

RESEARCH ARTICLE

# Invasive species cover, soil type, and grazing interact to predict long-term grassland restoration success

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Grasslands are undergoing tremendous degradation as a result of climate change, land use, and invasion by non-native plants. However, understanding of the factors responsible for driving reestablishment of grassland plant communities is largely derived from short-term studies. In order to develop an understanding of the factors responsible for longer term restoration outcomes in California annual grasslands, we surveyed 12 fields in Davis, CA, U.S.A., in 2015 that were seeded with native species mixtures starting in 2004. Using field surveys, we investigated how invasive plant richness and cover, native plant richness and cover, aboveground biomass, grazing, soil type, and restoration species identity might provide utility for explaining patterns of restoration success. We found a negative relationship between invasive cover and restoration cover, which was attributed to the slow establishment of seeded species and subsequent dominance by weeds. The relationship between invasive cover and restoration cover was modified by grazing, likely due to a change in the dominance of exotic forbs, which have a more similar growing season to restoration species, and therefore compete more strongly for late season moisture. Finally, we found that soil type was responsible for differences in the identity and abundance of invasive plants, subsequently affecting restoration cover. This work highlights the value of focusing resources on reducing invasive species cover, limiting grazing to periods of adequate moisture, and considering soil type for successful long-term restoration in California annual grasslands. Moreover, observations of long-term restoration outcomes can provide insight into the way mechanisms driving restoration outcomes might differ through time.

**Key words:** *Elymus glaucus*, *Elymus triticoides*, management, native grass, revegetation, *Stipa pulchra*

## Implications for Practice

- Invasive plant cover is important for predicting long-term cover of restoration species, suggesting that the ability to withstand resource competition can be a useful trait for identifying restoration candidates.
- Grazing during drought can have a negative effect on restoration cover by benefiting exotic annual forbs, which have a similar growing season to seeded natives. Practitioners should consider using low intensity grazing in years that are not characterized by drought conditions or right after a rainfall event.
- Soil type can limit restoration success by modifying the identities of dominant invasive plant species. Practitioners can improve revegetation efforts by choosing restoration candidate species based on their functional similarity to invasive species because trait redundancy can confer resistance to invasion.

## Introduction

Temperate grasslands are undergoing large-scale degradation as a result of climate change, land conversion, and invasion by exotic species. These systems are particularly susceptible to disturbance because relatively small changes in resource availability or environmental conditions can produce large and, often, unexpected changes in native plant communities (e.g. Chabot

& Mooney 1985; Heisler-White et al. 2009). Some of the more well-documented effects of environmental change on grasslands include biodiversity loss (Harrison et al. 2015), increased incidence of catastrophic wildfire (Brooks et al. 2004), loss of wildlife habitat (Grant et al. 2004), and modifications of soil nutrient cycling (Evans et al. 2001). The decline in the ecological integrity and economic value of grassland habitats worldwide requires immediate and effective implementation of restoration strategies. However, high diversity restoration of these systems—particularly xeric grasslands—is notoriously difficult because grasslands can be characterized by low annual precipitation and low productivity (Stromberg et al. 2007), which directly limits establishment and growth rates of seeded species.

Many factors can modify the likelihood and the degree to which goals are achieved in restored grasslands. These can include underlying abiotic conditions of soil heterogeneity

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(Baer et al. 2005), soil disturbance (Tilman 1983), and resource availability (Baer et al. 2004), as well as biotic conditions such as the identity and abundance of soil fungi (Bell et al. 2015), and the dominance of invasive plants (Costello et al. 2000). Historic, current, and follow-up management approaches deployed at a site can also play a role in modifying restoration outcomes (Bartolome 1981; Brockway et al. 2002; Halpern et al. 2012). Understanding how these variables interact to ultimately drive the response of restored species in grasslands is critical for making predictions of intervention outcomes, as well as for the development of effective restoration approaches.

