species, this approach takes advantage of extant native species and is less resource intensive. Although this strategy has proven successful in some cases (Barbaro et al. 2001; Wilson & Clark 2001), many more studies have shown that managing disturbance regimes alone is insufficient to

restore community composition (Muller et al. 1998; Seabloom et al. 2003a). This result is likely caused by a lack of native propagule source (i.e. dispersal limitation), which limits recruitment even at small spatial scales (Bakker et al. 1996; Martin & Wilsey 2006). Therefore, it may be necessary to combine managed disturbances with introducing native species for restoration success (Muller et al. 1998; Maret & Wilson 2005). These methodologies are best tested in highly invaded, disturbance-dependent systems with a number of displaced species, such as California grasslands (Hobbs & Mooney 1995; Leiva et al. 1997).

California's grasslands, like temperate and Mediterranean grasslands worldwide (Hoekstra et al. 2005), are highly threatened ecosystems and the focus of extensive restoration efforts. Of particular concern are the more mesic and species-rich coastal prairies in California (Stromberg et al. 2002), which are threatened by development and changing disturbance regimes, and contain an increasing number of endangered species (Ford & Hayes 2007). Similar to most grasslands, they evolved

with disturbance, including grazing by the Pleistocene megafauna, lightning-strike fires and those used by Native Americans, and then cattle grazing for the past 250 yr (Axelrod 1985; Edwards 1992). Over the past three centuries, California grasslands have experienced continual shifts in composition with exotic species invasion, creating challenges to restoration and management (Seabloom et al. 2006). The disturbance factors with which these grasslands evolved are no longer extant, so managers seek alternatives to maintain grassland species.

Options for managing disturbance regimes are, however, often limited by compatibility with nearby land use. Prescribed burning is commonly restricted because of smoke-related health issues and risks of fire escape from the target area (Riebau & Fox 2001; Keeley 2002). Livestock grazing is controversial owing to conflicts with recreational use and potential negative environmental effects (Huntsinger et al. 2007); moreover, livestock grazing is challenging to manage in increasingly fragmented landscapes. Therefore, mowing (clipping) is often used as a disturbance surrogate that is more compatible with other human land uses (Zobel et al. 1996; Wilson & Clark 2001).

In this paper, we present results of a 10-year long, multi-site mesic Mediterranean grassland study to answer the following questions:
1. Can disturbance regimes be managed to favor native over exotic plant guilds?
2. Are grassland responses to disturbance regimes consistent over time and across sites?
3. Does seeding native species in combination with managing disturbance regimes shift the balance towards native species?

We compared the effect of different clipping frequencies on long-term grassland plant community composition to no disturbance and cattle grazing, both common management regimes. Clipping was a primary treatment for several reasons. First, it is applicable to the widest range of conservation managers and is likely to become more common as cattle grazing becomes less economically viable in some regions (Luick 1998; Liffmann et al. 2000). Second, it allowed us to answer questions about effects of different frequencies of disturbance on the balance of native and exotic species. Although many authors have suggested that frequency of disturbance strongly affects species composition (Collins et al. 1995; Fynn et al. 2005), few studies have systematically compared different within-season disturbance frequencies. Third, by clipping we could experimentally test litter removal effects on grassland community composition; past studies have suggested that litter accumulation affects grassland vegetation dynamics (e.g. Facelli et al. 1988). After our first 4 yr of data suggested that distur-

bance regimes alone did not increase native species, we initiated seeding experiments to test whether seeding and disturbance together would prove to be more successful in restoring native species. Experimentally manipulating clipping frequency, litter removal, and seeding not only furthers our mechanistic understanding of disturbance effects on grassland dynamics but is also important to inform resource-constrained land managers, who are eager to identify minimum disturbance regimes that favor native species.

Methods

Study system and site description

California's coastal prairies are mesic Mediterranean grasslands patchily distributed from southern Oregon to the Channel Islands of California, USA below 1000 m a.s.l. within the moderating effects of the ocean (< 100 km from the coast). Characteristic native perennial grass species of coastal prairies include tussock-forming *Danthonia californica*, *Hordeum brachyantherum* and *Bromus carinatus* (Ford & Hayes 2007). We conducted research at three coastal prairie sites all within 4 km of the coast at elevations of < 150 m a.s.l. Sites are each separated by 25 km along a largely north–south gradient near Santa Cruz, California. All research sites were selected to meet the following criteria: (1) had been actively grazed by cattle until the beginning of study; (2) contained characteristic coastal prairie plant species; (3) had slopes of < 10% facing south to southeast; (4) had sandy loam soils, deeper than 1 m; and (5) had long-term conservation protection status. We refer to the sites as: 'Elkhorn' (near the Elkhorn Slough, 3652′4.3″N, 121°44′23.8″W), 'UCSC' (on the University of California, Santa Cruz campus, 36°59′5.5″N, 122°3′0.9″W), and 'Swanton' (near the community of Swanton, 37°4′ 13.4″N; 122°15′00″W). All sites had been grazed by cattle since at least the 1950s, but Swanton and UCSC were not grazed in the early 1990s. All sites were probably surface tilled (to < 5 cm) using a harrow in the early 1900s.

