Post-Fire Resilience of Restored Coastal Sage Scrub and Grassland Communities

Our study site in Bee Flat Canyon, Santa Ana Mountains, Irvine, CA.

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Abstract

California coastal sage scrub (CSS) and native grassland systems are experiencing increased fire frequencies and extreme droughts due to climate change. These stressors, in addition to historical and ongoing disturbances, make native-dominated communities vulnerable to vegetation-type conversion to communities of non-native grassland. The challenge is to restore resilient native plant communities under these shifting conditions. Our study site, Bee Flat Canyon in the Santa Ana Mountains, contains CSS, grasslands, and other plant communities degraded by historic agricultural and rangeland use. The area was restored by the Irvine Ranch Conservancy (IRC) over 10 years and burned, shortly after project completion, in the 2020 Silverado Fire, presenting a unique opportunity to assess restoration resilience to fire. We studied how CSS communities in restored treatments recovered compared to unrestored degraded and unrestored intact control areas post-fire, whether physiological traits influence post-fire cover of CSS species, and how restored grassland changed over time in relation to temperature, precipitation, and fire. We found no significant difference between restored and intact CSS sites for abundance and survivorship of crown sprouting shrubs and cover of native/non-native forb seedlings, indicating that restored sites were as resilient as intact sites. Degraded sites remained in a degraded state post-fire and contained almost zero native shrubs. There were differences in CSS plant community composition amongst degraded, intact, and restored CSS sites such that restored sites contained some native species that were seeded but absent from intact sites and vice versa. Plant physiological traits did not correlate with cover of CSS species, indicating that traits were not predictors of fire response. In restored grassland, cover did not significantly correlate with temperature and precipitation. Forbs and non-native grasses recovered post-fire, but the native grass *Stipa pulchra* continued to decline, possibly due to competition. Grassland plant community composition shifted significantly toward a higher dominance of non-native grasses in the second year post-fire compared to previous years, indicating a need for non-native control measures after fire. From these assessments, we recommend to IRC that they (1) continue monitoring and managing weeds in CSS and grasslands, (2) enhance the diversity of their restoration seed mixes with additional native species, and (3) develop a post-fire recovery plan to limit the reestablishment of non-native species and support resilience of native species.

Keywords: post-fire resiliency, restoration, crown sprout, recruitment, coastal sage scrub, native perennial grassland, *Stipa pulchra*, physiological plant traits

Executive Summary

Introduction. California is expected to experience longer dry periods due to climate change, which increases the chances of more frequent, high-intensity fires. While fire is a natural disturbance in many California plant communities, these shortened fire intervals can leave disturbed areas vulnerable to land degradation and provide an open space for community assembly of aggressive non-native species to colonize. Due to physiological traits that allow high seed dispersal and rapid growth in an environment free of competition, non-native invasive species often have a competitive advantage over native perennial shrubs and bunchgrasses when reestablishing post-fire. These conditions often do not leave enough time or resources for coastal sage scrub (CSS) species and native grasses to establish through seed reproduction or shrub crown sprout after fire. Thus indicating that morphophysiological plant traits can play an important role in the ability of CSS and grassland species to recover following fire. Despite being historically fire-adapted, native plant communities are declining in Orange County due to urban development and agriculture. To prevent further degradation and habitat loss, IRC began restoring Bee Flat Canyon in the foothills of the Santa Ana Mountains in Irvine, California in 2011. The restoration burned in the 2020 Silverado Fire, creating an opportunity to assess the recovery and resilience post-fire and provide recommendations for future restoration methods.

Goals and Methods. The project goals were to assess post-fire resiliency of CSS and grassland in Bee Flat Canyon and inform IRC management. To understand this complex landscape post-fire, we conducted studies in both CSS and grasslands in unrestored intact control sites, unrestored degraded sites, and restored sites and performed climatic and species traits analyses. We surveyed native shrub crown sprouting and recruitment in the November

following the Silverado Fire, and native and non-native shrub, grass, and forb surveys in the following spring. Focusing on dominant CSS species, we then assessed traits that might influence growth rate. We also compared vegetative cover and species composition of native and non-native forbs and grasses (*Stipa pulchra* in particular) over time, relative to precipitation and temperature before and after the fire.

CSS Shrub Recovery. Our study took place post-fire and after a summer of drought–conditions that exemplify overlapping issues facing managers as a result of global warming. Our shrub recovery analyses showed no significant difference in crown sprout or recruitment shrub size between intact and restored sites, but did show more seedling abundance in intact sites and more crown sprouts in restored sites. The proportion of seedlings that survived the fire and the proportion of crown sprouts that survived to the Fall following the fire did not vary between restored and intact sites. Both seedlings and crown sprouts had high survivorship overall at ~90%. Taken together, these analyses imply that restored sites are doing comparably well after fire and drought.

CSS Seedling Recruitment. The abundance of native forb and grass seedlings was higher in intact areas due to the sites having precomposition of natural occurrences and therefore, a resistance to invasibility. However, restored sites showed similar success with native forb resiliency and no significant difference compared to intact sites, pointing to a successful restoration. Non-native forbs and grasses had more seedling recruitment in degraded sites compared to intact and restored sites due to the ability of invasive plants to act as colonizers of disturbed sites and readily take advantage of ecosystem resources after fire. Species composition differences showed there was not a significant relationship between the year of measurement and ordination space. However, there was a significant effect of restoration status in ordination space. Overall, there were similarities of species composition between restored and intact sites. Moreover, restored sites had just as many natives as intact sites. Yet, there was a difference in native annuals species composition between intact and restored sites, which can be attributed to the species included in the seed mix.

CSS Functional Traits. We compared species abundance from the Springs before and after the fire to determine what species reappeared post-fire and if there are any correlations with a plant's functional traits. Of the species we analyzed, only two came back after the fire and had a positive fire response value. These two forb species were *Deinandra fasciculata*, a native*,* and Brassica *nigra, an* invasive. When looking at functional traits specifically, we found that there was no correlation between any of the traits we analyzed and species' fire response. We also found that there was no significance in fire response depending on a plot's water or nitrogen treatment. There could be a variety of reasons for these results, one of which being that the abundance data was collected only a few months after the fire and did not allow enough time for plants to reestablish post-fire. It is also important to note that of the two species that did reestablish post-fire, one of them was invasive.