Interactions among biotic and abiotic factors must be considered in restoration because they commonly drive plant community dynamics (Stromberg & Griffin 1996; Craft et al. 2002). For example, in highly invaded grasslands, such as those typically found in the California central valley, plant community dynamics and restoration outcomes are largely driven by how invasive plants interact with habitat characteristics to outcompete native species for resources (e.g. Dyer & Rice 1999). As a result, many studies have documented the significant independent and interactive effects of invasion and cattle grazing (e.g. Harrison et al. 2003; Kimball & Schiffman 2003), and site and soil conditions (Lulow et al. 2007; Holl et al. 2014) for restoration outcomes in California grasslands. Characteristics of seeded species, such as identity (Lulow et al. 2007; Wilson 2015) and year planted (Young et al. 2015), are also commonly invoked as important for restoration success in California, due to effects of annual weather variation on invasive plant cover. However, this knowledge is mostly predicated on short-term assessments (Ruiz-Jaen & Aide 2005), and might not be useful in making predictions of long-term restoration outcomes. As might be expected by community assembly rules and succession theory (e.g. Young et al. 2001), more than 8 years is typically required to achieve a relatively successful, stable cover of restoration species in grasslands (e.g. Muller et al. 2002). In California annual grasslands, the slow establishment and subsequent subordinate competitive ability of most native perennial bunchgrasses are largely responsible for the time lag between restoration deployment and adequate native species coverage (e.g. Bugg et al. 1997; Porensky et al. 2012).

Reviews of longer term restoration outcomes might provide a more relevant assessment of intervention efforts as plant community response to vegetation management is rarely linear (Bakker & Berendse 1999; Zedler & Callaway 1999; Hayes & Holl 2011; Lennox et al. 2011). In grasslands, this can be caused by differences in the identity of the natural drivers of community composition through time. For example, short-term dynamics are largely driven by interannual variability in precipitation (Hobbs & Mooney 1995; Knapp et al. 2002), whereas longer term dynamics can be driven by values of average precipitation, across years (Harrison et al. 2015). The regular inclusion of assessments of long-term restoration project outcomes through basic observational studies can elicit data that can be used to test whether mechanisms driving short-term restoration outcomes also do so in the longer term. For example, long-term studies can be used to distinguish between natural variation and significant trends in restoration species cover.

In this study, we evaluated the long-term success (defined as achieving high native seeded species cover) of a multi-field grassland restoration project initiated in 2004. Field characteristics that have been shown to be important for short-term restoration success (soil type, field size, year seeded, restoration mixture type, the presence of grazing, invasive species richness and cover, and native species richness and cover) were estimated to identify factors that could provide particular utility for explaining longer term patterns of seeded restoration species cover. First, we expected that year seeded and restoration mixture type would play a role in mediating restoration outcomes because the indirect effects of weather variability on these characteristics have been shown to be important for California grassland community dynamics (Stromberg et al. 2007). We also expected to find a negative relationship between the cover of invasive species and restoration species (e.g. Bakker & Wilson 2004) because exotic annual plants can be the most important driver of native perennial bunchgrass dynamics through competition for soil moisture (Hamilton et al. 1999). Moreover, we expected restoration species cover to be higher in fields exposed to grazing, which lowers the prevalence of exotic annual grasses (Bullock et al. 2001). Finally, we expected soil type to play a role in modifying long-term restoration success because native perennial grass cover can scale with soil clay content (Keeley 1993).