Mean rainy season temperature for the sites is 12.1 °C and mean dry season temperature is 16.4 °C. Rainfall occurs almost entirely between Nov and Apr of each year, but summer drought is greatly moderated by summer fog, which contributes to positive water balance for native perennial grasses (Corbin et al. 2005). Rainfall was highly variable throughout the study (range 251–1228 mm yr^{-1}; see the Supporting Information, Appendix 1), as is typical in Mediterranean systems; 1997 to 1998 (the year before the study started) was an El Niño year, with higher than average rainfall, but overall rainfall during the study was slightly below average. Rainfall was always lowest at

Elkhorn and highest at Swanton, whereas inter-annual fluctuations were similar at all sites (Appendix 1). Soils at all sites are sandy loams with minor variations in pH, organic matter, and major nutrients (Hayes & Holl 2003). The Elkhorn site has more sand (Elkhorn 68%; Swanton 56%; UCSC 43%) and less silt (Elkhorn 20%; Swanton 32%; UCSC 35%), whereas the UCSC site has slightly more clay (Elkhorn and Swanton 12%; UCSC 22%).

Experimental design

At each of the three sites, we fenced a 52 m × 52 m area to exclude primarily cattle and secondarily feral pigs. Within each fenced area, we randomly allocated 30, 7 m × 7 m plots to three replicates of nine clipping treatments (described in detail below) and a no-disturbance treatment beginning in Jan 1999. The plots were separated by a 1-m buffer, which was mowed every 2 to 3 months during the growing season. The first level of treatments consisted of three vegetation clipping regimes using a motorized rotary trimmer to clip vegetation to ca. 5 cm. The three vegetation clipping regimes were: (1) minimal clipping (2 yr^{-1}), where vegetation was clipped once in the spring (Apr) and once in the autumn (Sep); (2) bimonthly clipping (3 yr^{-1}), where clipping was done every other month through the growing season (Jan, Mar, May); and (3) continual clipping (6 yr^{-1}), where vegetation was clipped once monthly through the growing season (Jan–Jun). We designed these disturbance regimes to provide a gradient of disturbance frequencies and to mimic common management regimes (Hayes & Holl 2003).

For the first 4 yr of the study, each of the three clipping frequencies was subjected to one of three secondary treatments designed to test three types of cattle grazing-related disturbances: reducing live vegetation cover (clip and leave clipped material on the ground), litter removal (clip and remove litter with leaf rakes) and soil disturbance (clip, remove litter, and disturb the soil surface). We disturbed the surface of the soil by stepping forcibly with cow hooves attached to boots (Hayes & Holl 2003). Because the soil disturbance treatment had no significant effect on either bare soil or plant community composition (Hayes & Holl 2003), we ceased this treatment in year 5 of the study. Thereafter, we managed these plots the same as litter removal plots and used them for seeding experiments (described below).

We also measured vegetation in three 7 m × 7 m plots grazed by cattle that were outside, but within 15 m of, the exclosures. At Elkhorn, cattle grazed these plots at a stocking rate of 4 to 9 animals ha^{-1} for approximately 4 d at 45- to 60-d intervals from Dec to Apr, which is roughly equivalent in frequency to our 3 yr^{-1} treatment. The grazing regime at Swanton mimicked Elkhorn but the

stocking rate was lower during the first half of this study and similar to Elkhorn during the second half. At UCSC, cattle grazed the site continuously from Dec to Jun at a lower stocking rate of 3 animals ha^{-1}, more equivalent to our 6 yr^{-1} treatment. In the second half of the experiment, UCSC was also lightly grazed (0.5 animal ha^{-1}) from Jun to Dec. Feral pigs disturbed grazed plots at Swanton during the 2000 and 2001 growing season but not thereafter.

Rainfall and litter

We compiled rainfall data from nearby government-managed meteorological stations for Elkhorn and UCSC; for Swanton we obtained data from long-time neighbors of the site (McCrary, unpublished data). Stations were located at similar elevations within 4 km of each research site. We took 10 litter depth measurements at 40-cm intervals along a diagonal of each plot in Sep 2007 (year 9 of the treatments).

Vegetation community data

In each plot, we monitored plant community cover in late Mar of each year from 1999 to 2008 using the point-intercept method. We placed four grids at the corners of a 2.5 m × 2.5 m square centered in each plot, so all plots were 2.25 m from the plot edge and 3.25 m from other treatments. We recorded each species only once at each sample point if it intersected a 1.5 mm metal pin lowered at points spread across a 0.5 m × 0.5 m grid at 10 cm intervals (25 points total). We categorized species origin (native or exotic) using Hickman (1993).

Seeding

In years 5 and 6 of the study, we seeded eight native species into three of the six litter removal plots at each clipping frequency at Swanton and UCSC (nine seeded plots total at each site). A total of 500 seeds m^{-2} of each species were hand-broadcast in the inner 3 m × 3 m area of each plot in Oct 2003 and 2004; we reseeded in 2004 as we recorded no seedlings of seeded species in our sampling quadrats and observed few seedlings elsewhere in the plots during our spring 2004 sampling. We seeded *D. californica* and *Nassella pulchra* (native perennial grasses), *Castilleja exserta* ssp. *exserta* and *Gilia capitata* (native annual forbs), and *Sisyrinchium bellum* (native perennial forb) in both years at both sites. We seeded *Calandrinia ciliata*, *Eschscholzia californica* and *Lupinus nanus* (native forbs) in 2004 only.

