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RESEARCH ARTICLE

Fire versus grazing as tools to restore serpentine grasslands under global change

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Grassland restoration in a world of change—including nitrogen deposition and invasion—requires solutions that can be sustained and effective in the face of novel drivers. This challenge is amplified in systems characterized by high spatiotemporal variability, as management to address novel drivers may affect a system differently across its range of variability. California serpentine grasslands epitomize this challenge: they host a high diversity of native species, are characterized by temporal and spatial variability, and are experiencing atmospheric nitrogen deposition that leads to a conversion from native annual forbs to non-native annual grasses. Here, we test the interactive effects of grazing and fire to restore native serpentine species following annual grass invasion and litter accumulation. We assess management outcomes (burned-grazed, burned-ungrazed, and unburned-ungrazed) using a long-term (2004–2012) monitoring dataset. A 2004 wildfire led to a reduction in annual grasses and a transient increase in native species (forb) richness. In 2008, cattle grazing was reintroduced and crossed with the burn legacy, which sustained post-fire diversity and eventually led to native recovery in unburned areas, with a caveat that a period of high precipitation promoted the growth of annual grasses. Our study indicates that short-term management, such as fire, can promote native forb recovery in invaded serpentine grassland communities, but that ongoing treatments like grazing are necessary to maintain restoration outcomes. We speculate that this recovery may be due to the presence of a robust native seed bank, which may persist despite a period of annual grass conversion.

Key words: annual grass invasion, biomass removal, litter accumulation, native recovery, nitrogen deposition

Implications for Practice

- Ecosystems may benefit from continual and varied management in the face of global change. For example, burning and grazing can be used (either alone or in combination) to remove litter buildup from annual grass invasion facilitated by nitrogen deposition.
- While systems-based interventions such as burning and grazing do not control the external forcing of global changes, our results suggest that they can target proximal mechanisms driving changes in non-native and native plant cover in the serpentine grassland system.
- In the context of ongoing nitrogen deposition, we highlight that active, recurrent management is needed to control litter levels and maintain native plant diversity in this system. We suggest that a burn and continual grazing are most effective in combination.

Introduction

Global change poses a challenge to ecological restoration: how to "restore" an ecosystem when the world has changed around it? While traditionally restoration has aimed to recover a historic, self-sustaining ecosystem, ongoing external change may render this goal impossible (Hobbs et al. 2006; Hallett et al. 2013). For example, external inputs of both resources (e.g. nitrogen deposition) and new species (e.g. invasive species propagules) may override the effect of one-time restoration efforts. This challenge is amplified in systems characterized by high temporal variability, as management to address novel drivers may affect a system differently across its range of variability (Vaughn & Young 2010). Consequently, grassland restoration may increasingly require ongoing interventions that counteract the local effects of global change (Hobbs et al. 2011). This may involve redirecting communities to novel but desired trajectories, introducing a new element to the system that counteracts proximate effects of global change, or a combination of the two. While interest has grown in shifting from classic restoration ecology to systems-based intervention ecology,

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long-term studies that develop and test interventions targeting ongoing change are needed.

California serpentine grasslands are emblematic of the challenges facing ecological restoration in a changing world. Serpentine systems have high conservation value, hosting 10% of California's endemic plant species despite only comprising an estimated 1% of the state's landscape (Kruckeberg 1984). Soil derived from California's state rock, serpentine, is generally rocky and shallow, low in nutrients, and high in heavy metals, resulting in vegetation with low resource-use traits and high native species diversity adapted to these conditions (Kruckeberg 1984; Brady et al. 2005; Anacker et al. 2011). In addition, serpentine grasslands serve as key hosts and habitat for other endemic species, such as the federally threatened Bay checkerspot butterfly (*Euphydryas editha bayensis*) (Murphy & Weiss 1988; USFWS 2009). Unlike grasslands on more nutrient-rich soils in California, serpentine grasslands have largely resisted dominance by non-native annual grasses—likely because low resources are a barrier to entry, where non-native annual grasses cannot overcome serpentine soil's deficiency in nitrogen (N) (Hobbs et al. 1988; Huenneke et al. 1990; Going et al. 2009; Vallano et al. 2012).

Nitrogen deposition, however, is reshaping California serpentine grasslands. Specifically, serpentine grasslands concentrated around the highly urbanized San Francisco Bay Area receive anthropogenic N inputs from vehicles, agriculture, and other sources (Weiss 1999). A global change driver, atmospheric N deposition generally favors plant species with high resource-use traits, such as non-native annual grasses, simplifying grassland communities while simultaneously increasing plant biomass (Zavaleta et al. 2003; Clark & Tilman 2008; Bobbink et al. 2010; Stevens et al. 2010). Similarly, studies using N fertilizer to simulate local N deposition rates in serpentine grasslands have shown that N addition increases non-native annual grass growth and dominance via enhanced resource acquisition, reducing native species abundance (Hobbs et al. 1988; Huenneke et al. 1990; Weiss 1999; Vallano et al. 2012). Furthermore, high interannual rainfall variability may interact with N deposition, where wetter years spike non-native annual grass abundance (Hobbs & Mooney 1991; Hobbs et al. 2007; Eskelinen & Harrison 2015). Once non-native annual grasses senesce in spring, their high biomass production becomes a thick litter layer that can prevent native forb recruitment and provide fuel for fire (Hobbs et al. 1988; Huenneke et al. 1990; D'Antonio & Vitousek 1992). Consequently, attempts to restore invaded serpentine grasslands must address chronic effects of N deposition in the system, such as litter accumulation.

Grazing and burning are interventions that may counteract the proximate effects of N deposition on native serpentine species. Livestock grazing has been an important tool for restoration and management of Californian serpentine grasslands threatened by non-native annual grasses (Weiss 1999; Safford & Harrison 2001; Harrison et al. 2003; Weiss et al. 2007). Most directly, cattle grazing affects the plant community by selectively consuming non-native grasses in preference to native forbs, resulting in greater abundance of native annual forbs in cattle-grazed compared to ungrazed areas (Huenneke et al. 1990). Cattle grazing can also remove dense litter—which excludes native forbs—by trampling and feeding during the dry season (Heady 1956; Bartolome et al. 1980, 2002; Huenneke et al. 1990). To date, most grazing studies have been relatively short term, although the cumulative effect of trophic and non-trophic grazing effects on species composition may be lagged (Dudney et al. 2017), necessitating long-term study. Furthermore, the effect of grazing on composition may depend on site history, particularly if native species' storage of seeds in the soil, typically through multiyear dormancy, or a seed bank, has been reduced by long periods of grazing removal (Menke 1992; Sternberg et al. 2003).