## Methods

### Existing Restoration Project

This study was conducted in fields on Russel Ranch (38.547921, -121.805087), which is associated with the Putah Creek Riparian Reserve, owned and managed by the University of California. The ranch encompasses 380 acres, and is surrounded by a matrix of rural residential and agricultural areas west of Davis, CA, U.S.A. The area is characterized by a Mediterranean climate with 24.6°C average temperature and 41 cm total annual precipitation that occurs mostly in the late fall and winter. The fields were previously cultivated as agricultural lands (row crops and orchards) that were abandoned in the 1980s. Soil data were collected from USDA NRCS maps ([www.nrcs.usda.gov](http://www.nrcs.usda.gov)), which have a minimum size of delineation of 1.4 acres. The soils of the study area were a mix of fine-silty, mixed superactive thermic Mollic Xerofluvents; fine, mixed active Typic Palexeralfs; and fine, smectitic, thermic Typic Haploxerepts (Table 1). At the start of the study, the fields reflected a typical California valley grassland habitat (Heady 1977), largely composed of invasive annual grasses such as *Avena fatua* (Wild oats), *Festuca perennis* (Italian rye grass), and *Elymus caput-medusae* (Medusahead) with little to no woody cover.

Starting in 2004, restoration projects were initiated across approximately 190 acres of flat land at the ranch with the goal of reestablishing native perennial bunchgrass communities. Between 2004 and 2007, 12 fields of various sizes (Table 1) were seeded with a native grass (Table 2). Grass-only mixes were initially used because of the need to apply a one-time broadleaf herbicide (Garlon® 4 at a rate of 15 gal/acre) across

**Table 1.** Site and vegetation characteristics of restored fields. Mix indicates the identity of the seed mix used at each site (see Table 2) and the year the mix was seeded into each field. Invasive cover, mix cover, and biomass values are means (SD).

Field	Size (acre)	Soil Type	Mix (Year)	Grazing	Invasive Cover (%)	Invasive Richness	Mix Cover (%)	Mix Richness	Biomass (g)
M1	14.0	Corning gravelly loam	1 (2004)	N	85.9 (18.5)	4.2 (1.7)	3.3 (4.9)	0.6 (0.5)	32.0 (1.8)
M2a	17.6	Corning gravelly loam	1 (2004)	Y	97.6 (4.2)	4.6 (1.2)	5.3 (5.2)	0.1 (0.3)	35.0 (5.1)
M2b	8.8	Corning gravelly loam	1 (2004), 5 (2006)	Y	94.1 (17.7)	5.1 (0.9)	4.2 (2.7)	0.1 (0.3)	34.3 (4.2)
M3	28.3	Brentwood silty clay loam	3 (2005)	N	15.6 (7.0)	1.1 (0.3)	85.0 (16.5)	0.0 (0.0)	26.0 (4.2)
M4	14.7	Rincon silty clay loam	1 (2004), 4 (2011)	Y	91.9 (15.0)	6.4 (1.1)	4.1 (2.9)	0.3 (0.5)	28.9 (2.2)
M5	50.4	Yolo silty loam	2 (2004), 4 (2011)	Y	20 (7.9)	1.7 (0.5)	45.6 (15.6)	0.1 (0.3)	30.7 (3.6)
L2a	82.3	Rincon silty clay loam	1 (2004)	N	50.9 (28.7)	4.8 (1.2)	26.6 (26.1)	1.0 (0.0)	26.1 (8.7)
L2b	20.6	Rincon silty clay loam	1 (2004), 5 (2010)	N	17.6 (11.1)	3.3 (1.4)	46.1 (24.5)	0.1 (0.3)	23.5 (3.0)
L3	26.9	Rincon silty clay loam	1 (2004)	N	41.7 (31.3)	2.9 (0.9)	28.6 (14.4)	0.4 (0.5)	26.7 (6.0)
K1	14.5	Yolo silty loam	3 (2005), 4 (2011)	N	34.9 (10.9)	1.9 (0.6)	32.7 (15.8)	0.0 (0.0)	41.3 (6.2)
K2	7.07	Yolo silty loam	3 (2005), 4 (2011)	N	50.4 (29.6)	3.0 (1.1)	30.7 (34.5)	0.0 (0.0)	46.9 (3.0)
K3	23.0	Yolo silty loam	3 (2005), 4 (2011)	N	44.7 (22.2)	1.7 (0.5)	34.2 (11.3)	0.0 (0.0)	45.7 (9.2)
K4	26.8	Yolo silty loam	1 (2007)	N	58.1 (13.0)	2.0 (0.9)	11.6 (12.2)	0.0 (0.0)	37.3 (6.9)
K6	5	Yolo silty loam	3 (2006)	N	16.8 (18.3)	2.3 (0.7)	78.3 (22.1)	0.0 (0.0)	38.7 (14.3)

**Table 2.** Identities (and lbs of seed/acre) of native species used in each seed mix. Mixes 1–3 were grass mixes and mixes 4 and 5 were forb mixes.