We monitored abundance of seeded species in late Mar/ early Apr of subsequent years in the same 0.5 m × 0.5 m grids used for community composition measurements. We recorded the total number of individuals of each of

seeded species not present at sites before seeding. For species that were present at the sites before seeding (*E. californica* and both native perennial grasses) it was impossible to distinguish introduced seedlings from those naturally occurring, so we compared cover from community composition monitoring described previously.

Statistical analysis

All analyses were done using SAS 9.1.3 (Cary, NC, US). We compared plant cover, focusing on vegetation guilds as the goal of our study was to evaluate whether different disturbance regimes would serve to shift the dominance from exotic to native guilds of plants. Because of their similar growth form and life histories, we grouped native perennial sedges (Cyperaceae), rushes (Juncaceae) and grasses (Poaceae) into 'native perennial graminoids.' Cover data are number of intercepts by guild/100 vegetation-pin intercepts per plot. We summed all intercepts in a given plant guild, which resulted in cover values > 100% in cases where species in the same guild overlapped.

We analysed the effect of disturbance regime on vegetation communities using multivariate repeated measures ANOVA with disturbance treatment as a fixed factor, sampling year as the repeated factor, and the absolute cover of various plant guilds as the dependent variables. Because vegetation rarely differed in plots with and without litter removal, we pooled data from these two treatments and focused on comparing no disturbance, grazing and the three clipping frequencies, although we report the effect of all treatment combinations on litter depth. We used Tukey's LSD mean comparison procedures to compare treatments in individual years. For individual-year comparisons, we report significance levels of $P < 0.05$ and $P < 0.005$. Values were log transformed when necessary to meet assumptions of normality and homogeneity of variances. For vegetation community analyses, we used only data from unseeded plots in order to test whether managing disturbance regimes alone could shift the balance between exotic and native guilds. We conducted analyses separately for each of the three sites because earlier analyses (Hayes & Holl 2003) showed highly site-specific responses.

To test whether the high inter-annual variability in guilds could be explained by rainfall patterns, we summed rainfall data into total rainfall (Jul–Jun), fall rainfall (Sep–Nov) and winter rainfall (Dec–Feb) following categorizations by Hobbs et al. (2007) for California grasslands. We calculated Spearman rank correlation coefficients of the rainfall totals, as well as the Palmer drought index (averaged over the previous 1 yr and 5 yr) with major plant guilds in individual unseeded treatments and averaged across sites. Given that the relationships for

individual treatments were generally consistent with site averages, we report the latter.

To evaluate whether seeding in combination with clipping served to increase seeded species cover, we compared individual species abundance in seeded and unseeded plots which were managed identically (clipping and raking). Initial analyses showed no clipping frequency effect on seeding success, so we pooled data from the three clipping frequencies. For species with sufficient abundance, we conducted a multivariate repeated-measures ANOVA with seeding, year, and a seeding × year interaction term for each site. For species where there was a significant seeding × year interaction term, we compared individual years using a one-way ANOVA.

Results

Disturbance effects on vegetation community dynamics

Litter depth in the no-disturbance plots was at least double that in all other treatments at all sites in year 9 of the study (Fig. 1). Otherwise, differences among
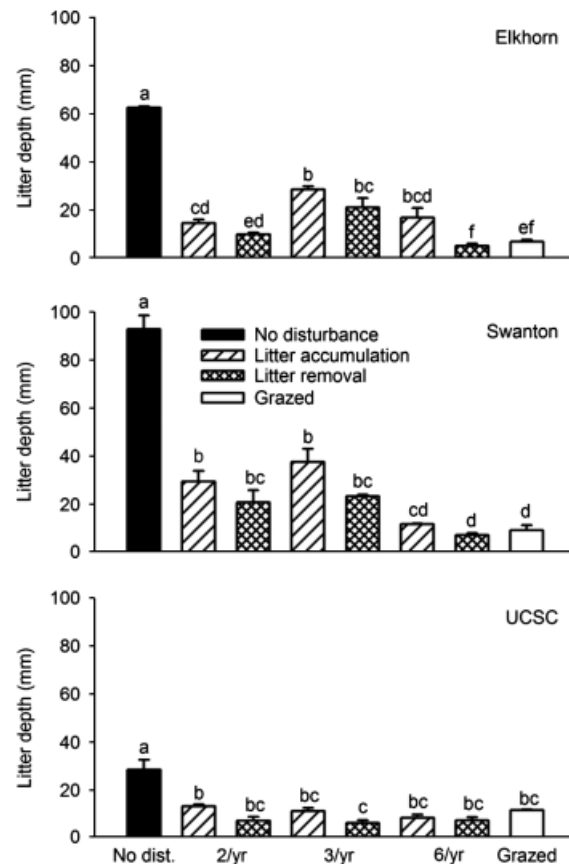

Fig. 1. Litter depth in all treatments in 2007 (year 9 of the study). Values are means ± 1 SE. Means with the same letter are not significantly different ($P > 0.05$, Tukey's LSD test). UCSC = University of California, Santa Cruz.

treatments were much smaller with no consistent trends across clipping frequencies (Fig. 1). Surprisingly, in only one of nine site × frequency combinations was litter depth significantly lower in litter removal than litter accumulation plots, and litter depth in grazed plots was similar to 6 yr^{-1} treatments at all sites. There were no significant litter removal effects on vegetation guild cover over the duration of the study; therefore, in subsequent analyses, we report the clipping frequency effect pooling data from litter accumulation and removal plots.