Fire is another potential tool to remove litter buildup; however, this is not as well studied as grazing in serpentine systems. Previous studies show that fire has variable effects on California grasslands, but like grazing, generally increases forb germination, flowering, and biomass (Hervey 1949; Parsons & Stohlgren 1989). By reducing accumulated litter (Heady 1956), increased light and temperature at the soil surface favors forb and bulb germination, while physical scarification from fire favors legumes. While several studies show that fire effectively reduces non-natives and enhances native cover (Menke 1989; Parsons & Stohlgren 1989; Meyer & Schiffman 1999), fire can also promote non-natives (Heady 1972; D'Antonio 2000). Harrison et al. (2003) found that these effects were environment-dependent, where fire increased species richness of natives on serpentine soils, while increasing species richness of non-natives on non-serpentine soils. This relationship is likely due to native forb prevalence on serpentine soils and non-native forb prevalence on non-serpentine soils, resulting in different seed banks available to respond after fire (Harrison et al. 2003). Across ecosystems, seed banks play a key role in ecosystem response to fire, and thus managers must consider fire history and frequency for plant biodiversity goals (Kiss et al. 2018). Historically, fire was not a common occurrence in low-productivity serpentine grasslands, and its similarities, differences, and synergies with grazing as a management tool have not been tested.

Here, we capitalize on a long-term monitoring study (2004–2012) to understand burning and grazing effects on native serpentine grassland communities in both the short and long term and assess how these two restoration techniques can be used most effectively either alone or in combination. We use this unique dataset to test the following hypotheses: (1) Burning and grazing have similar effects on native species richness, cover, and composition because they both decrease non-native cover and remove accumulated litter biomass. (2) Burning has a greater effect on the composition of ungrazed than grazed communities, because the effects of grazing and burning are redundant (i.e. both reduce non-native cover and litter accumulation). Alternatively, if these communities have already lost a native seed bank, burning will have less of an effect on ungrazed communities. (3) Burning effects are temporary. We expect that burning will initially increase native diversity, but this response will only persist in grazed communities. (4) Grazing reintroduction will have a lagged effect in which communities slowly shift to resemble continually grazed communities, as native seed availability may initially be limiting.

This process may be faster in previously burned compared to unburned communities.

Methods

Site Description and History

Our study is situated on Tulare Hill, approximately 130 ha area of serpentine grassland in south San Jose, Santa Clara County, California (37°13′16.6″N, 121°45′17.2″W). Since at least the 1980s, the site has been invaded by non-native annual grasses such as *Festuca perennis* and *Bromus hordeaceus*, likely due to N deposition from nearby highway sources (i.e. vehicle emissions) (Weiss 1999). From the mid-1980s to 2001, the entire site was heavily grazed (0.83 cattle/ha year-round). Starting in 2001, grazing was reduced to more typical levels for California grasslands (0.20–0.25 cattle/ha, with grazing primarily in the spring and occasionally over the summer) throughout most of the hill, but the northern 90 ha were fenced off and not grazed. A wildfire occurred in late May 2004, which was characterized by high winds and surface burning, and burned all the grazed area and some of the adjacent ungrazed area. No prescribed burns took place. In summer of 2008, cattle were reintroduced to all ungrazed areas. Spring and occasional summer grazing was maintained in ungrazed areas through 2011.

We sampled species composition in 0.5 m × 0.5 m permanently marked quadrats. Ten independent quadrats were positioned evenly along 50 m transects (10 quadrats/transect; Fig. S1). These transects were used to aid with positioning and locating quadrats in the field and not for grouping like quadrats (in some cases, quadrats from opposite ends of the same transect are farther apart than quadrats on two different transects; Fig. S1). Serpentine grasslands are characterized by fine-scale heterogeneity and are dominated by species with high stem densities and small seed dispersal kernels (several thousand stems/m^2 and dispersal kernels <1 m, Hobbs & Mooney 1985). As quadrats were a minimum of 5 m apart, we considered them to be independent; this distance between independent replicates is typical of previous long-term studies in this ecosystem (e.g. Hobbs & Mooney 1985, 1991; Weiss 1999; Hallett et al. 2018). Also, to ensure treatment effects are not due to site-specific effects, we accounted for site variation in our analyses and show within-transect variation in Figure S2.

Percent species cover was visually estimated once annually at peak biomass (March–April) and percent litter cover was recorded from 2006 onward. The initial design aimed to capture thermal effects of slope and aspect on composition; here, we focus exclusively on moderate thermal conditions (habitat stratified between 15 and 16.49 MJ/m^2 insolation; Murphy & Weiss 1988) with shared slope and aspect to facilitate comparison between grazing and burning. Four transects (40 quadrats) were established in 2001-grazed areas; all these quadrats were burned in 2004. Following the fire, two additional pairs of transects on either side of the burn line (within 20 m of each other) were established in the ungrazed area, resulting in 20 burned-ungrazed and 20 unburned-ungrazed as well as the 40 nearby burned-grazed quadrats. Because the fire covered all grazed areas, we could not include a grazed-unburned contrast. As such, the design allows for a crossing of burn legacy and grazing, with three out of four potential treatment interactions. Over the time period following the burn (2005–2012), we evaluated plant community composition, functional group cover, litter dynamics, and species-specific responses to these three treatment combinations. Grazing was introduced to the previously ungrazed plots in 2008. Therefore, we focus on two time periods: (1) how plant communities changed following the 2004 fire and (2) how grazing reintroduction in 2008 further altered community trajectories.