Mix Type	Species
Mix 1	<i>Elymus multisetus</i> (3), <i>Festuca microstachys</i> (1), <i>Melica californica</i> (3), <i>Stipa pulchra</i> (8), <i>S. cernua</i> (3), <i>Poa secunda</i> (2)
Mix 2	<i>Elymus glaucus</i> (4), <i>Elymus trachycaulus</i> (2), <i>Hordeum brachyantherum</i> (6), <i>Elymus triticoides</i> (6)
Mix 3	<i>Elymus glaucus</i> (4), <i>E. trachycaulus</i> (2), <i>H. brachyantherum</i> (6), <i>E. triticoides</i> (6), <i>S. pulchra</i> (8)
Mix 4	<i>Achillea millefolium</i> (1), <i>Calandria ciliolatum</i> (1), <i>Eschscholzia californica</i> (4), <i>Grindelia camporum</i> (2), <i>Lotus unifoliolatus</i> (1), <i>Lupinus bicolor</i> (1), <i>L. nanus</i> (1), <i>L. succulentus</i> (3), <i>Trifolium bifidum</i> (1), <i>T. microcephalum</i> (3), <i>T. willdenovii</i> (3)
Mix 5	<i>Achillea millefolium</i> (2), <i>C. ciliolatum</i> (1), <i>E. californica</i> (4), <i>L. unifoliolatus</i> (1), <i>L. bicolor</i> (3), <i>L. nanus</i> (4), <i>Madia elegans</i> (1), <i>T. bifidum</i> (1), <i>T. gracilentum</i> (1), <i>T. microcephalum</i> (1), <i>T. willdenovii</i> (2)

fields to reduce the extensive weedy forb seed bank. Native forb mixes were seeded one to several years later (between 2005 and 2011) on a subset of fields (on both entire fields, and on portions of fields; Table 1). After seeding, herbicide was used infrequently (approximately every 3 years) to control annual grasses (Roundup Pro® Dry at a rate of 9 gal/acre). In 2012 (17 days, 25 cows) and 2013 (3 months, 18 cows), several fields were treated with spring cattle grazing in order to achieve a 15 cm optimal foraging height for Swainsons Hawk (Table 1). A linear mixed-effects model demonstrated that in 2015 there was no difference in biomass between ungrazed fields and grazed fields (SE = 1.86,  $t = -1.17$ ,  $p = 0.25$ ), likely because all fields were mowed approximately every year for fire prevention.

Three permanent transects (20 m in length) were installed in each field for vegetation surveys. In two fields (M2 and L2), a total of six transects were installed because different areas of these fields received different combination of seed mixes (three were installed in an area receiving one seed mix and three were installed in an area that received a different seed mix; Table 1). Transects were deployed randomly in the fields, with at least 20 m separating each transect. Transects were deployed in May 2015, and all field work was completed at this time as well.

#### Data Collection

At the beginning, middle, and end of each transect, plant richness and cover of each species was visually estimated and

recorded to species in a 1-m<sup>2</sup> plot (three plots per transect and nine plots per field). Species were also characterized as “invasive,” “native,” or “restored.” Species characterized as “native” included only native species that were not part of a restoration seed mix. We assumed that any seeded species found in a plot that was included in the restoration seed mix applied to the field being surveyed (Table 2) was present due to seeding activities and not due to natural colonization from non-seeded areas.