Total cover (vegetation hits) was relatively constant over time and across treatments. Mean total cover was lower at UCSC (137%) than Swanton (174%) or UCSC (164%). Bare ground was minimal (Elk < 2%, Swanton < 3%, UCSC < 6%).

At Elkhorn and Swanton, exotic annual grass (EAG, comprised primarily of *Bromus* spp., *Lolium multiflorum* and *Vulpia* spp.) cover was significantly higher in plots with no treatment, especially in comparison to 6 yr^{-1} plots, in most of years 3 to 10 of the study (Fig. 2, Table 1); 3 yr^{-1} and 2 yr^{-1} plots tended to have intermediate EAG cover, but this trend was variable over time. At UCSC, EAG cover was higher in grazed plots 2 yr out of 10, but otherwise there were no differences across treatments (Fig. 2). In addition to the annual grass species found at the other sites, UCSC had substantial cover (25–44% average in years 3–10 of the study) of *Brachypodium distachyon*, an extremely short-statured exotic annual grass. Cover in grazed plots at all sites had high inter-annual variation.

Exotic annual forbs (EAF, largely *Erodium* spp., *Geranium dissectum* and *Trifolium* spp.) were a substantial component of the vegetation at all three sites, although populations fluctuated greatly among years (Fig. 3, Table 1). This guild generally had opposite clipping response to that of EAGs (Fig. 3). At Swanton, EAF cover was consistently much lower in the no-disturbance treatment in years 2 to 10; in 3 years EAF cover was significantly higher in 6 yr^{-1} compared with 3 and 2 yr^{-1} treatments. In certain years, Elkhorn and UCSC showed the same, albeit weaker, trend of lower EAF cover in no-disturbance plots, and in other years there was no difference among treatments.

Exotic perennial forbs (EPF) clipping response varied across sites, despite *Plantago lanceolata* and *Rumex acetosella* being common at all sites (Fig. 4, Table 1). The EPFs were generally less common in grazed and no-disturbance plots at Swanton, whereas EPF cover was lower in grazed and 6 yr^{-1} sites in some years at Elkhorn. At UCSC, EPF cover differed across treatments, but declined significantly in all treatments over time.

Elkhorn had the highest initial abundance of native perennial graminoids (NPG, primarily *D. californica*). the
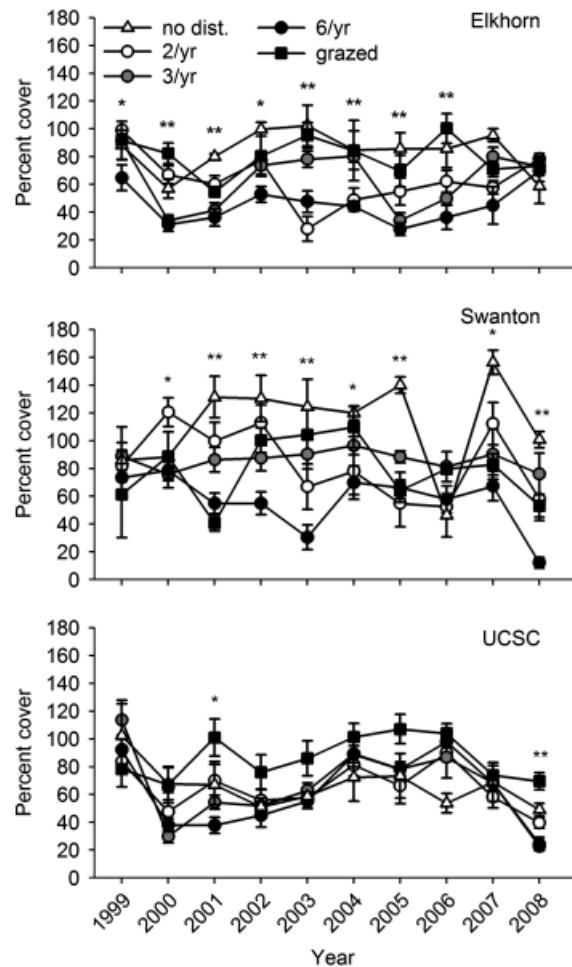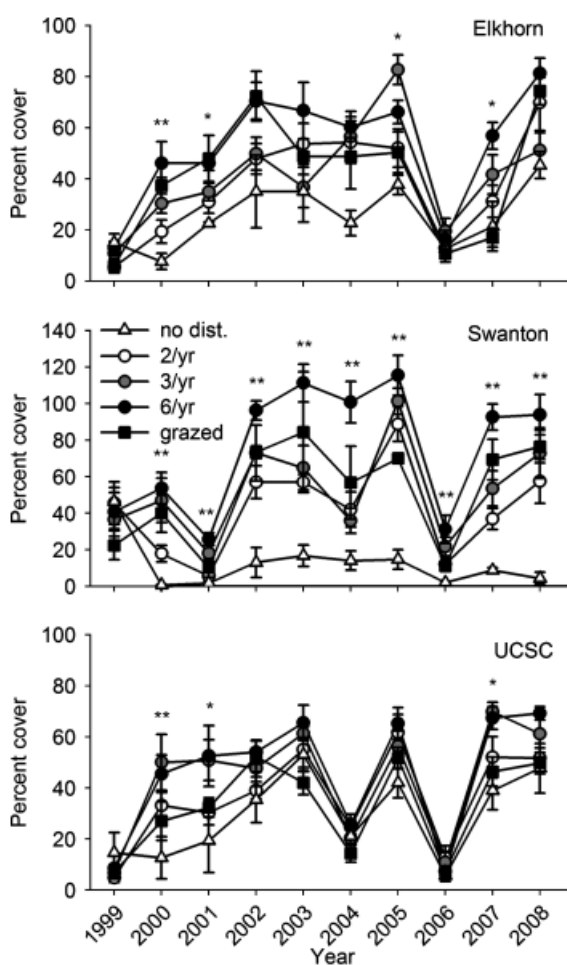