We include a focus on *Plantago erecta*, the primary host of the federally threatened Bay checkerspot butterfly (Weiss 1999). While we analyze this species within the same time window (2005–2012), we include a longer time series (2001–2018) with lower replication in the supplement to explore potential climate-contingent effects.

Data Analysis

All analyses were performed in the R statistical computing environment (R Core Team 2018). Prior to analysis, quadrats that comprised >80% bare rock cover were removed from plant cover data used in all subsequent analyses—a total of 3 out of 80 quadrats were dropped. We calculated species richness within year, plot, and functional group (i.e. native forb, native grass, non-native forb, non-native grass). Due to low cover and richness of native grasses and non-native forbs (Fig. S3), we focused our analyses on native forbs and non-native grasses. We focused on relative species cover (species cover divided by total plant cover). For the purpose of subsequent analyses, we refer to burned-grazed, burned-ungrazed, and unburned-ungrazed quadrats as "treatments" from this point forward. We calculated annual growing season precipitation as all rainfall from October to April (PRISM Climate Group 2019).

Species Diversity and Cover Over Time

We used a repeated-measures approach to test for treatment effects over time on native forb and non-native grass relative cover and richness, and on the absolute cover of litter (visualized in Fig. 1). We divided the data into two time periods: (1) 2005–2008 after the wildfire and prior to grazing reintroduction and (2) 2009–2012 after grazing reintroduction. To test for effects of burning and grazing during each of these time periods, we built separate linear mixed effect models using the "lme" function in the *nlme* package where treatment, year, and treatment*year were fixed effects. Quadrat was included as a random effect to control for site-specific effects over time. We followed this with post hoc pairwise comparisons of treatments by year using least-square means tests in the *emmeans* package with Tukey adjustments for multiple comparisons. To understand the relationship between native forbs and litter, we also built general linear regressions of species richness and relative cover of native forbs against absolute cover of litter across years irrespective of treatment. For all tests, we accepted significance at p values less than 0.05.

Community Composition Over Time

To test if burning and grazing affected community composition over time, we performed non-metric multidimensional scaling

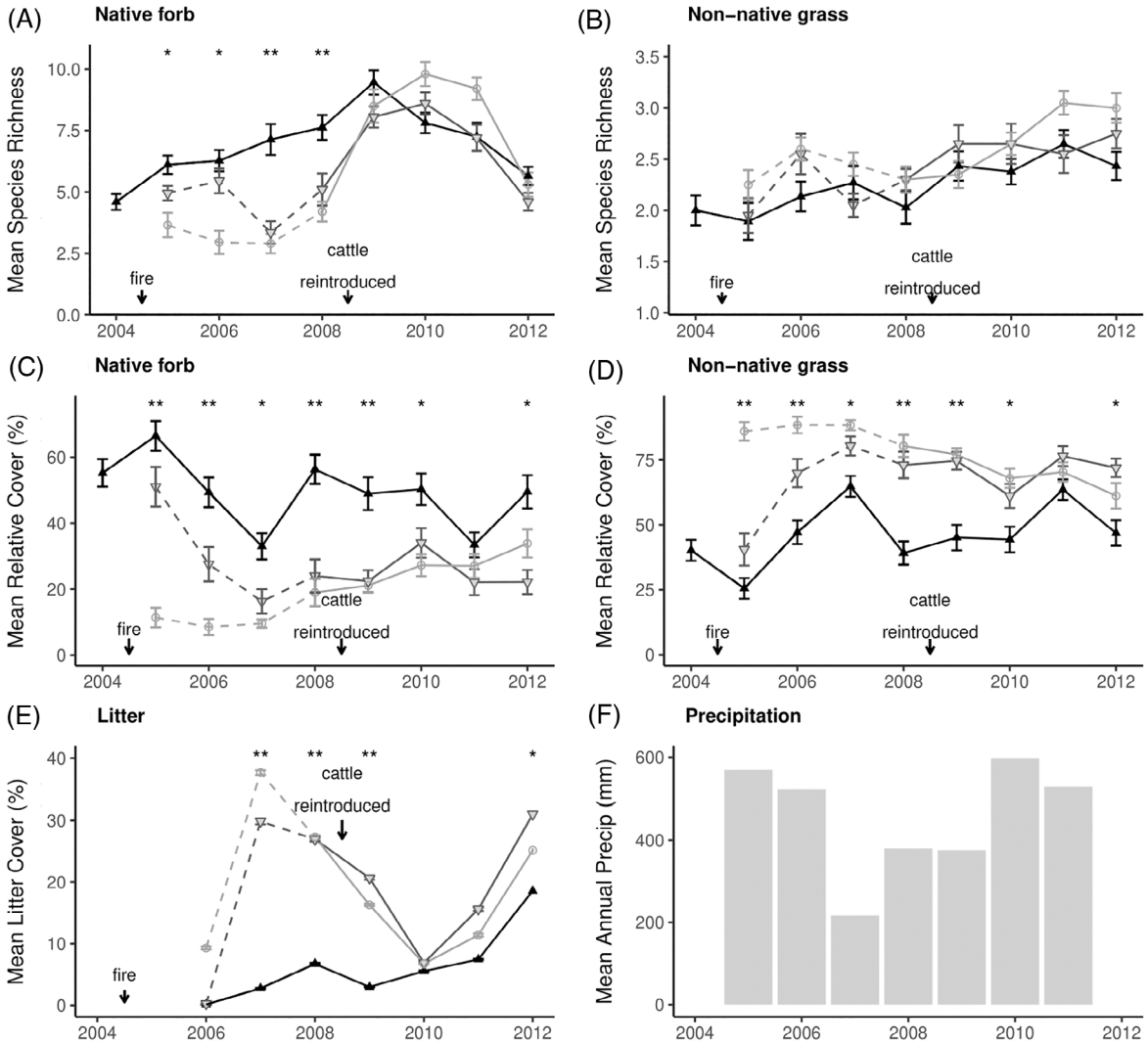

Figure 1. Time series of species richness of (A) native forb and (B) non-native grass, relative cover (%) of (C) native forb and (D) non-native grass, absolute cover (%) of (E) litter, and (F) annual precipitation (mm) of the growing season, October to April, from 2004 to 2012. Litter cover data for 2005 and 2006 were not available. Shapes indicate means, error bars represent ± SE, and treatments are differentiated by color and shape: Burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). Solid lines indicate periods of grazing and dashed indicates periods in which quadrats were not grazed. Arrows point to two treatment events: Wildfire in May 2004 and grazing reintroduction in previously ungrazed quadrats in summer 2008. In panels (A) through (E) asterisks are used to represent significant least-square means post hoc results of yearly treatment effects (Table S2). Each asterisk represents a significantly different pair of treatments, ranging from zero (none of the treatments are different), one (two most distant points are different), two (most distant pairs are different), and three (all of the treatments are different).