We also collected standing biomass 0.5 m NW of each transect (one associated with each transect,  $n = 3$  per field). Above-ground biomass was clipped to 2 cm in a 30 × 30-cm quadrat. At the point of collection, most of the invasive annual grasses had reached maturity. Biomass was dried for 48 hours at 65°C and weighed.

### Data Analysis

We initially collected data for nine fixed factors that could be used to explain differences in the cover of restoration species, including soil type (Table 1), year seeded (between 2004 and 2011), seed mix type (Table 1), grazing (absent or present), standing biomass (in grams), invasive cover (%), invasive richness (#), native cover (%), and native richness (#). To conserve parsimony, we first identified the subset of factors that would best describe differences in restoration species cover. To do this, we used a multivariate model that included all factors, and interaction terms (including an error term for plot nested within transect, nested within field) and then used an automated backward stepwise model selection process. Variables were considered for the final models only if their significant level in the full model was less than 5% (Yamashita et al. 2007). The selection procedure used exact Akaike Information Criterion (AIC) values, and  $k = 2$  degrees of freedom ( $df$ ) were used for the penalty (Burnham & Anderson 2002).

The stepwise approach identified three factors with significance levels of less than 5%: invasive cover, grazing, and soil type. These were then included as fixed factors in a linear mixed-effects model (which also included an error term for plot nested within transect, nested within field). Linear mixed effects models are generalized models in which parameters are allowed to vary by group (Bolker et al. 2008). This approach was used because these types of models are particularly useful for nested designs, and can economize the number of degrees of freedom used up by the treatment levels. To understand how the strength of relationships among explanatory variables and long-term restoration species cover change, as highlighted by the mixed model, we also performed correlation testing. Finally, we conducted ordination analysis on the plot level community data using non-metric multidimensional scaling (NMDS; Clarke 1993). A final solution for the NMDS was reached after two iterations. Contributions of grazing and soil type to community composition were tested using permutational multivariate analysis of variance (PERMANOVA), a non-parametric method that operates on distance matrices, allowing for multivariate analysis. All analyses were conducted in R version 3.1.1 (R Development Core Team 2012) using the MASS, vegan, and nlme packages.

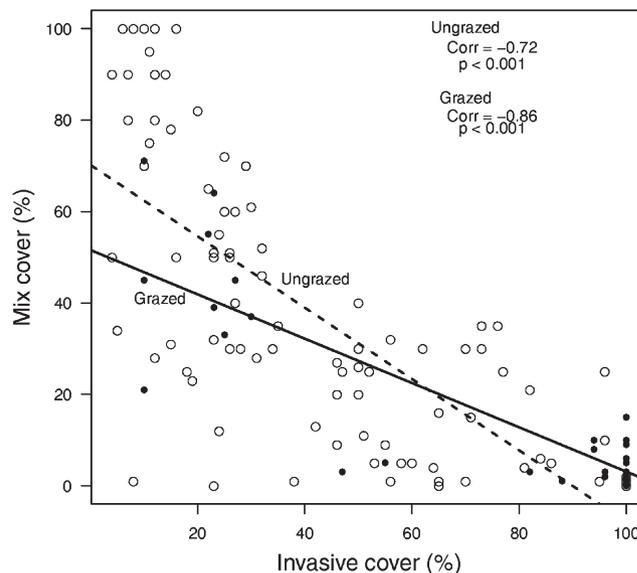


Figure 1. Correlations between invasive cover and restoration species cover in ungrazed fields (open circles, dotted line) and in grazed fields (closed circles, straight line).

### Results

We found a total of 31 species across among all restored grasslands, including 24 invasive species (12 grasses and 12 forbs), two native unseeded species (both forbs), and five restoration species (Table 1). Dominant invasive species across all plots included *Avena fatua* (average cover = 25%), *Bromus hodeaceus* (Soft brome; average cover = 30%), and *Medicago polymorpha* (Bur clover; average cover = 29%). The two natives found were *Achyrachaena mollis* (Blow wives; average cover = 2.6%) and *Amsinckia menziesii* (Fiddleneck; average cover = 1%). The restoration species (Table 2) found in our surveys included four grasses: *Elymus glaucus* (Blue wild rye; average cover = 11%), *Elymus triticoides* (Creeping wild rye; average cover = 34%), *Stipa pulchra* (Purple needle grass; average cover = 29%), and *Melica californica* (California melic; average cover = 2%); and one forb: *Lupinus bicolor* (Miniature lupine; average cover = 4%).