Fig. 2. Exotic annual grass cover in no-disturbance (no dist.), clipped and grazed plots at three sites. Values are means ± 1 SE. *$P < 0.05$, **$P < 0.005$. UCSC = University of California, Santa Cruz.

NPG cover at Elkhorn remained level for 4 yr but in years 5 to 9 showed substantial decline in the no-treatment plots and an increase in all clipping plots (Fig. 5, Table 1). The NPG cover was low in all plots at Elkhorn in the final year, but was still higher in clipped than no-disturbance plots. The NPG cover at Swanton was a patchy mix of *B. carinatus*, *D. californica*, and *H. brachyantherum* that did not show consistent responses to treatment effects over time. At Swanton, one grazed plot initially had higher NPG abundance, although this declined after 3 yr likely owing to pig disturbance. The UCSC site initially and throughout the study had very low (< 1%) NPG cover in all treatments (data not shown).

Native perennial and annual forbs had < 5% cover in all treatments at all sites in most years, and their abundance did not change consistently over time with two exceptions. At UCSC, *E. californica* had 28% cover in no-disturbance plots in the year 1 and steadily declined to
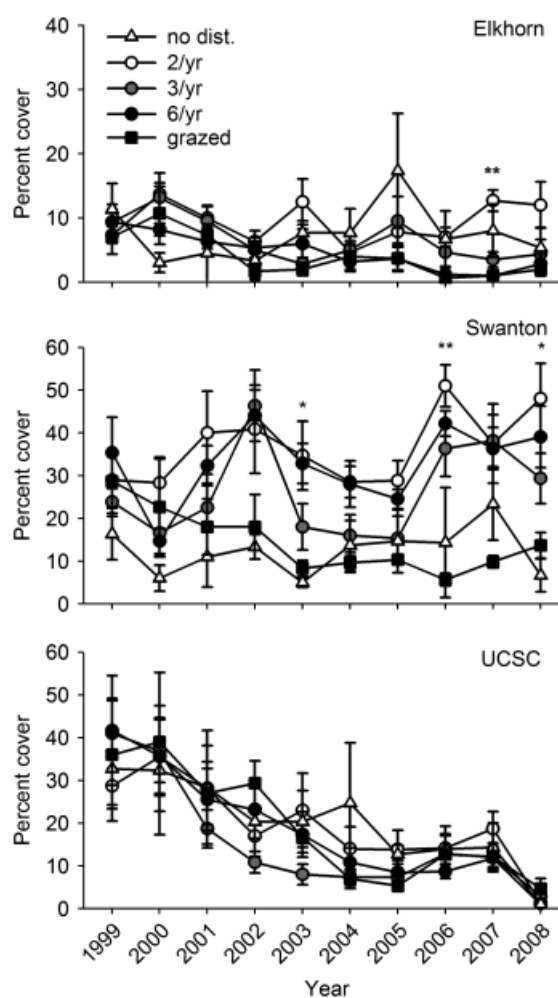
Table 1. Repeated measures ANOVA of disturbance effects on exotic annual grasses (EAG), exotic annual forbs (EAF), exotic perennial forbs (EPF), native perennial graminoids (NPG) and native annual sedges (NAS). Statistics are only reported for NPG and NAS in sites where they were sufficiently abundant to compare across disturbance treatments.

| Site	Variable	EAG		EAF		EPF		NPG		NAS	
		F	P	F	P	F	P	F	P	F	P
Elk	Disturbance	13.5	< 0.0001	50.5	< 0.0001	4.0	0.0172	23.4	< 0.0001	5.1	0.0070
	Year	10.5	0.0009	2.6	0.0011	9.0	0.0016	19.9	< 0.0001	6.1	0.0064
	Distance × year	2.7	0.0007	3.0	0.0495	1.1	0.3588	1.5	0.0844	1.2	0.2438
Swa	Disturbance	5.1	0.0066	38.5	< 0.0001	5.0	0.0067	1.2	0.3427		
	Year	18.1	< 0.0001	1.8	0.0274	4.1	0.0196	3.4	0.0345		
	Distance × year	4.2	< 0.0001	39.8	< 0.0001	1.5	0.0920	1.9	0.0204		
UCSC	Disturbance	3.0	0.0460	265.9	< 0.0001	0.2	0.9490				
	Year	29.9	< 0.0001	1.6	0.0656	9.4	0.0005				
	Distance × year	1.7	0.0442	5.4	0.0045	1.6	0.0645				