(NMDS) analyses using the "metaMDS" function in the *vegan* package (Oksanen et al. 2018). Using relative cover of plant species by plot, we determined the initial position of the community in multidimensional space using the Bray–Curtis distance coefficient. Separate NMDS analyses were run using years 2005–2008 and 2008–2012 to characterize responses to burning and grazing reintroduction with 4 and 5 dimensions, respectively. The number of dimensions were chosen by plotting stress versus number of dimensions and choosing the point at which stress was not improved by including additional dimensions. NMDS ordinations were run using 1,000 permutations and stress values ranged from 6.3% (burn NMDS, Fig. 2) to 8.3% (graze NMDS, Fig. 3), where a stress value less than 10% is ideal (Clarke 1993). We followed NMDS ordinations with permutational multivariate analysis of variance (perMANOVA) to test if communities significantly differed by treatment (burned-grazed, burned-ungrazed, and unburned-ungrazed) for each individual year from 2005 to 2012 (Table S1). Multiple perMANOVA analyses were run using 1,000 permutations on the Bray–Curtis distance matrix using the "adonis" function in the *vegan* package and subsequent pairwise comparisons between groups with corrections for multiple testing were performed using the 'pairwise.perm.manova' function in the *RVAideMemoire* package (Hervé 2019). Lastly, to determine species whose occurrences and abundances have significant associations with each treatment and combinations of treatments, we performed indicator species

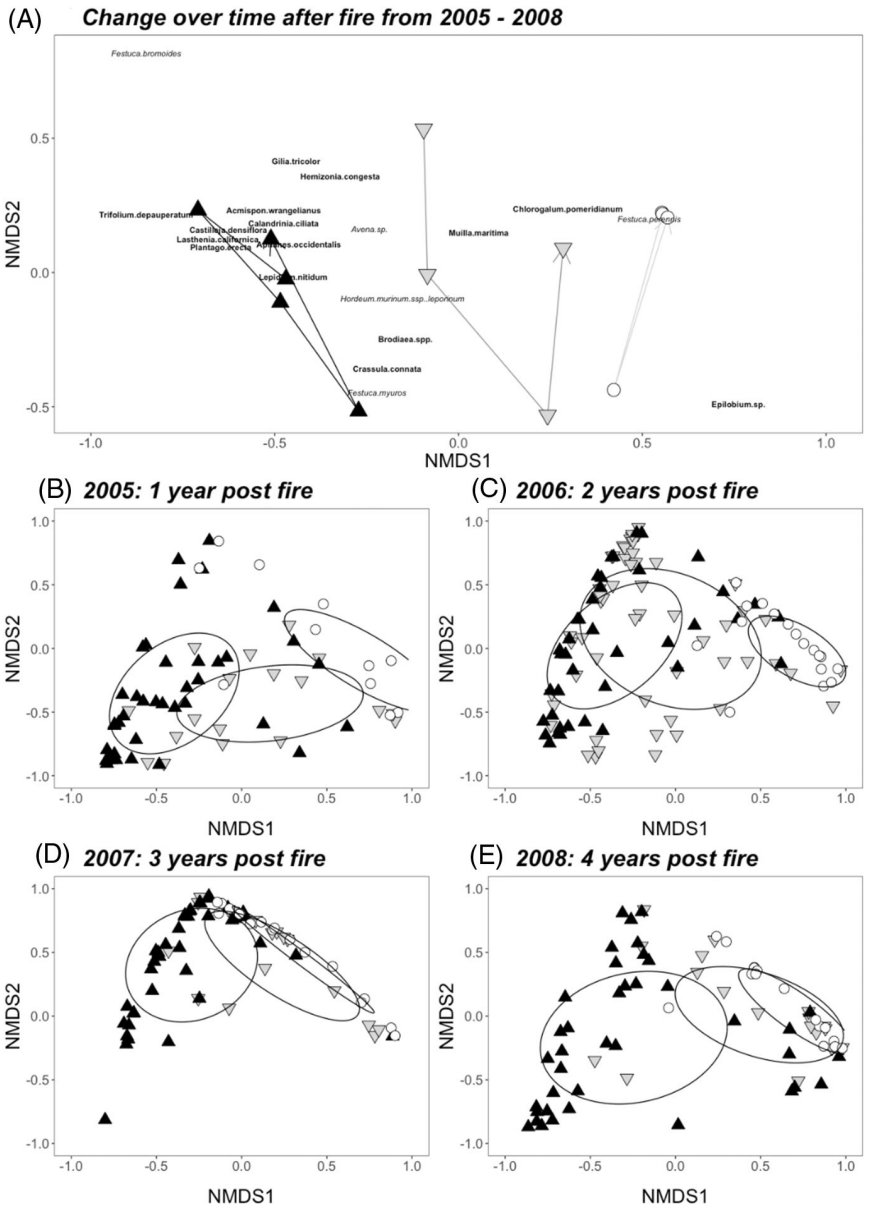

Figure 2. Non-metric multidimensional scaling ordinations of plant community cover data following a 2004 fire for burned and unburned quadrats by grazing treatment over time. Treatments are differentiated by color and shape: Burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). (A) Mean community compositional change by treatment over time. Vectors show the compositional shift in ordination space with arrows indicating the direction of change over time, with each point representing a year. The burned-grazed quadrats include 2004 (pre-fire) through 2008 community data. Pre-fire data were not available for ungrazed quadrats and 2005–2008 data are shown. Significant indicator species identified by multilevel pattern analysis (see Table 1) are overlaid on the community ordination, non-native grasses are shown in *italic* and native forbs are shown in **bold**. (B–E) Community ordinations of all quadrats from 2005 through 2008, respectively. Ellipses show a 95% confidence interval around the mean of each treatment's cloud of points.

analyses using the "multipatt" function in the *indicspecies* package (De Caceres & Legendre 2009).