Grassland Monitoring. Grassland cover and composition changed significantly over time, especially post-fire. The cover data show that grassland restoration was successful pre-fire with consistently higher cover of *S. pulchra* than non-native grasses. There was less discrepancy between native and non-native forbs overall, with slightly higher cover of native forbs. Cover of all functional groups decreased the first year after fire as expected, though native forbs and grasses experienced higher loss than non-natives. Cover in the second year post-fire showed low resilience of restored *S. pulchra* indicating a need for post-fire management to maintain desired cover of this species. Native forbs, non-native forbs, and non-native grass recovered, with a strong increase in non-native grasses, but *S. pulchra* continued to decline. This response is likely attributed to the ability of non-native grasses to outcompete native perennials for resources and quickly reestablish in the spring season. Temperature and precipitation were not significant predictors of cover, perhaps due to a small sample size, but they did correlate with differences in species composition across years. Species composition in 2022 was significantly different than previous years and was highly correlated with higher cover of non-native grasses. Overall, the grassland restoration was successful and forbs were resilient post-fire, but the focal species *S. pulchra* was not.

Seed Mix Assessment. Due to their post-fire and post-drought resilience, we also suggest considering the addition of native species found in restored sites that were not a part of the restoration palette, those found in intact sites that were not a part of the restoration palette, and those found in grasslands that were not part of the original seed mix (see Table 2).

Conclusions. Given our results and assessments, we recommend the following to IRC: 1) continue monitoring and managing weeds in CSS and grassland communities, 2) enhance the diversity of restoration seed mixes with additional native species, and 3) develop a post-fire recovery plan to help limit the reestablishment of non-native species to support resilience of native species after a wildfire event.

1. Introduction

1.1. Goals & Objectives

The goal of this project was to evaluate the post-fire recovery of restored coastal sage scrub (CSS) and grassland habitats. Our study site was a large restoration project of a previously grazed and heavily invaded site in Bee Flat Canyon, located in the Santa Ana Mountains of Orange County, California (Figure 1). Increasing fire frequency and non-native invasion threaten the resiliency of native CSS and grassland habitats, leading to the question of whether restored CSS and grassland communities returned to pre-fire conditions. This work was conducted to assist our community partners at Irvine Ranch Conservancy (IRC) in the active adaptive management of this unique landscape.

Our project consisted of three goals that measured restoration resilience and a fourth goal for restoration engagement: (1) Assess the resilience of restored CSS with crown sprouting shrubs and seedling recruitment surveys across three habitat conditions (unrestored intact control, unrestored degraded, restored); (2) Relate CSS resilience to functional traits of native and non-native plants by a comparison based on changes in species composition pre- and post-fire; (3) Assess vegetation cover of grassland restoration (with a focus on the native perennial bunchgrass, *Stipa pulchra*) relative to regional precipitation, temperature, and the 2020 Silverado Fire; and (4) Present our work at an IRC research symposium and mentor students from the IRC-Crystal Cove Conservancy high school internship program. See Table 1 for a detailed breakdown of our goals and objectives.

1.2. Research Questions

We outlined five research questions to determine how resilient restored communities are to wildfire. In coastal sage scrub (CSS), crown-sprouting and recruiting from seed are the two strategies by which shrubs re-establish following wildfire. For this community we asked (1) Does the prevalence of one shrub re-establishment strategy or another vary depending on restoration status (restored, degraded, or intact); (2) Does the total cover of seedling recruitment of herbaceous functional groups (native and non-native forbs and grasses) and species composition vary depending on restoration status; and (3) Is there a relationship between CSS species' functional traits and their change in abundance in response to wildfire, and does that relationship vary depending on water and nitrogen levels? In our grassland studies, we asked (4) Is there a significant difference in total cover of grassland functional groups (native and non-native forbs, non-native grasses, and *S. pulchra*) over time; (5) Does the total precipitation and average monthly temperature during the growing season significantly predict total cover of grassland functional groups and community composition; and (6) How is the community composition of grassland changing over time in relation to functional group cover and abiotic factors?

1.3. Significance

CSS and grassland communities are unique habitats that support high biodiversity and provide ecosystem services, making the conservation, protection, and restoration of these communities vital. A significant portion of the state's coastal vegetation consists of drought-deciduous CSS which supports a large number of sensitive, endangered, and threatened species such as the coastal cactus wren (*Campylorhynchus brunneicapillus ssp.*), Quino checkerspot butterfly (*Euphydryas editha quino*), and California Gnatcatcher (*Polioptila californica*; Stephenson, 1999). California's grasslands are considered biodiversity hotspots that host 90% of rare and endangered plant species (Agee et al., 2000) and 40% of total native plant species in the state (Wigand et al., 2007), and wildlife such as the giant kangaroo rat (*Dipodomys ingens*), California red-legged frog (*Rana draytonii*), and California tiger salamander (*Ambystoma californiense*; (Bartolome et al., 2014). In addition to habitat, CSS and grassland also provide important ecosystem services such as carbon storage, improved air and water quality, flood protection, erosion control, and recreation (Sala & Paruelo, 1997; White et al., 2000).

The post-fire resilience of CSS is dependent on how likely shrub skeletons are to crown sprout and seed to recruitment after fire and then survive possible drought conditions (Figure 2). CSS shrubs crown sprout success rates vary by species and age (Hobbs, 1985; Keeley, 2006) and seedling recruit survivorship is affected by drought (Jacobsen et al., 2018). Studying the success of these growth strategies supports management in creating and sustaining long term habitat resilience after the fire.

These habitats are in serious decline. CSS is one of the most threatened habitat types in North America (Noss et al., 1995) with some studies indicating that more than 30% of CSS in California was converted to exotic grassland land between 1930 and 2009 (Cox et al., 2014). It is estimated that native perennial grasses now comprise only two percent of California grasslands (Elstein, 2004). While much of this loss is attributed to anthropogenic causes such as urban development, these ecosystems are also threatened by shorter intervals in natural wildfire cycles. These disturbances can lead to vegetation type conversion (Keeley, 2005), a subsequent shifting from one plant community to another.

Maintaining or returning a CSS landscape to a canopy state has been shown to reduce the likelihood of type conversion to non-native grasses and decreases fuel load for potential wildfires (Rejmánek, 1989). Moreover, non-native annual grasslands carry more fire risk than native perennial grasses (Setterfield et al., 2013) thus ensuring that these native ecosystems maintain post-fire resiliency contributes to future fire mitigation efforts. Physiological traits and establishment strategies, such as seeding, recruitment, and dispersal also play an important role in CSS post-fire resiliency (Bartolome & Gemmill, 1981; McGill et al., 2006). If these communities cannot recover from contemporary fire and climate trends, practitioners will need to adjust their strategies to ensure future project success.

Our study site, Bee Flat Canyon, is a mosaic of native habitats that lies in the foothills of the Santa Ana Mountains and is owned by Orange County Parks. The outcomes of this project are targeted primarily toward supporting IRC restoration management of Bee Flat Canyon, yet studying restoration after the Silverado Fire could provide broader management implications both in terms of ecological integrity and addressing future climate conditions. Given the range of CSS and perennial grassland across California, other restoration practitioners and conservation land managers may benefit from this research both to assess post-fire recovery and to consider recommendations to support post-fire resiliency in these communities.