Fig. 3. Exotic annual forb cover in no-disturbance (no dist.), clipped, and grazed plots at three sites. Note different *y*-axis scales. Values are means ± 1 SE. *$P < 0.05$, **$P < 0.005$. UCSC = University of California, Santa Cruz.
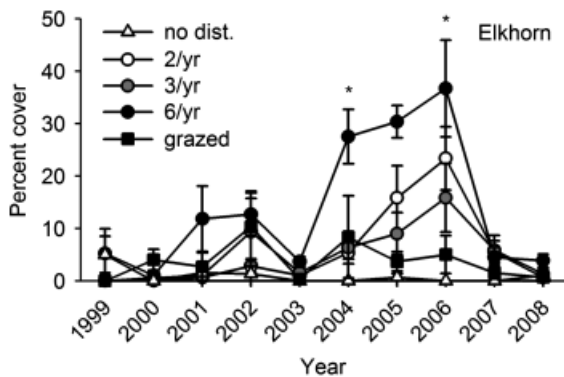

Fig. 4. Exotic perennial forb cover in no-disturbance (no dist.), clipped and grazed plots at three sites. Note different *y*-axis scales. Values are means ± 1 SE. *$P < 0.05$, **$P < 0.005$. UCSC = University of California, Santa Cruz.

< 5% by year 5. Similarly, *Madia sativa* covered > 5% of 6 yr^{-1} plots in the first 3 yr at Swanton, but was rarely recorded after year 4. Short-statured native annual sedges

(*Juncus bufonius* and *Scirpus koilolepis*) were only recorded at Elkhorn, where they were more common in the most frequently clipped plots 3 yr out of 10 (Fig. 6).
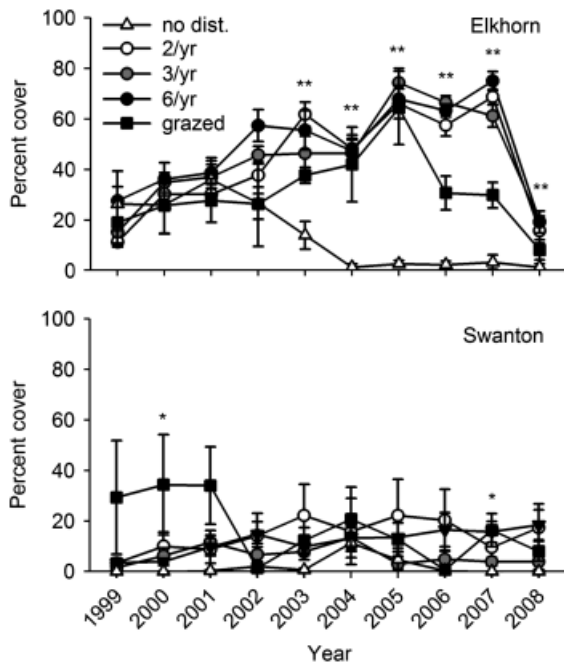
Fig. 5. Native perennial graminoids (grasses, sedges and rushes) in no-disturbance (no dist.), clipped and grazed plots at three sites. The UCSC (University of California, Santa Cruz) site data is not shown as native perennial grass cover was < 1% in all years. Values are means ± 1 SE. *P < 0.05, **P < 0.005.

Fig. 6. Native annual sedge cover in no-disturbance (no dist.), clipped and grazed plots at three sites. Native annual sedge values at other sites were < 1% cover overall. Values are means ± 1 SE. *P < 0.05, **P < 0.005.

Rainfall and vegetation dynamics

Surprisingly, neither EAG or NPG cover was significantly correlated with fall, winter, or total rainfall, or the Palmer drought index (PDI) 1-yr and 5-yr averages when treatments were considered individually or when cover was averaged across treatments ($P > 0.05$ in all cases). The EAF cover was strongly negatively correlated with the previous year's PDI at all sites (Elkhorn $r = -0.92$, $P = 0.0002$; Swanton $r = -0.71$, $P = 0.0217$; UCSC $r =$

-0.84, $P = 0.0021$); in other words, EAF cover was higher in years when the previous year had greater drought pressure. The EPF cover was not related to any rainfall parameters at Swanton or Elkhorn and was positively correlated with the 5-yr prior PDI at UCSC ($r = 0.91$, $P = 0.0002$); at UCSC, however, EPF cover declined throughout the study in all treatments, simultaneous to the increasing severity of the 5-yr PDI (correlation between 5-yr PDI and year of study: $r = -0.78$, $P = 0.0075$).
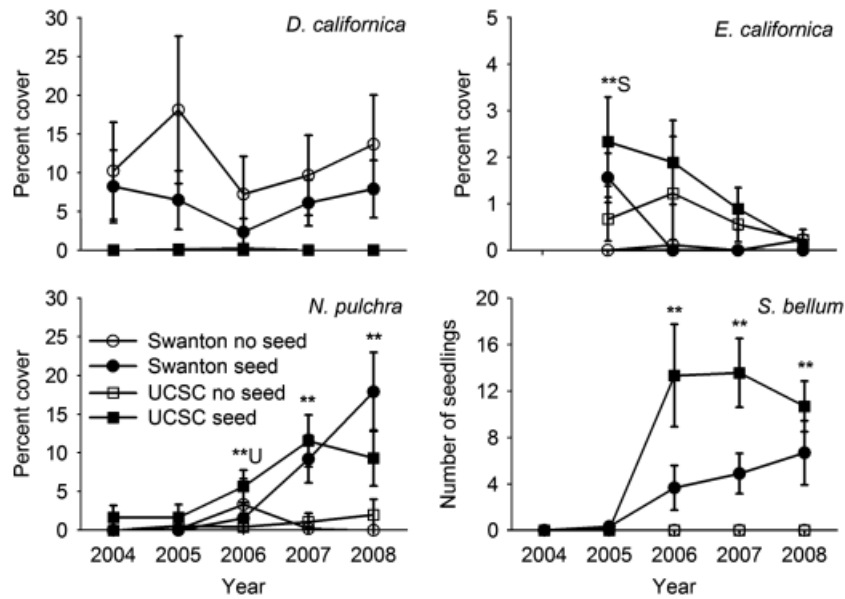
Native species seeding