Results

Effects of the 2004 Fire

Native forb richness was significantly greater in the burned-grazed areas than the unburned-ungrazed in all years following the fire prior to cattle reintroduction (2005–2008; Fig. 1A, Table S2). Burning increased native forb richness (Fig. 1A, Table S2), but this effect in ungrazed areas was temporary. Specifically, native forb richness in burned-ungrazed areas increased and was no different from burned-grazed areas in 2005 and 2006 (Fig. 1A). In the subsequent 2 years, all the ungrazed areas, regardless of prior burn, had native forb richness that was significantly lower than the burned-grazed (Fig. 1A, Table S2). There was no effect of burning on non-native grass richness (Fig. 1B).

Paralleling changes in richness, native forb relative cover was significantly greater in burned-grazed compared to

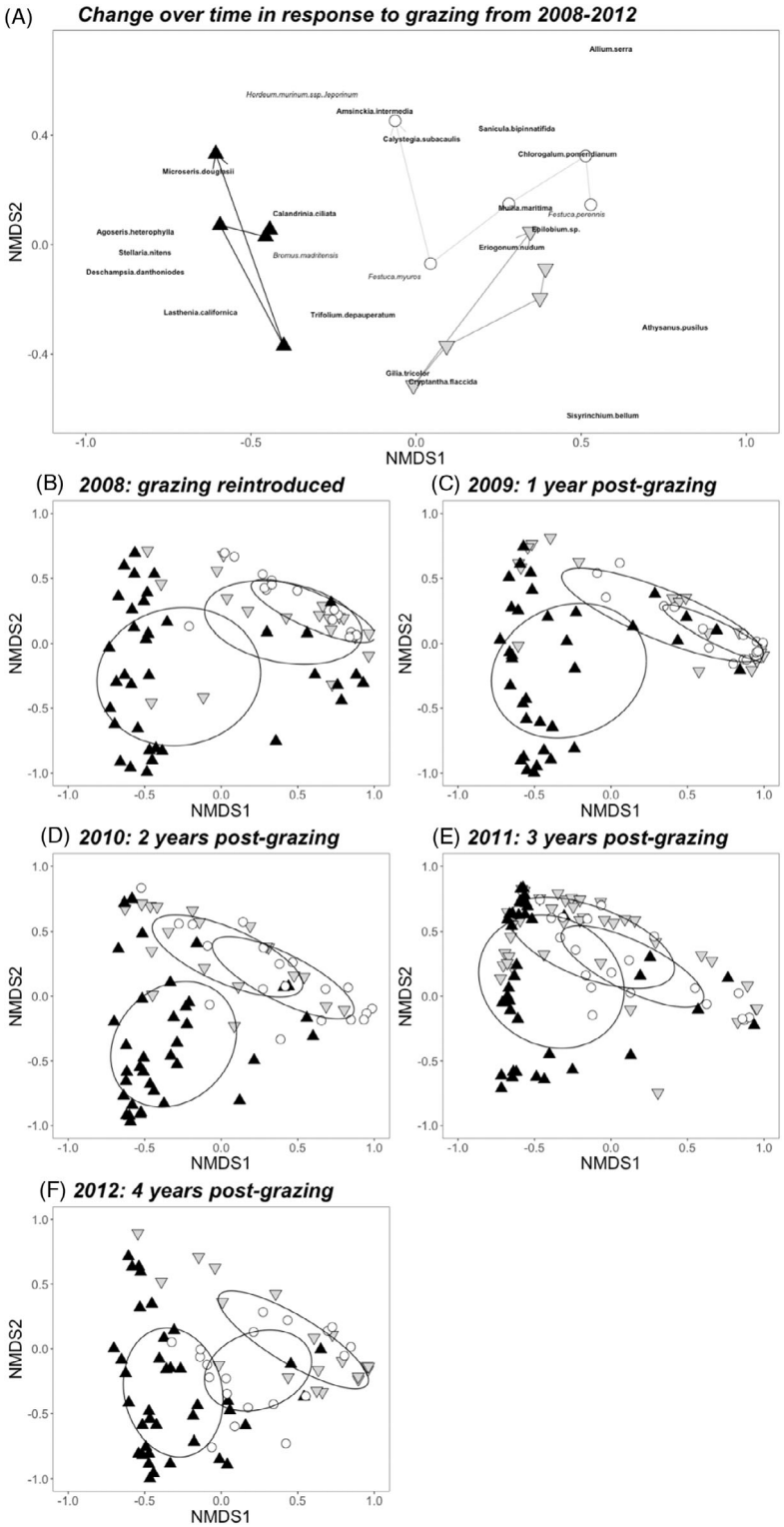

Figure 3. Non-metric multidimensional scaling ordinations of plant community cover data following the reintroduction of grazing for previously burned and unburned quadrats by grazing treatment over time. Grazing was reintroduced in summer 2008. Treatments are differentiated by color and shape: Burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). (A) Mean community compositional change by treatment over time. Vectors show the compositional shift in ordination space with arrows indicating the direction of change over time, with each point representing a year from 2008–2012. Plant species significantly correlating with treatments (see Table 1) are overlaid on the ordination, non-native grasses are shown in *italic* and native forbs are shown in **bold**. (B–F) Community ordinations for all quadrats from 2008 through 2012, respectively. Ellipses show a 95% confidence interval around the mean of each treatment's cloud of points.

Table 1. Multilevel pattern analysis results showing significant indicator species ($p < 0.05$) for (A) native forbs and (B) non-native grasses. Results shown are indicator species in burned-grazed (●), burned-ungrazed (◍), and unburned-ungrazed (○). Only species that were significant indicator species more than one time during the 8 years of this study are shown here. For a full list of indicator species, see Table S4.