1.4. Background

The ecology of Southern California’s native grasslands and CSS species evolved with fire and drought over millions of years. The area’s Mediterranean climate produces wet winters with high primary productivity and increased fuel load followed by hot dry summers that result in regular fire regimes (Keeley, Bond, et al., 2011). Additionally, researchers estimate that between 5.6 and 13 million acres of California burned annually from fires started by lightning as well as Indigenous peoples' fire regimes, which began 10,000 years ago (Martin & Sapsis, 1992; Sugihara et al., 2006). By the late 1800s, colonial settlers had introduced invasive species, developed large scale industrial farming, and conducted intensive harvesting, grazing, and fire suppression practices that resulted in a legacy of degradation that shifted plant community composition (Barry et al., 2006; Irvine Ranch Conservancy, 2011, 2012). In the last twenty years, longer drought periods (National Drought Mitigation Center et al., n.d.) and a drastic increase in the number of acres burned due to wildfires (Porter et al., 2020) have left CSS and native grassland habitats vulnerable to vegetation type conversion (Cayan et al., 2008; Conlisk et al., 2016; Kimball et al., 2014), necessitating a high level of resiliency when restoring California's plant communities.

While native habitats evolved with historic Southern California fire intervals every 30 to 40 years (Keeley & Fotheringham, 2001), recent increases in fire frequency have had major consequences for native habitat resilience, including in Bee Flat Canyon. In October and November of 2020 the Silverado Fire burned over 12,000 acres in Orange County including all of Bee Flat Canyon, which had previously burned in the 2007 Santiago Fire (Orange County Fire Authority, 2020).

The Bee Flat Canyon adaptive management restoration mosaic of native habitats provides a unique opportunity to evaluate post-fire CSS and grassland recovery. CSS is the dominant plant community in Bee Flat Canyon, covering 50% of the acreage with scattered patches of native grasslands. Within the 84 acres of heavily degraded habitat, 79 polygons were chosen for restoration in areas with less than 50% native cover. Site preparation included removal of non-native weed cover, soil ripping, and disking. The native plant palette (Table 2) was based on site observations, nearby reference sites, and propagule availability from local seed growers and wild sources. Some plants were specific fire followers to these habitats, and a small number of select species were added as plantings. Mixes were planted in strips to facilitate adaptive management experiments and regular site maintenance (DeSimone, 2011; DeSimone & Zedler, 1999; Irvine Ranch Conservancy, 2012).

2. Literature Review

Many variables affect the ability of native CSS shrub, forb, and grassland species to recover and resist post-fire vegetation type conversion. While most above ground CSS biomass is killed during fires, CSS shrub species are predominately facultative seeders, regenerating both through crown sprouting and recruitment from the seedbank (Keeley, Bond, et al., 2011). While increased fire intervals can prevent reproduction of certain non-sprouting native California plant communities like chaparral (Jacobsen et al., 2004), CSS shrub species have higher crown sprouting success at younger ages (Keeley, 2006) and it remains unclear how more fire events will affect CSS community resilience. Herbivory can also limit post-fire resprout growth which may have implications for their stand structure (Jacobsen et al., 2004; Ramirez et al., 2012). Moreover, non-sprouting shrub species are dependent on germination from the seedbank, but increased fire frequency can prevent shrubs from reaching maturity for seed dispersal. Assessing the resilience of restored CSS sites adjacent to intact areas contributes to adaptive management that can expand intact native habitat and support obligate species, including birds that can further increase native plant dispersal (Bowler, 2000).

Several studies suggest that one of the greatest impacts of invasive plants on California CSS ecosystems is changing fire regimes (Lambert et al., 2010) that then provide invasive annuals a competitive advantage (Fleming et al., 2009; Haidinger & Keeley, 1993; Keeley et al., 2011; Talluto & Suding, 2008). Invasive species can out-compete native shrub seedlings for vital resources like water, due to early germination and rapid growth rates (Kimball, Principe, et al., 2018). Native shrub seedlings also must face increasingly longer dry seasons in California (Ullrich et al., 2018) that make these young plants more susceptible to water deficits due to their shallow roots (Jacobsen et al., 2018). Many of the factors that pose a threat to the establishment of native shrub seedlings extend to native grasslands communities as well.

The native perennial bunchgrass, *S. pulchra*, is a drought-adapted species that recovers quickly with bare ground after fire (Bartolome & Gemmill, 1981). However, its resilience and recovery can be severely compromised when these disturbances are prolonged and occur in tandem (Larios et al., 2013; Schellenberg et al., 2020). Since invasive annual grasses and forbs begin their growing season earlier, they can quickly recolonize disturbed sites post-fire, resulting in vegetation type conversion to invasive annual grassland, more ignitable fuel for wildfire, and more frequent fires (Conlisk et al., 2016).

A plant's functional traits can also provide information on a plant's ability to recover post-fire. Functional traits are morpho-physio-phenological traits that impact the fitness of individual species throughout their growth, reproduction, and survival (Violle et al., 2007). Research on functional traits indicates how species relate and respond to their environment to address ecological questions (McGill et al., 2006). The availability of resources following a fire event combined with favorable functional traits can allow faster invasive recruitment. Determining traits that provide successful outcomes for natives can facilitate management and seed mix strategies that support post-fire resiliency.

Southern California is expected to experience more extreme weather events including severe droughts and increased fire intensity and frequency in coming years (Williams et al., 2019), making adaptive management research on this subject more vital than ever. Our study and analyses of CSS, grasslands, and functional traits will help to fill the knowledge gap and provide insights for practitioners to accomplish successful CSS and grassland restoration under anthropogenic environmental change.

3. Methods

3.1. Study Area

Located in Limestone Canyon in Orange County, CA, Bee Flat Canyon is a 293-acre subwatershed that was once part of the historic Irvine Ranch. The restoration site is situated over 84 acres of heavily degraded agricultural rangeland and native habitat, both of which have been invaded by exotic grasses and forbs. A total of 79 polygons were targeted for restoration, specifically in areas with less than 50% native cover (Irvine Ranch Conservancy, 2012).

3.2. Data Analyses and Availability

For a complete list of our data and sources, see Table 3. All data analyses were conducted using R software (R Core Team, 2020) and data manipulation and visualization was done using tidyverse (Wickham et al., 2019). Datasets and reproducible analyses for this project are available on the Dryad data repository at https://doi.org/10.7280/D1D40D.