Nassella pulchra and *S. bellum* gradually increased in seeded compared with unseeded plots (seeding × year interaction for *N. pulchra*: Swanton $F = 30.6$, $P = < 0.0001$; UCSC $F = 11.0$, $P = 0.0006$; seeding × year interaction for *S. bellum*: Swanton $F = 33.9$, $P < 0.0001$; UCSC $F = 93.3$, $P < 0.0001$), so that by 2007 and 2008 cover of both species was higher in seeded plots at both sites with addition of seed (Fig. 7). *Danthonia californica* cover did not differ in seeded and unseeded plots in any year at either site (Fig. 7). *Eschscholzia californica* cover was higher in seeded plots at Swanton in 2005, immediately following seeding, but not thereafter at either site (Fig. 7). We recorded 49 *Gilia capitata* seedlings at Swanton and 17 at UCSC in 2005, all in seeded plots, but no seedlings were observed in subsequent years. For the remaining three seeded species (*Calandrinia ciliata*, *Castilleja exserta*, and *Lupinus nanus*, we recorded < 4 seedlings total in all plots at all sites from 2004 to 2008.

Discussion

Can disturbance regimes be managed to favor native over exotic plant guilds?

Regardless of frequency or litter removal, clipping generally shifted community dominance from exotic annual grasses to exotic annual forbs, rather than consistently favoring native species. Others have demonstrated that grazing or clipping, compared with no disturbance, shifts grassland dominants from grasses to forbs (Bullock et al. 2001; Cox & Allen 2008) and from taller- to shorter-statured species (Fynn et al. 2005; Diaz et al. 2007). Our results are consistent with this past work, as clipping favored exotic annual forbs, which are primarily low-statured. Moreover, exotic annual grass cover was higher in no-disturbance plots at the two sites with primarily taller-stature EAG (e.g. *Bromus* spp. and *L. multiflorum*), whereas clipping did not affect EAG cover in the site where the short-statured species *B. distachyon* was abundant.

Our results show that more frequent clipping had stronger effects on abundance of certain guilds, for example EAF and native annual sedges (NAS), but not others

Fig. 7. Per cent cover or number of seedlings of four native species (*Danthonia californica*, *Eschscholzia californica*, *Nassella pulchra* and *Sisyrinchium bellum*) in seeded and unseeded plots at two sites. Values are means ± 1 SE. Note different *y*-axis scales. All species were seeded in 2003 and 2004 except *E. californica* which was seeded in 2004 only. *$P < 0.05$, **$P < 0.005$ for seeding effect at both sites. **S and **U indicate significant difference at Swanton or UCSC (University of California, Santa Cruz) site only.

(e.g. NPG). Results from other systems similarly reflect lack of consistent responses to within-season disturbance frequency variation (Biondini & Manske 1996; Schiborra et al. 2009). Past research suggests that adapting disturbance frequency or timing during a single growing season can control single exotic species (Rinella & Hileman 2009) or benefit specific desired species (Zimmer et al. 2010). Indeed, our results show that clipping strongly favored the NPG *D. californica* at Elkhorn but did not affect the NPG guild at the site with multiple NPG species (Swanton). Our research is consistent with previous literature showing that, in invaded grasslands, clipping and grazing, even at specific frequencies, hold little promise for shifting the balance between native and exotic plant species guilds (Wilson et al. 2004), given that many exotic species are well-adapted to these disturbances and native propagules are often limiting (discussed below).

Are grassland responses to disturbance regimes consistent over time and across sites?

For the most abundant guilds (EAG and EAF) disturbance treatment effects were relatively consistent over time after the second year of the study, although there tended to be reduced treatment effects in years when overall abundance of a guild was low. The inter-annual variability in cover of guilds, particularly annuals, was high, which is the rule in Mediterranean climates where large yearly differences in rainfall are typical (Hobbs et al.

2007). Teasing out the cause of this variation is challenging because the plant communities were responding over time to the simultaneous effects of our treatments, variation in climate, and inter-annual differences in other biotic interactions (e.g. disease outbreaks, seed predator and herbivore abundance). Many previous studies demonstrate the strong effect of climate on both native and exotic annuals and perennials in Mediterranean grasslands (Seabloom et al. 2003a; Alhamad 2006; Hobbs et al. 2007). In our study, only exotic annual forb cover was correlated at all sites with a climate parameter (1-yr PDI); the higher EAF cover when rainfall in the preceding year was lower may result from the fact that annual forbs (both exotic and native) with long-lived seed banks are likely to increase in abundance following dry years, when grass seed output is lower (Levine & Rees 2004). Other authors have suggested that total rainfall alone is an insufficient predictor of grassland dynamics, but rather that the size and number of rainfall events (Swemmer et al. 2007), periods of drought during the rainy season (Reever-Morghan et al. 2007) or the temperature following the first major rainfall event (Levine et al. 2008) are more important.