	2005	2006	2007	2008	2009	2010	2011	2012
(A) Native forbs								
Agoseris heterophylla			●		●	●		
Microseris douglasii				●	●			
Trifolium depauperatum	●		●	●		●	●	
Plantago erecta	●◍	●◍	●	●◍	●			
Lasthenia californica		●◍	●	●	●◍	●◍		
Lepidium nitidum	●◍	●◍	●◍	●◍				
Aphanes occidentalis		●◍	●◍			◍○		○
G. tricolor		●◍	●					
Calandrinia ciliata				●◍	●◍			●
Castilleja densiflora	◍		●					
Crassula connata			●	●◍				
Brodiaea sp.		●○	●○	●○	●○			
Epilobium sp.			○	○	◍○	○	○	
Chlorogalum pomeridium				○		◍○	◍○	◍○
Muilla maritima					◍○	○	○	
Hemizonia congesta					◍○	◍○		
A. wrangelianus							◍○	●○
(B) Non-native grasses								
Festuca perennis	◍○	◍○	◍○	◍○	◍○	◍○	◍○	◍○
Festuca sp.	●◍						●	
Hordeum murinum					●○		●○	●○
Avena sp.			●		●◍			

unburned-ungrazed treatments from 2005 to 2008 (Fig. 1C, Table S2). The relative cover of native forbs in burned-ungrazed shifted over time. Specifically, in 2005, the native forb relative cover in the burned-ungrazed and burned-grazed areas did not differ, and both were significantly greater than in unburned-ungrazed (Fig. 1C). By 2006, native forb relative cover in the burned-ungrazed was comparable to unburned-ungrazed, and significantly lower than in burned-grazed areas (Fig. 1C, Table S2). *Plantago erecta* cover increased in the grazed area prior to fire (2001–2004) but steadily declined after fire (Fig. S4). Similar to native forb relative cover, *P. erecta* cover remained greater in burned-grazed compared to burned-ungrazed or unburned from 2005 to 2012 (Fig. S4).

The non-native grass relative cover exhibited the inverse pattern of native forb relative cover in response to burning and grazing treatments; whenever non-native grass decreased, there was a corresponding increase in native forb cover and vice versa (Fig. 1C & D). Specifically, non-native grass relative cover was significantly lower in both burned plots compared to unburned in the first year following the fire (Fig. 1D), but recovered 2 years post-fire in ungrazed and grazed areas (Fig. 1D). Litter data for 2004 and 2005 were not available and immediate effects of burning on litter could not be tested. There were no burning effects on litter cover in subsequent years. However, absolute litter cover was significantly greater in ungrazed plots compared to grazed plots between 2007 and 2008 (Fig. 1E, Table S2). Litter cover in ungrazed treatments peaked in 2007, mirroring peaks of non-native grasses (Fig. 1D & E). Within 2 years of cattle reintroduction, litter cover decreased in previously ungrazed plots and became indistinguishable from grazed plots.

Following the 2004 wildfire, both burned-grazed and burned-ungrazed treatments differed from the unburned-ungrazed in their community composition (perMANOVA, $p = 0.002$ and 0.002 for grazed and ungrazed, respectively, Table S3). Within burned treatments, the community composition differed by grazing treatment over time (Fig. 2). Specifically, the effects of the fire lasted 2 years on the ungrazed treatment, where the burned-ungrazed was most similar to the burned-grazed in 2005 and 2006 (Fig. 2A–C), but shifted and was no different from the unburned-ungrazed community composition by 2007 (Fig. 2A & D; perMANOVA, $p = 0.385$, Table S3) and remained no different in 2008 (Fig. 2A & E; perMANOVA, $p = 0.256$, Table S3). Continually grazed plots remained different from the unburned-ungrazed treatment through 2008 (Fig. 2A & E; perMANOVA, all $p < 0.05$, Table S3).

Indicator species analysis showed that burned plots, regardless of grazing treatment, shared five native forb indicator species in the first 2 years following the fire, including *P. erecta* and *Lasthenia californica* (Table 1). Immediately following the fire (2005–2006), the burned-grazed treatment contained an additional two native forbs indicators, while an additional native forb, *Castilleja densiflora*, was an indicator for burned-ungrazed (Table 1). In the ungrazed plots, regardless of burn treatment, the non-native grass *Festuca perennis* was a

significant indicator species in all years (Table 1). As communities shifted in 2007, fewer indicator species were shared between both burned treatments, and native forbs were more associated with the burned-grazed, but not burned-ungrazed treatment (Table 1). Several species, including *Trifolium depauperatum*, *Agoseris heterophylla*, and *Microseris douglasii* were only associated with burned-grazed quadrats over time (Table 1).

Effects of Cattle-Grazing Reintroduction in 2008

Grazing reintroduction in previously ungrazed quadrats immediately increased native species richness to the same levels as continually grazed quadrats and had no effect on non-native richness, which remained no different between treatments (Fig. 1A & B). Three years after grazing reintroduction, there was no difference in the relative cover of forbs and non-native grasses for previously burned-ungrazed and unburned quadrats (Fig. 1C & D). Prior burning in ungrazed quadrats did not accelerate the recovery of native forb richness or cover relative to unburned-ungrazed quadrats. Litter significantly decreased following grazing reintroduction in ungrazed quadrats until 2010 (Fig. 1E), when litter increased across all treatments following two wet years in 2010 and 2011 (Fig. 1E & F). During this time, previously ungrazed quadrats maintained 5–10% more litter than continually grazed quadrats. In addition, increased litter resulted in a corresponding decline in forb richness despite continual grazing presence (Fig. S5). In 2012, the treatment with the greatest litter cover (previously burned-ungrazed) had the lowest native forb cover and highest non-native grass cover (Fig. 1E, C, & D).