The mixed effects model showed that invasive cover negatively affected restoration species cover ( $F_{[1,116]} = 180.71$ ,  $p < 0.001$ ). There was also a significant effect of the interaction between grazing and invasive cover on restoration species cover ( $F_{[1,116]} = 5.63$ ,  $p = 0.02$ ). Correlations between invasion cover and restoration species cover (Fig. 1) suggest that the strength of this relationship differs in the absence and presence of grazing. Finally, the mixed model results indicated that the interaction between invasive cover and soil type also demonstrated significant contributions to differences in restoration species cover ( $F_{[1,116]} = 4.19$ ,  $p = 0.02$ ).

The community analysis highlighted a potential mechanism driving the relationship between invasive cover, soil type, and restoration species cover. The ordination converged on two dimensions with a stress of 0.24 (Fig. 2). PERMANOVA results demonstrate a significant effect of soil type (increasing

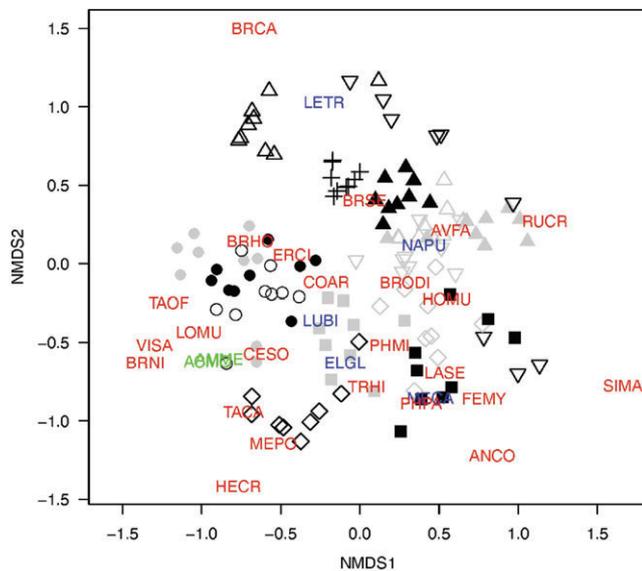


Figure 2. Results of the NMDS ordination. Letter codes indicate species identity. Red, invasive species; blue, native species (seeded); green, native species (unseeded). Symbols indicate sites (plot level). Symbols of different shapes indicate different soil types: triangles, Yolo silt loam; squares, Rincon silt clay loam; circles, Corning gravelly loam; crosses, Brentwood silt clay. Similarly, shaded/colored symbols indicate plots within the same transect group. Restored species identity codes were ELGL, *Elymus glaucus*; LETR, *Elymus triticoides*; LUBI, *Lupinus bicolor*; MECA, *Melica californica*; NAPU, *Stipa pulchra*. Native species identity codes were: ACMO, *Achyrachaena mollis*; AMME, *Amsinckia menziesii*. Invasive species identity codes were: AVFA, *Avena fatua*; ANCO, *Anthemis cotula*; BRNI, *Brassica nigra*; BRCA, *Bromus caroli-henrici*; BRDI, *Bromus diandrus*; BRHO, *Bromus hordeaceus*; BRSE, *Bromus secalinus*; CESO, *Centaurea solstitialis*; COAR, *Convolvulus arvensis*; ERCI, *Erodium cicutarium*; FEMY, *Festuca myuros*; LOMU, *Festuca perennis*; HECR, *Hedypnois cretica*; HOMU, *Hordeum murinum*; LASE, *Lactuca serriola*; MEPO, *Medicago polymorpha*; PHMI, *Phalaris minor*; PHPA, *Phalaris paradoxa*; RUCR, *Rumex crispus*; SIMA, *Silybum marianum*; TACA, *Taenatherum caput-medusae*; TAOF, *Taraxacum officinale*; TRHI, *Trifolium hirtum*; VISA, *Vicia sativa*.