3.3. CSS Shrub Recovery

The CSS shrub recovery study used the initial IRC restoration design to determine sampling areas in burned parts of Bee Flat Canyon. Data were collected in established polygons of restored treatment and unrestored intact control and unrestored degraded areas (Figure 3). We sampled 12 replicates using 1 x 5 m quadrats. All sampling was conducted with a randomized method employing a blind toss of PVC pipe that was used to then designate a specific corner of the plot. The data collection occurred in November and December 2021 and included measurement of all species of shrub crown sprouts, unburned living shrubs, shrub recruitment, shrub size, and total number of dead shrubs (Figure 2). We measured the height, the widest width, and a second width perpendicular to the first width of each shrub crown sprout or each recruited seedling. We calculated the canopy volume of shrubs using the ellipsoid volume formula [Height * π (Width1/2 * Width2/2)] (Thorne et al., 2002).

The data were separated by shrub growth forms (crown sprout and seedling recruitment) because we were interested in separately assessing the ability of shrubs to crown-sprout versus establishment from seed following fire. We performed mixed models ANOVAs with the aov function (R Core Team, 2020) on the total number of all shrub seedlings and crown sprouts, regardless of species, with restoration status (intact or restored) as the independent variable and polygon as a random factor. We also ran separate mixed ANOVAs on the most abundant species found in both intact and restored treatments (*Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia mellifera)* to determine whether there was a species specific response to fire.

We performed an ANOVA using the aov and lmer functions (R package *lme4*, Bates et al., 2015) with shrub seedling and crown sprout shrub size (log transformed volume) differences across treatments (intact and restored) . We calculated the standard error and visualized the total shrub size for living crown sprouts and recruitment by treatment. Where residuals and QQ Plot results did not confirm normal distribution, we log-transformed the data prior to analyses (R package *rstatix,* Kassambara, 2021).

We calculated survivorship for post-fire shrub seedlings, post-fire crown-sprouting shrubs, and post-drought (from the first to the second year after fire) crown-sprouting shrubs. This analysis was performed with a logistic regression model using the function glmer with binomial data (alive or dead) using the R packages *lme4* and *lmerTest* (Kuznetsova et al., 2017) with restoration status (intact or restored) as a fixed factor and polygon as a random factor.

3.4. CSS Seedling Recruitment

For each restoration treatment (restored, intact, degraded), we collected point intercept and species presence/richness data within three different treatments (Figure 4) and used four replicates with 1 x 1 m gridded quadrats for a total of 12 plots and 36 replicates. Each quadrat contained 25 possible hits. Sampling locations were randomly selected by blind toss method within restored areas that CEB researchers had previously designated for 2021 analyses. Data were collected in April 2021 and March 2022, to capture recruitment during the first two spring seasons after the Silverado Fire of 2020.

A mixed model ANOVA using *nlme* package (Pinheiro et al., 2021) was conducted to assess differences in species abundance by functional groups across all treatments. Data were log transformed to improve normality. Functional groups included native and non-native forbs and grasses. To assess the degree of dissimilarity in community composition amongst sample plots, we conducted non-metric multidimensional scaling (NMDS) analysis using the *vegan* R package (Oksanen et al., 2022). We used Bray-Curtis distance measures on presence/absence data.

3.5. CSS Functional Traits

We utilized two different datasets for this analysis: functional trait data collected from shrubs and seedlings at the old IRC seed farm (Kimball, Vose, et al., 2018) and abundance data of CSS species collected before and after the fire in the Loma Ridge Global Change Experiment, located adjacent to Bee Flat Canyon (Figure 1). The Loma Ridge data we used was based on various manipulations of water and nitrogen in shrubland plant communities to understand their response to conditions under climate change. We determined how the cover of each species changed in response to wildfire. We analyzed the abundance of 10 different CSS and grassland species and their response to wildfire by comparing the average species abundance from the springs before and after the Silverado Fire. A fire response value was calculated as (cover in 2021 after fire – cover in 2020 before fire). We calculated z-scores on this dataset so that response values ranged from -1 to +1, with 0 values indicating no change. We also analyzed relationships between species composition and plant traits to determine whether traits influenced response to wildfire. The specific traits we analyzed were photosynthetic rate, relative growth rate, percent nitrogen, specific leaf area, and root system. Correlation matrices and linear regressions were analyzed to identify relationships between species response to wildfire and a given trait value using R package *GGally* (Schloerke et al., 2021). We used

ANCOVA to test for relationships between a plant's functional traits or the water and nitrogen treatments.

3.6. Grasslands Monitoring

The IRC established 57 permanent 50 m transects for full, partial, and passive restoration in CSS, grassland, and oak woodland for their habitat monitoring program that began in 2011. This analysis was based on the IRC monitoring data and focused on six 50 m grassland transects in restored polygons that were sampled before the Silverado Fire in 2015, 2017, 2019, and afterward in 2021 (Figure 5; Freese, 2021; Irvine Ranch Conservancy, 2021). We collected a second year of post-fire data on the six transects in March 2022 (Ta et al., 2022). Point-intercept data were collected at 1 m intervals along the transect including plant canopy height, tallest intercepting canopy species, all other intercepting species, and ground cover. Plant species were categorized by native status (native, non-native) and functional group (forb, grass). The native grass functional group in this dataset consisted primarily of *S. pulchra* with one observation each of *Elymus glaucus* and *Bromus carinatus*, and was therefore synonymous with *S. pulchra*. Absolute percent cover (percent cover) was calculated by dividing the total cover by 50 (transect points) and multiplying by 100. Percent cover data were log transformed for analysis. Two extreme outliers were detected but included in the analysis due to the small sample size of the dataset. Assumptions of normality were violated in four year-functional group samples using a Shapiro-Wilk's test. Normality was further tested with QQ plots for each sample and met.

We conducted a repeated measures ANOVA to assess if mean differences in absolute percent cover (log-transformed cover) were a function of the interactions between functional group, native status, and year with an error term of transect per year to account for natural variation between transects. Assumptions of sphericity were tested with the anova_test function from the *rstatix* package. Corrections were not applied, and the assumption of sphericity was met. We ran a multiple linear regression to assess whether total precipitation (cm) and mean monthly temperature (°C) during the growing season predict total percent cover using temperature and precipitation data at Bee Flat Canyon from 2014 - 2021 (PRISM Climate Group, 2022). We used log transformed precipitation data in the regression and defined the growing season for a given year as the period between October in the previous year through March of the given year (e.g., October 2021 to March 2022; Kimball et al., 2018). We visualized the changes in species composition over time in species space with an NMDS analysis using the *vegan* R package and Bray-Curtis distance measures (Faith et al., 1987; Kimball et al., 2018). Total cover of species observed in three or more samples was used to calculate the distance matrix. After the ordination was completed, we correlated abiotic variables with ordination space. Precipitation and temperature in the growing season and total cover of *S. pulchra* and non-native grasses were represented with linear vectors on the ordination.