Before grazing reintroduction in summer 2008, burned communities with different grazing histories differed in composition from one another (Fig. 3A). Burned-grazed also differed from the unburned community (Fig. 3B; perMANOVA, $p = 0.002$, Table S3), while the burned-ungrazed group did not (Fig. 3B; perMANOVA, $p = 0.256$, Table S3). Following grazing reintroduction, community composition shifted by treatment over time (Fig. 3), where all communities differed after the first year of grazing (Fig. 3C; perMANOVA, all $p < 0.05$, Table S3). While previously ungrazed communities became more similar to the continually grazed community over time (Fig. 3A), community composition by treatment remained significantly different up to 4 years post-grazing (Fig. 3D, E & F; perMANOVA, all $p < 0.05$, Table S3). Previously burned-ungrazed plots recovered high *P. erecta* abundance 6 years after cattle reintroduction (Fig. S4).

Indicator species analysis showed that before the reintroduction of grazing in 2008, burned groups shared four native forb indicator species (*P. erecta, Lepidium nitidum, Calandrinia ciliata*, and *Crassula connata*, Table 1). In addition, both previously ungrazed groups shared a non-native grass indicator, *Festuca perennis*, prior to grazing reintroduction, which they continued to share throughout the remainder of the study (Table 1). Following grazing reintroduction in 2009, previously ungrazed communities gained native forb indicators, including *Epilobium* sp., *Chlorogalum pomeridium*, *Hemizonia congesta*, and *Muilla maritima* (Table 1). The forb indicator species gained after grazing reintroduction differed from the indicator species present in earlier years following the fire (Table 1). In 2011, following two wet years (Fig. 1F), burned and unburned groups shared less native forb indicator species, but shared more non-native grass indicator species.

Discussion

Systems-based interventions are a promising tool for restoration ecology, allowing a proactive approach to counteract ongoing global change effects. While promising, few long-term studies have assessed these interventions in real-world situations. Long-term monitoring of the plant community at our study site provided the unique opportunity to assess immediate and long-term interactive potential of burning and grazing as interventions for serpentine grasslands experiencing N deposition. We found that burning and grazing had similar effects on native diversity, supporting our first hypothesis: both native forb cover and richness underwent the same positive directional change, while non-native grass cover declined following a fire and grazing reintroduction into the system. However, community change trajectories were dependent on previous grazing or burning history, supporting our second hypothesis. Specifically, burning had the greatest effect on previously ungrazed quadrats, which became more similar to the burned-grazed quadrats, while the burned-grazed had a much smaller shift in community composition with fire. Trajectories after grazing reintroduction did not depend on prior burn history, but instead on duration of grazing, where under continual grazing the relative higher forb cover was maintained compared to reintroduced areas. Finally, the response time and effect duration of fire and grazing differ. While burning resulted in an immediate response in community composition that lasted for 2 years, consistent with our third hypothesis, there was a lagged response to grazing reintroduction, with communities slowly becoming more similar over time, supporting our fourth hypothesis.

While changes to N availability are likely the ultimate cause for shifting dominance patterns in serpentine systems, non-native annual grasses reinforce their dominance via the establishment of a thick litter layer, which promotes their germination but excludes many natives, especially native forbs (Huenneke et al. 1990; Meyer & Schiffman 1999). Our results demonstrated that native forb richness and cover declined with increasing litter cover. Yet, burning and grazing are both effective strategies to reduce litter cover. Burned quadrats had lower litter cover 2 years after the fire and continually grazed quadrats had lower litter cover than ungrazed quadrats. Similarly, the reintroduction of grazing onto previously ungrazed quadrats had immediate negative effects on litter cover. However, litter accumulation is also strongly correlated to rainfall, where high precipitation years are related to high grass biomass production, and subsequently litter accumulation (Bartolome et al. 2002; Dudney et al. 2017). We also found that litter cover increased across all quadrats following the two wettest years (2010 and 2011), resulting in a corresponding decline in forb richness despite continual grazing. While litter cover was not significantly correlated with precipitation in our study, we speculate this may be due to precipitation influencing litter depth more than cover. Identifying a limit of this restoration tool, we highlight here that high litter cover overrides grazing's effectiveness for

promoting native forb richness and stress the need to account for other drivers of variability (i.e. precipitation patterns).

Both fire and grazing were effective in reducing the litter layer, allowing native forb recruitment. Other studies show greater native forb emergence and diversity in serpentine grasslands after a one-time fire (Harrison et al. 2003) and with cattle grazing, respectively (Safford & Harrison 2001; Harrison et al. 2003); however, on non-serpentine California grasslands, fire increased non-native forb cover (Harrison et al. 2003; Seabloom et al. 2003) and grazing had little effect on native composition (Jackson & Bartolome 2002). Across ecosystems, seed banks are critical in determining restoration trajectories under stresses, such as climate change (Kiss et al. 2018), and the differential responses in serpentine and non-serpentine grasslands suggests that the presence of a native seed bank is key to native recovery after litter removal by fire or grazing. Non-serpentine grasslands have likely already lost their native seed bank over a long period of non-native annual grass dominance (Hamilton et al. 1999; Seabloom et al. 2003; Brandt & Seabloom 2012), while serpentine grasslands likely still have a reserve seed bank allowing for recovery (Seabloom et al. 2003). While the seed bank was not measured in this study, we speculate an intact seed bank aided in native forb recovery following burning and grazing.

The effects of fire on serpentine grassland communities were immediate, but transient, disappearing after 2 years. Other studies have also found that effects often disappear within a few years of a one-time fire (D'Antonio et al. 2002; Harrison et al. 2003). For example, in a meta-analysis, D'Antonio et al. (2002) found that in the first 2 years after a burn, fire had a positive effect on native plant richness and a negative effect on non-native grass cover in California annual grasslands; however, these effects disappeared 2 years post-burn. While fire initially clears non-native annual grass litter and improves growing conditions for forbs, a lagged but high resurgence of non-native grasses has been observed by 2 years post-fire (Hervey 1949; Keeley & Keeley 1981; Menke 1989; Parsons & Stohlgren 1989; D'Antonio 2000). We also observed a lagged, but high recovery of non-native grasses by 2 years post-fire in both grazed and ungrazed quadrats. This lagged response may be attributed to the nutrient input from fire ash (Menke & Rice 1981), which favors fast-growing, resource acquisitive non-natives (Stohlgren et al. 1999). While burned quadrats with continual grazing also experienced a resurgence of non-native grasses, grazing appears to control non-natives after the initial resurgence while ungrazed quadrats continue to gain non-native grass cover. These responses depend on the timing of fire and are tightly tied to each group's seed bank density. For example, besides litter layer removal, fire can also reduce non-natives if fire occurs early in the growing season prior to non-native seed dispersal (Eller 1994; Pollak & Kan 1998; Meyer & Schiffman 1999). Similarly, summer burn may also be effective by decreasing the seed bank of exotic grasses *Bromus hordeaceus* and *Taeniatherum caput-medusae* (Menke & Rice 1981). Because the fire at our study site occurred in May 2004 after seed dispersal, we expect it was more effective at reducing litter accumulation, with smaller effects on the non-native seed bank.