NMDS1 scores indicate decreasing soil porosity,  $F_{[1,116]} = 4.02$ ,  $p = 0.004$ ), invasive cover ( $F_{[1,161]} = 12.38$ ,  $p = 0.001$ ), grazing (grazed plots are characterized by more negative NMDS1 scores,  $F_{[1,116]} = 5.79$ ,  $p = 0.001$ ), and the interaction between soil and invasive cover (highest invasive cover values in loamy (comparatively high porosity) soil;  $F_{[1,116]} = 4.14$ ,  $p = 0.002$ ) on community composition. This suggests that soil type may have driven differences in both the abundance of invasive species as well as the identity of the dominant invasives in particular plots (Fig. 2). Plots on Yolo silt loam were dominated by species such as *A. fatua* and *Bromus caroli-henrici* (Weedy brome). Plots on Rincon silt clay loam were dominated by species such as *Lactuca serriola* (Prickly lettuce), *Phalaris paradoxa* (Canary grass), and *Trifolium hirtum* (Rose clover). Plots on Corning gravelly loam were dominated by *B. hordeaceus*. Lastly, plots on Brentwood silt clay were dominated by *Bromus secalinus* (Rye brome).

## Discussion

We surveyed 12 sites almost 10 years following restoration to understand long-term management outcomes that would not be discernable from short-term monitoring (Block et al. 2001). We found that invasive plant cover, the interaction between invasive plant cover and grazing, and the interaction between invasive plant cover and soil type were important for predicting cover of restoration species. Unexpectedly, the year a site was seeded and the identity of sown species were found to be relatively unimportant for restoration success. As these two factors are often identified as critical for understanding early restoration outcomes in California annual grasslands (Stromberg et al. 2007), our finding highlights dissimilarities between drivers of short-term and long-term revegetation success. We found that only three species used in the restoration mixes maintained any appreciable cover: *Elymus glaucus*, *Elymus triticoides*, and *Stipa pulchra*. In previous studies, these species have demonstrated competitive equivalence or dominance to some of the more noxious invaders of these grassland systems (Lulow et al. 2007; Young et al. 2009), suggesting that the ability to withstand resource competition can be a useful trait for identifying restoration candidates (e.g. Pywell et al. 2003). Using a trait-based approach to grassland restoration could also be useful for conferring invasion resilience to the restored community (Funk et al. 2008).

California grasslands are some of the most heavily invaded systems in the world. And this invasive plant cover can hinder restoration success (Cione et al. 2002). The suppression of restoration species by exotics documented in this study was likely driven by competitive dynamics at the seedling stage (Bartolome & Gemmill 1981; Dyer et al. 1996) because this is the point in the life cycle that can be the most important for driving overall reestablishment (e.g. Gornish et al. 2015). Identifying locally adapted (Smith et al. 2011) restoration candidates based on establishment traits could provide utility for enhancing population growth rates and stability (Silvertown & Charlesworth 2001). Strategies that prioritize management at these early stages would also enhance restoration success. In California, for example, the use of grass-specific herbicides early in the spring season, when exotic annuals are much more vulnerable to management efforts than native perennials, could provide a more suitable environment for increasing restoration species cover and species richness (Grubb 1977; Marushia & Allen 2011).