Interestingly, at the one site where we had substantial initial cover of the native perennial grass *D. californica*, 4 yr passed before the species responded to treatments, consistent with previous research noting long-term declines in native perennial grass abundance with reduced disturbance (e.g. Bartolome & Gemmill 1981). Time lags are

especially pronounced in arid systems (Wiegand & Milton 1996; Valone et al. 2001) and suggest that, particularly for perennial species, it is necessary to monitor the results of management actions for several years before evaluating the effects.

Plant community composition grazing effects in our study were highly variable across sites and years, making it difficult to compare grazing with clipping or no disturbance. This variability can be explained in part by different patterns of grazing timing and intensity between years and sites, and in relation to the timing of our vegetation sampling. Moreover, grazing is patchy and selective on certain species, especially when less intense, allowing species with varying traits to persist (Knapp et al. 1999; Vickery et al. 2001). The variability associated with grazing may explain why previous studies have reported highly inconsistent grazing effects on the balance of native versus exotic species (Corbin et al. 2004; Huntsinger et al. 2007). Clipping has more homogeneous plant community impacts (Vickery et al. 2001) and, therefore, may be a more predictable management tool.

Our results concur with past multi-site studies, which demonstrate site-specific treatment effects (Bartolome & Gemmill 1981; Leiva et al. 1997; Zimmer et al. 2010). Such results highlight the importance of replicating studies at multiple sites to make broad-reaching conclusions, as well as the challenge of providing generally applicable guidance to land managers.

The varied responses of some guilds across sites likely reflect a combination of differences in initial species composition, site characteristics, and land-use history (Leiva et al. 1997; Zimmer et al. 2010). We initially chose sites with similar suites of common species, but differences in relative abundances of these species, as well as distinctive less common species at the sites, may have affected the responses. Moreover, variable site conditions (e.g. soil nutrients, drainage, microclimate, microbial and/or herbivore communities) may also be important. Indeed, UCSC, where total cover, litter-depth, and above-ground biomass were lower (Hayes 2002), tended to show less response to clipping than other sites; this result is consistent with suggestions that management regime's effects at reducing competition (e.g. grazing, clipping) will be greater in sites with higher productivity where interspecific competition is stronger (Tilman 1993; Alhamad & Alrababah 2008).

Does seeding native species in combination with managing disturbance regimes serve to shift the balance towards native species?

The lack of increase in native cover in response to a range of disturbance regimes suggests that shorter-statured

exotics are favored by disturbance, (discussed previously) and/or that native propagules are limiting. The latter is likely in our system given that native cover, particularly forbs, was low in most plots at the outset (Hayes & Holl 2003) and that few species in this or other grassland systems have adaptations for long-distance dispersal (Bakker et al. 1996), which often results in dispersal limitation (Coulson et al. 2001; Seabloom et al. 2003a). Mediterranean grasslands often have long-lived seed banks (Bakker et al. 1996; Satterthwaite et al. 2006), but recruitment is episodic (Hobbs & Mooney 1991) and our sites had been lightly tilled historically and grazed for many decades, which may have degraded seed banks.

Many authors have suggested the possibility of restoring grasslands by seeding native species along with managing disturbance regimes (Seabloom et al. 2003b; Martin & Wilsey 2006), whereas our results suggest the contrary. We seeded a total of eight species known to be common in California coastal prairie in two different years, but only two species established and had higher cover in seeded plots after 3–4 yr. The species that did not establish included four short-stature annual forbs that we predicted would be favored by clipping, as well as *D. californica*, which responded favorably to clipping in plots where it was present at the outset of the study. We surface-seeded rather than burying seeds, so high predation, seed desiccation or poor seed soil contact may have reduced establishment (Rotundo & Aguiar 2004, 2005). Other factors could include: species selected being ill-adapted to local conditions (McKay et al. 2005), climatic conditions incorrect (Holl & Hayes 2006) or herbivory, possibly from exotic mollusks (Maze 2009).

Conclusions

Our results indicate that even the resource-intensive approach of introducing propagules along with managing disturbance regimes does not guarantee native species establishment and that maintaining and restoring broader suites of native species in invaded grasslands is extremely challenging. Increasing numbers of highly competitive tall- and short-statured exotic species guarantees communities dominated by exotics, unless there is an extensive native community present or efforts to seed in natives are successful. It is increasingly evident that the correct timing, intensity, type and frequency of disturbance are narrowly limited to individual species, or perhaps more narrow sets of species than previously appreciated. While further work to better understand species-specific habitat needs and reintroduction methods is critical, it is highly probable that landscape-level management (Salwasser et al. 1987; Alhamad 2006) of varied disturbance regimes in locations where native species are already present will

provide the most positive results for maintaining all species given environmental stochasticity, changing climate and our limited knowledge (Doak et al. 2008). Long-term studies are essential as native perennial grasses, often a key target for conservation, are slow to respond to management, and native annual forbs, many of which are species of concern, show high interannual variability owing to complex germination cues and long-term seed banks (Levine & Rees 2004; Satterthwaite et al. 2006).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Total rainfall (mm) at each site between Jul 1 and Jun 30 of each rainfall year at the three study sites.

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