3.7. Seed Mix Assessment

We also created species lists with the original CSS and grassland restoration seed mixes and the observations of each species from the 2021 shrub recovery study, the spring 2022 seedling recruitment study, and the spring 2022 grassland monitoring study. We compared species observed in restored sites to species from the original seed mix to determine the representation of the seed mix (Table 2).

4. Results

4.1. CSS Shrub Recovery

We found a total of eleven native shrub species across restored, intact, and degraded treatments in our shrub crown sprout study (Table 2). Crown-sprouting shrubs were generally larger than individuals that were recruited from seed, and *Malosma laurina* was the largest of the crown sprouting species measured. Certain species, such as *M. laurina* and *Salvia apiana,* were only observed once in both intact and restored treatments (Figure 6). As expected, there was no increase of native species in degraded plots after the fire, so degraded treatments were removed from analyses.

Our results showed that there were more individual seedlings in intact sites compared to restored sites and more crown sprouts in the restored sites compared to intact sites (Figure 7). Our analysis of recruitment abundance including species (*Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia mellifera)* as a factor showed no significant difference between treatments (Table 4). Crown sprout and recruitment shrub size did not differ between intact and restored treatments (Table 4). The proportion of seedlings that survived the fire did not vary depending on restoration status (z = -0.189, p = 0.85, n = 194) nor did the proportion of crown sprout vary depending on restoration status (z = 1.749, p = 0.08, n = 528). The proportion of seedlings that survived to the fall of the first year after fire did not vary depending on restoration status (z = -0.406, p = 0.685, n = 215). Additionally, the average values of seedling survivorship after the fire and crown sprouts after the fall of the first year were ~90% (Figure 8).

4.2. CSS Seedling Recruitment

Differences in percent cover of species recruitment cover varied across the three levels of treatment (degraded, restored, intact; Figure 9). Using a mixed model ANOVA for the different functional groups (native and non-native forbs and grasses), we found no significant difference of native forbs between restored and intact sites, with both treatments having relatively similar percent cover (Table 5). Degraded sites had fewer native forbs compared to intact and restored sites, and greater numbers of non-native forbs than restored and intact sites. Native grasses succeeded better in intact sites compared to restored sites, with restored sites having slightly less observations of native grasses than degraded. Non-native grasses differed across all treatments with more percent cover in degraded and restored sites compared to intact sites.

Species composition differences showed there was no significant relationship between year of measurement and ordination space ($p = 0.751$); however, there was a significant effect of restoration status in ordination space ($p = .0001$, Figure 10). Degraded sites had a non-native species dominated plant palette, with slight overlap into intact areas. There was no similarity of species composition between restored and degraded sites. Overall, there were similarities of species composition between restored and intact sites (Table 6); however, restored sites had more native species that were originally seeded in the restoration palette, while the intact sites had native species assumed to originate from the seed bank.

4.3. CSS Functional Traits

Of the 10 species we analyzed, all had a negative response to wildfire, suggesting that there was a decline in species cover after the Silverado Fire, except for *B. nigra* and *D.*

fasciculata, which had a positive response to wildfire with a value of 0.400 and 0.266 respectfully. The species *E. fasciculatum* and *Malacothrix saxatilis* both had a wildfire response value of 0. We ran the correlation matrix to include perennials and annuals together, as well as separately. In all scenarios there was no correlation observed (Figures 11, 12, 13, 14). There also were not any significant correlations between species response to fire and functional trait values upon running the linear regressions (Table 7). Lastly, multiple ANCOVAs were run to see if there were any significant relationships between a plant's functional traits and the water and nitrogen treatments. There were no significant relationships observed.

4.4. Grassland Monitoring

The grassland community significantly changed over time with overall increases in native and non-native forbs and non-native grasses, and a decrease in *S. pulchra*. Forbs generally had lower mean percent cover compared to grasses, with non-native grasses having the highest cover across all samples in 2022 (Figure 15). The repeated measures ANOVA showed that functional group, year, native status-by-year interaction, functional group-by-year interaction, and native status-by-functional group-by-year interaction had statistically significant effects on percent cover. Differences by native status alone and the native status-by-functional group interaction were not statistically significant (Table 8). Post-hoc pairwise t-tests were conducted on each native status-functional group between years and year-functional group between native status using the Bonferroni *p* adjustment method. Percent cover of native forbs and non-native grasses increased significantly post-fire from 2021 to 2022, non-native forbs were significantly higher in 2022 compared to 2017, and *S. pulchra* was significantly lower in 2021 and 2022 post-fire compared to 2019 before the fire (Table 9). Percent cover of non-native grasses (M = 90.33, SD = 50.82) was significantly higher than *S. pulchra* (M = 15, SD = 11.01) in 2022 (t_5 = -3.00, p_{adj} = .03). All other comparisons between native status by year and functional group were not significant.

Temperature and precipitation in the growing season are shown in Figure 16. The multiple linear regression showed that percent cover of native forbs and grasses were weakly and positively correlated with temperature and precipitation, while non-native forbs were moderately negatively correlated and non-native grasses weakly negatively correlated. However, these relationships were not statistically significant (Table 10). The NMDS analysis indicated that species composition was significantly different in 2022 with a higher cover of non-native grasses compared to previous years (Figure 17). Axis 1 of the ordination was negatively correlated with non-native grass cover and positively correlated with precipitation (n.s.) and *S. pulchra* cover. Axis 2 positively correlated with both native and non-native forbs and was negatively correlated with temperature (Table 11). The most significant species correlations were *B. nigra* and *Bromus spp.* which were positively correlated with Axis 2, and *S. pulchra* which was positively correlated with Axis 1 (Table 12).

5. Discussion

5.1. CSS Post-fire Resilience

Our study provided a unique opportunity to assess a ten-year restoration situated in a canyon that had entirely burned, allowing us to compare post-fire resiliency in replicate across a large mosaic of restored and unrestored areas. As we measured, we found that CSS shrubs were resilient although composition differed from intact areas because of the original restoration seed mix. Native grasslands were negatively impacted, with the dominant native *S. pulchra* declining post-fire and non-native annual grasses recovering quickly.

5.1.1. Shrub Recovery

While some post-fire resiliency studies of intact CSS project community composition convergence (Conlisk et al., 2016; Keeley, 2006) and others provide meta analyses on available strategies for initiating post-fire restorations (Scheper et al., 2021), there remains a critical lack of studies on post-fire resilience in restorations of CSS communities and few for shrubland restorations in general. One study on Mediterranean shrubland post-fire resiliency in restored sites suggested that not until 15-21 years of succession was the seedbank sufficient to produce equivalent post-fire resiliency to that of intact sites (Meira-Neto et al., 2011). Crown sprouting invasive shrubs like *Cytisus scoparius* (Scotch broom) disrupt post-fire resiliency in neighboring CSS communities in the Santa Monica Mountains (Bossard & Rejmanek, 1994), but our study system does not have invasive species in the shrub functional group. Overall, the results of our study suggest that crown sprouting native shrubs are able to grow just as well in intact sites as restored sites, implying that initial growth strategies will lead to future resiliency.