Although many studies have demonstrated the value of using well managed grazing for maintaining restoration species establishment, cover, and diversity in grasslands (e.g. Gibson et al. 1987; Smith et al. 2000; Wilsey & Martin 2015), we found that grazing had an indirect negative effect on the cover of native seeded species. It is possible that weather played a role in this unexpected outcome. In California annual grassland systems, grazing tends to have a negative effect on plant communities in resource poor environments (Bakker et al. 2006; Beck et al. 2015). This occurs because high resource environments are characterized by high productivity, and grazing serves to reduce competition for light among species through biomass removal. Alternatively, in low resource environments,

productivity is low, and biomass is mostly allocated below-ground, where grazing animals have little impact. The 2 years in which the restored fields were exposed to grazing were some of the driest in the history of the state (Griffin & Anchukaitis 2014; Swain et al. 2014). As productivity was likely limited by the low availability of soil moisture across fields, competition for light was not likely an important driver of community dynamics. However, the lack of a positive effect of grazing during drought conditions does not explain why grazing modified the relationship between restoration cover and invasive cover to ultimately reduce the abundance of seeded species.

Grazing has been shown to disproportionately benefit exotic annual forbs (Bullock et al. 2001), which favor low resource and disturbed environments (Gerlach & Rice 2003). Under these conditions, perennial restoration species would experience stronger competitive effects from invasive forbs (which have a similar growing and flowering season) than from invasive grasses. This occurs because invasive annual forbs directly compete with native perennial bunchgrasses for residual soil moisture resources that are available far too late in the season for invasive annual grasses (Gerlach 2000). Moreover, in California, many of these invasive annual forbs demonstrate copious seed production. For example, large individuals of *Centaurea solstitialis* (Yellow starthistle) can produce over 100,000 seeds/plant with a germination rate of 90–100% a single week after seed dispersal (DiTomaso et al. 2006). This seed production replenishes the seed bank and ensures coverage the following year. These results suggest that site-appropriate low intensity grazing (Campbell et al. 2006) can still provide value for restoration in years that are not characterized by drought conditions or soon after a rainfall event. However, as the benefits of grazing on seeded native species can take up to 5 years to be discernable (Pykälä 2003), broadleaf herbicides can be applied for the short-term reduction and maintenance of competitively dominant invasive annual forbs.

Soil type, quality, and character are important drivers of plant community dynamics (Prober et al. 2002), and, subsequently, restoration outcomes (Bassett et al. 2005; Heneghan et al. 2008; Zhang & Dong 2010). Even small patterns of soil variability within a degraded site can enhance the likelihood of restoration failure (e.g. Eviner & Hawkes 2008). This occurs because soil types can differ in moisture retention, nutrient cycling, and cultivation of various microbial communities (Berg & Smalla 2009). We found that small deviations within soil type across fields resulted in large differences in the identity of dominant invasive plant species. These community-level differences ultimately affect restoration success because the performance of seeded species can depend on the identity of neighboring exotics (Daehler 2003). These results suggest that restoration candidate species should be chosen based on their functional similarity to invasive species, because trait redundancy can confer resistance to invasion (Bakker & Wilson 2004). Practitioners can also consider using soil type to inform invasive plant management strategies that target specific problematic weeds.

This study was conducted during severe drought conditions, which are known to affect both native and invasive plant dynamics in California grassland systems (e.g. Bartolome et al. 2007; Harrison et al. 2015), and might limit how generalizable results are from this study. However, drought conditions in many areas of the Western United States are predicted to increase in frequency and intensity (Seager et al. 2007). These results, instead of providing a snapshot of grassland community dynamics during an anomalous weather event, may demonstrate the types of community patterns more commonly expected in areas experiencing increasing changes to average precipitation values.

The rapid conversion and ecological degradation occurring on temperate grasslands highlight the need for field-derived explanations of the mechanisms driving successful restoration of these systems. Observational studies that capture long-term outcomes of restoration efforts can lead to an understanding of how abiotic and biotic factors interact to ultimately mediate the response of restoration species in grasslands. We encourage researchers to revisit established restoration sites, when possible, in order to assess restoration success. Researchers should also take advantage of the many opportunities available in existing long-standing grassland restoration projects to conduct observational studies in order to develop general principles that can be used to reestablish functional plant communities on working and natural landscapes.

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