We found that native forb relative cover increased more slowly after grazing reintroduction compared to fire. This could be due to slow reduction in non-native grass and litter cover following grazing reintroduction, low forage selectivity by grazers, or patchy, localized changes in non-native cover. Similarly, Meyer and Schiffman (1999) found that litter reduction via grazing was not as effective as complete litter removal (e.g. to bare ground via fire) at promoting native forbs because bare ground provides specific environmental cues that improve annual forb species germination and survivorship (Rice 1989). In our study, grazing reduced, but did not completely remove litter cover. On the other hand, forb recovery after grazing may have a slow response time if the native seed bank has been reduced by years of non-native annual grass dominance. We expect this is not the case, as native forb cover recovered immediately after burning in the ungrazed plots, indicating the presence of a native seed bank for ungrazed quadrats. Thus, the effectiveness of grazing is most likely dependent on grazing intensity (Pasari et al. 2014), timing, and frequency, where greater grazing intensity over the summer may have a faster impact on native forb resurgence from litter removal. However, with a more intensive grazing regime, cattle may consume their preferred nitrogen-rich annual grasses and then move on to consuming the less palatable native forbs. In addition, the presence of grazers introduces localized deposits of nutrients via their feces and urine, which may promote or sustain non-native species. While the effects on soil nutrients vary, grazing in California's grasslands generally increases soil nitrogen availability while decreasing phosphorus and sulfur (Vaughn et al. 1986; Stromberg & Griffin 1996) and concentrates nutrients in animal-gathering areas (e.g. under shade and near food/water containers; Jackson & Bartolome 2007).

In the serpentine system, both fire and grazing address a proximate driver (e.g. litter accumulation from annual grass invasion) of native species loss, but they also have differences that may shift ecosystem trajectories. These trajectories are important in restoration decisions. For example, while the fire increased native forb populations in the short term, the highly productive grasses also flourished following the fire in the absence of grazing and regained dominance after only 2 years. This suggests that a one-time fire alone is likely insufficient to control non-native grass populations. Previous studies also show that sustained increases in native forbs require annual burns in ungrazed areas (D'Antonio & Chambers 2006). While we acknowledge that we could not compare burned-grazed to unburned-grazed quadrats (as the wildfire at the site burned all of the grazed quadrats), the burned and continually grazed quadrats supported the greatest native forb and lowest non-native grass populations. This suggests that a burn paired with continual grazing is a promising management approach for removing annual grass litter and supporting native forb populations in serpentine grasslands. We also acknowledge that dynamics in this study may differ across the landscape with topographic variability. However, similar dynamics have been qualitatively noted across serpentine grasslands in high N-deposition zones over nearly three decades, first noted in Weiss (1999)—intensified grass invasions, accumulation of litter, loss of forb cover and diversity, followed by more gradual recovery over several years

when grazing is reintroduced. The same responses have been observed across different slopes, and grazing has been a required management action on all conserved lands at our study site.

Success in native plant recovery can extend to other restoration goals, such as supporting higher-trophic species. Here, we focused on *P. erecta* recovery, a primary host plant for the federally threatened and endemic Bay checkerspot butterfly. In 1987, the Bay checkerspot butterfly population was estimated in the low hundreds at our study site (Harrison et al. 1988). It disappeared by 1990 following several years of drought. A few butterflies were observed in 1995, and by 2002, the population was estimated in the low thousands. By 2004, the lack of grazing on the northern part of the hill led to habitat deterioration, and only a small Bay checkerspot butterfly population remained on the southern 40 ha, where annual sightings of adult butterflies ranged 1–5 per year. Indirectly, our results support the use of burning and grazing as management tools that can aid the butterfly through bolstering populations of *P. erecta*. We found that the burn increased *P. erecta* abundance immediately, whereas grazing reintroduction appeared to have a lagged effect in which *P. erecta* did not recover for 6 years. However, *P. erecta* exhibits a cyclical population dynamic with a peak and trough about every 5–10 years (Hallett et al. 2018), and the burn occurred during a peak whereas cattle were reintroduced during a trough in its cycle. This patterning highlights the need for long-term studies that assess intervention success across a range of natural variability. While we did not measure the direct effect of grazing or burning on butterfly populations, in theory, larval populations could be affected positively or negatively depending on when the management tool is implemented. This, along with potentially different effects on plant functional and community composition, is motivation to consider the timing and intensity of the implemented fire and grazing regimes in future studies.

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Supporting Information

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

Table S1. Permutational multivariate analysis of variance (perMANOVA) tests.
Table S2. Pairwise Least-Square Means post-hoc contrasts for linear mixed effects models
Table S3. *p*-values for pairwise comparisons between burned-grazed, unburned-grazed, and burned-ungrazed treatments.
Table S4. Multilevel pattern analysis results listing significant indicator species within group and combination of groups by year.
Figure S1. Map of experimental transects at our study site, Tulare Hill, California.
Figure S2. Native forb relative percent cover (A), richness (B), and non-native grass relative percent cover (C), and richness (D) by transect from 2005–2012.
Figure S3. Cover and richness response of native grasses and non-native forbs.
Figure S4. Time series of absolute cover (%) of *Plantago erecta* from 2001 to 2018.
Figure S5. Litter and precipitation lag effects on native forb richness and cover + correlation between prior year precipitation and litter cover.

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