The moderately higher abundance of crown sprouts in restored treatments is more than likely due to the restoration strip seeding design that would inherently increase shrub abundance in those plots (Irvine Ranch Conservancy, 2012). The higher abundance of seedlings in intact sites could be due to a more substantial seed reserve (Cox & Allen, 2008) that built up in the absence of agricultural disruptions like tilling and overgrazing. Planted in 2011, the restored sites are younger with less mature seed banks, but with time they could equal intact seed bank reserves.

While longitudinal studies on post-fire resiliency of specific species (for instance, *A. californica*) have been conducted to determine management strategies and favorable environmental conditions for resilience (Thomson et al., 2021), few researchers have been able to look at CSS systems as a whole. Interestingly, there was no difference in recruitment abundance for the three most abundant species common to both intact and restored sites in our study (*A. californica*, *S. mellifera*, *E. fasciculatum*). There were abundant species commonly found in both intact and restored sites; Some species like Desert Wishbone Bush (*Mirabilis laevis*) and Laurel Sumac (*Malosma laurina*) were highly abundant in intact but not restored sites. California Bush Sunflower (*Encelia california*) was planted and present in restored, but not present in intact.

Pre- and post-fire drought conditions negatively affect post-fire resiliency of crown sprouting shrub species (Werner et al., 2022). While CSS species are adapted to fire and periodic drought, survivorship within restored sites was threatened by having drought immediately following the Silverado Fire. Despite these concerns, our analysis demonstrated no observable differences in post-fire/drought CS survivorship across treatments or post-fire recruitment across treatments. In fact, post-fire recruitment survivorship was fairly high in both intact and restored treatments (~90%, Figure 8). Post-fire CS survivorship was slightly higher in the intact treatment (~60 in intact, ~40% in restored), which may be because of higher variation in shrub age in the intact due to seedbank regeneration (Figure 8).

5.1.2. Seedling Recruitment

Non-native forbs and grasses were expected to have more seedling recruitment in degraded sites as compared to intact and restored sites due to the history of agricultural activities conducted by Irvine Ranch in the 1900s (Irvine Ranch Conservancy, 2012) and no remediation thereafter. Non-native invasive plants act as colonizers of disturbed sites and can readily take advantage of ecosystems which lack resiliency, driving compositional change (Chabrerie et al., 2008; Didham et al., 2005). In conjunction with drought, an inability of biotic resistance in degraded sites may explain the lack of native seedlings in these areas and higher average cover of non-native species seedlings.

Since this ecosystem had been anthropogenically disturbed by agriculture, it shifted the balance of the disturbance regimes that were in the historic range of variation, offsetting the delicate equilibrium of natural recovery processes. Areas that generally maintained resilience to different disturbances often return to their prior conditions following a disturbance event (Meyer et al., 2021), explaining the ability of intact sites to resist transition to degraded states. Consequently, the abundance of native forb and grass seedlings were expected to be slightly higher in intact sites due to the sites having natural occurrences in the seed bank and therefore, a resistance to invasibility. Native forbs did not have significant differences in species abundance in restored and intact sites, pointing to a successful restoration in these areas and furthermore, supporting the presence of a biotic resistance to invasion.

The presence of non-native species across all treatments might be explained by a subset of the “driver/passenger” models, originally proposed by MacDougall and Turkington (2005). A subset of the “driver” model, coined as the “back seat driver” model by Bauer (2012), suggests that underlying environmental conditions such as environmental change and dispersal limitation encourage the non-native invasive species initial establishment. This model incorporates a temporal component. Thus, recovery and establishment of native species seedlings is only possible with removal of both the non-native species and the disturbance over time (Bauer 2012), which in this case would be the altered fire regime occurring in shorter intervals. This supports our findings of lower numbers of non-native grasses in restored sites as compared to intact sites due to the invasive weed management in these areas.

Frequent fire has been documented to cause losses in a native seed bank (Cione et al., 2002) explaining the small overlap between degraded and intact sites species composition, suggesting some intact sites that are less resilient to altered fire regimes become more prone to non-native invasion. Restored sites had just as many natives as intact sites. However, there was a difference in native annual species composition between intact and restored plots, which can be attributed to the species included in the seed mix. Moreover, *Cirsium occidentale,* a native forb, was significantly related to ordination space, having observations in all treatments. Native perennials were more similar between the two sites, showing species such as Encelia californica being similar in species space between restored and intact areas, and negating previous observations of higher persistence of native annual seed banks having more persistency than perennial shrub seed banks (Keeley & Keeley, 1984).

5.1.3. Functional Traits

Our overall results suggest that functional traits do not play a role in a plant's ability to reestablish themselves post-fire. Though we did not see any significant correlations, of the 10 species we looked at only two species, *B. nigra* and *D. fasciculata*, had a positive response value to the Silverado Fire. While *D. fasciculata* is native to California and the CSS communities, *B. nigra* (commonly known as Black Mustard) is an invasive species. Although fire is a natural occurrence in California, fire has been known to create a positive feedback loop with increases in invasive species in several plant communities including CSS (Lambert et al., 2010). This could explain why we observed a positive fire response and increase in abundance of Black Mustard post-fire.

It is also important to note that the abundance data we used for analysis was collected only a few months after the Silverado Fire, possibly not allowing enough time for species to recover and reestablish. Past studies suggest that even one year post-fire, species richness and plant canopy cover were low and highly variable (Lentile et al., 2007). It would be interesting and beneficial to continue the study of functional traits and fire response again, now that more time has passed since the fire event to see if we get the same results.

5.2. Grassland Post-fire Resilience

Long-term ecological monitoring is essential in helping practitioners understand how restored communities respond to disturbance, whether that response indicates a successful restoration, and how to adjust future restoration strategies (Lindenmayer, 2020). Bee Flat Canyon has a decade of transect data from their monitoring program, however only a subset of established transects were sampled every year. Our grassland analyses were limited to a five-year dataset which may have influenced the patterns and statistical power of our findings.

Given that fire is used as a restoration tool to reduce non-native annual grasses and create open space for native perennial bunch grasses to establish, we expected that *S. pulchra* would be resilient to fire. Yet, we found that *S. pulchra* had declined and non-native grass quickly recovered to be the dominant grass type in the two years since the Silverado Fire. Potts et al. (2012) showed that drought and prescribed fire have a negative effect on non-native grasses which contrasted with our post-fire results, and suggests that increased fire severity in wildfire may affect native and non-native grass recovery differently. Additionally, seasonal timing of fire may be a key factor that explains our results. Natural fires in California generally occur during the dormant season for herbaceous plants in summer and fall (Keeley, 2001). However, prescribed fires are done in the spring to prevent non-native annuals from setting seed and allow perennials to recover by vegetative resprouting (Keeley, 1991; Keeley & Fotheringham, 2001). The Silverado Fire occurred in late fall, so remnant annual grasses were able to set seed in Bee Flat Canyon, resulting in higher cover of *Avena* and *Bromus spp.*and displacement of *S. pulchra* (Figure 18). Although *Bromus spp.* can be highly flammable and susceptible to mortality in fire, seed germination is often high, and established seedlings are better at competing for water resources and rapidly developing higher biomass than *S. pulchra* (Monaco et al., 2016; Wainwright et al., 2012). Consequently, competition for water has major implications on reestablishment and recovery during periods of drought. An assessment on the post-fire recovery of *S. pulchra* in southern California showed high mortality and low resilience during drought and after a moderately severe fire, with drought likely having a greater effect on fire response than the type or severity of fire (Schellenberg et al., 2020).

When drought is factored in post-fire, the discrepancy in native/non-native response we observed in grasses falls in line with other case studies and suggests competition as a key factor in *S. pulchra* resilience. An analysis of long-term monitoring data in Orange County, California, following the 2007 Santiago Fire and extended drought from 2011 to 2016 showed a high cover of non-native annual grasses and a decline in *S. pulchra* over time (Kimball et al., 2018). These results reflect our study observations and indicate a strong effect of competition on *S. pulchra* resilience. Larios et al. (2013) also looked at grassland recovery after drought and the 2007

Santiago fire and found that non-native grasses (*Avena fatua*, *Bromus diandrus*, and *Festuca perenne*) recovered quickly while *S. pulchra* did not recover where it once dominated. Their study highlighted the role of species dominance before disturbance and propagule strategies which influence the composition of residual species that survive. In our case, *S. pulchra* had higher cover in the transects before the fire and also failed to recover, possibly due to differences in seed dispersal and germination success. Larios et al. (2013) also compared the seed rain and found significantly higher production in non-natives, making a dense, rapid spring growth of non-natives more likely. *S. pulchra* germinates slowly and most readily on bare ground except in extreme drought (Bartolome & Gemmill, 1981). This also supports the decline we saw in *S. pulchra* as 2021 was a drought year with approximately 15 cm of total rainfall in the growing season (Figure 16).

IRC management observed that annual non-native grasses outcompeted native perennial grasses during wet years in 2017 and 2019 and predicted that *S. pulchra* would be more abundant in dry years due to reduced competition with non-native grasses. Contrary to the prediction, percent cover of *S. pulchra* was higher than non-native grasses in both wet years though not statistically significant. Competition may have had less impact on *S. pulchra* cover these years because more water resources were available overall. Mature native grasses can outperform non-native grasses during drought (Hamilton et al., 1999) due to deeper roots that can better access below ground water resources (Koteen et al., 2011). For our dry year observations, we found that *S. pulchra* only had higher cover than non-native grasses in the pre-fire year in 2015 and lower cover in the post-fire years in 2021 and 2022, but these differences were not statistically significant.

5.3. Management Recommendations

5.3.1. Post-fire Monitoring

For the IRC, we suggest continuing the annual monitoring of CSS seedling recruitment in spring to assess seedbank reproduction rates and only surveying crown sprout shrub recovery subsequent to another fire event in the future. Based on our observed crown sprout and recruitment cover and survivorship, we suggest that managers consider diversifying their seed mix. Further functional trait analysis and long term monitoring of the introduced species would also be necessary to ensure an appropriate and effective seed mix in the long-term. To improve restoration success of native grasslands, we recommend the IRC continue to monitor the six transects in this study. Additional years of data will help characterize the recovery trend of *S. pulchra* and help reveal the relationship between temperature, precipitation and cover of grassland functional groups.

5.3.2. Seed Mix Assessment

In our CSS shrub recovery and recruitment studies, we observed 12 out of the 17 species listed in the CSS seed mix. In the grassland monitoring study, we observed seven out of the 21 species listed in the grassland seed mix. Based on our observations, we curated a list of candidate species that have demonstrated post-fire/drought resilience, were not in listed in the original seed mixes, and may be considered as additions to the seed mixes for future restoration: 5 CSS species found in restored sites, 16 CSS species that were found in intact sites, and 8 grassland species observed in the restored grassland monitoring transects (Table 2). However, the availability of any of the suggested species is dependent on seed source, cost, and inventory. Further investigation into adjusting the restoration seed mixes will require an abundance assessment of the candidate species, understanding their phenology and germination characteristics, and conducting a feasibility analysis for sourcing and storing seed.

5.3.3. Invasive Species Management

In the fire-prone CSS and native grassland habitats, we expect shortened fire frequency intervals could drive non-native invasion (Keeley & Brennan, 2012). These disturbances can put both CSS and native grasslands on a path to type conversion to non-native grasses and forbs which generate higher amounts of fine fuel and lower fuel moisture. Disturbances also lengthen the wildfire season and increase fire frequency, thus creating fire feedbacks (Davies & Nafus, 2013; Keeley & Brennan, 2012)**.** Post-fire data from the Loma Ridge Global Change experiment show an increase in invasive *B. nigra*, supporting evidence that invasive species tend to thrive post-fire.

In one study aimed at creating fire protection frameworks for sagebrush systems across five national parks impacted by more frequent fires, recommendations were made for a resiliency-based adaptive management approach, including pre-fire protection and post-fire triage classification and restoration strategies (Rodhouse et al., 2021). For Bee Flat, a plan for post-fire invasive plant control and removal could decrease invasive abundance and allow native species to recover thus reducing the possibility of fire feedbacks (Monaco et al., 2016) For grasslands, this plan should focus on limiting the reestablishment of non-native grasses and supplementing the native grass seed bank to improve diversity and potential germination of *S. pulchra*. Success of weed management with post-fire seeding varies due to a limited window of opportunity and depends on sufficient germination which may require additional years of seeding (Pyke et al., 2013).

5.3.4. Outreach and Education

Lastly, we recommend that the IRC continue their community outreach and education program through the high school fire ecology internship program. This program, in partnership with the Crystal Cove Conservancy, provides high school students with invaluable lessons in land stewardship, the scientific method, research methodology, and hands-on experience that can prepare them for future endeavors in the field of restoration.

6. Conclusion

In the coming years, California will continue to see an increase in drought and fire frequency and intensity. This makes adaptive management research essential for restoring resilient at-risk ecological communities such as CSS and grasslands. In order to continue restoration of habitats, proper steps must be taken. In the case of Bee Flat Canyon and the IRC, there are some expected overlaps and differences in the results of our studies as it applies to management.

Looked at together, our crown sprout, recruitment and trait findings demonstrated that CSS restoration remains successful following wildfire and drought. Despite maturity differences between shrub communities across intact and restored treatments, restored areas maintained relatively robust post-fire crown sprout survivorship. Additionally, native forb seedling recruitment was similar between intact and restored sites, pointing to a resilience in restored sites. Lower numbers of non-native grass seedlings in restored sites compared to intact sites, as well as no overlap of species composition between degraded and restored sites, implies that weed management and invasive removal was successful in these areas. Moreover, although we did not see any correlations between plant traits and fire response, we can still draw important conclusions to inform management. One such conclusion being that an invasive species was one of the two species that had a positive fire response value, suggesting the need for an adaptive post-fire management plan to combat the establishment of non-native invasives as necessary.

The monitoring data in grassland communities showed that *S. pulchra* was on a positive trend and was the dominant grass type before the Silverado Fire, indicating a successful restoration of native perennial grassland at Bee Flat Canyon. However, many biotic and abiotic factors influence the post-fire response of *S. pulchra*. Timing and severity of fire distinguish the benefit of prescribed burns from the negative effect we saw from wildfire. While we found no significant relationship between temperature and precipitation and percent cover, these abiotic factors influence the physiological responses that drive competition between native perennial and non-native annual grasses. We found that restored *S. pulchra* had low post-fire resilience and recovery compared to non-native grasses and will therefore require fire-responsive management action to maintain the desired level of restoration. This is challenging given the number of factors at play, which highlights the need for sustained long-term monitoring and adaptive management of grasslands.

We conclude that the IRC restoration plan to establish healthy plant communities in CSS and grasslands was successful, but only resulted in post-fire resiliency for native shrubs and forbs. With each fire event, monitoring the post-fire responses of both resilient and non-resilient functional groups in restoration results in valuable information to guide land managers. Such studies can provide insight for adapting seeding strategies for changing environmental conditions and developing post-fire management plans that effectively combat invasive species, prevent fire feedback loops, and assist native plant reestablishment.

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Tables

Table 1. Goals and objectives of the Bee Flat Canyon Post-Fire Resilience Project.

Goal 1:	*Assess the resilience of restored CSS post-fire in Bee Flat Canyon*	
	Objective 1:	Survey and analyze crown sprouting in restored, degraded, and intact CSS sites
	Objective 2:	Survey and analyze seedling recruitment in restored, degraded, and intact CSS sites
Goal 2:	*Relate CSS resilience to functional traits of native and non-native plants*	
	Objective 1:	Assess native and non-native species composition at Loma Ridge post-fire
	Objective 2:	Relate functional trait data from the old IRC Seed Farm to CSS species response to wildfire
Goal 3:	*Assess the resilience of restored grassland relative to environmental changes in Bee Flat Canyon*	
	Objective 1:	Survey vegetation cover on six grassland monitoring transects
	Objective 2:	Assess changes in functional group cover over time with a focus on *S. pulchra* as the native grass
	Objective 3:	Assess relationships between grassland cover and species composition over time relative to temperature, precipitation, and fire
Goal 4:	*Engage in community outreach on IRC restoration at Bee Flat Canyon*	
	Objective 1:	Present our final project at an IRC Research Symposium
	Objective 2:	Mentor students in the IRC/Crystal Cove fire ecology high school intern program through restoration field work and data analysis

Table 2. List of species in the IRC CSS and grassland (GL) restoration seed mixes and observed species in the 2021 CSS shrub recovery, 2022 CSS seedling recruitment, and 2022 grassland transect data. The letters indicate which type of treatment polygon the species was observed in (R - Restored, I - Intact, D - Degraded) and only conveys presence/absence. Species are sorted by functional group, native status, and alphabetical order. The Rs in the seed mix columns indicate that species was seeded in a restored site for that plant community. Six-letter species codes mentioned in this report can be identified in this list by the first three letters of the genus and first three letters of the species in the scientific name. **[Bold *]** denotes species found in restored CS sites but not original seed mix. **[Bold +]** denotes species found in intact CS sites but not original seed mix. **[Bold ^]** denotes species found in restored grassland sites but not original seed mix.

Native Status	Funct. Group	Scientific Name	CSS Seed Mix	CSS Shrub Recovery	CSS Seed. Recruit.	GL Seed Mix	GL Transects
Native	Forb	*Acmispon glaber*	R	I	I	R	R
Native	Forb	*Acmispon strigosus*				R	
Native	Forb	*Ambrosia psilostachya*			D		
Native	Forb	***Amsinckia menziesii var. Intermedia ^***			D		R
Native	Forb	*Calandrinia ciliata*			ID		
Native	Forb	***Calochortus catalinae +***			I		
Native	Forb	***Calystegia macrostegia + ^***		I	I		R
Native	Forb	***Castilleja foliolosa +***		I			
Native	Forb	*Chaenactis artemisiifolia*				R	
Native	Forb	***Chaenactis species ****			R		
Native	Forb	***Cirsium occidentale ****			RID	R	
Native	Forb	***Clarkia purpurea +***			I	R	
Native	Forb	*Cryptantha intermedia*	R			R	
Native	Forb	*Deinandra fasciculata*	R	I	RID	R	R
Native	Forb	*Dichelostemma capitatum*			ID		
Native	Forb	***Emmenanthe penduliflora ^***					R
Native	Forb	***Epilobium canum +***			I		
Native	Forb	***Eriogonum elongatum +***			I		
Native	Forb	*Eschscholzia californica*	R		RI	R	R
Native	Forb	*Eucrypta chrysanthemifolia*	R		I		
Native	Forb	***Galium aparine +***			I		
Native	Forb	***Galium species +***			I		
Native	Forb	*Grindelia camporum*			D	R	R
Native	Forb	***Lupinus bicolor +***			I		
Native	Forb	*Lupinus microcarpus*				R	
Native	Forb	*Lupinus succulentus*	R		RI	R	R
Native	Forb	***Malacothrix saxatilis ^***	R		RI		R
Native	Forb	***Microseris lindleyi ****			R		
Native	Forb	*Mirabilis laevis*	R	RI	R	R	
Native	Forb	*Phacelia cicutaria*				R	R
Native	Forb	*Phacelia parryi*				R	
Native	Forb	*Plantago erecta*	R				
Native	Forb	*Salvia columbariae*	R		R	R	
Native	Forb	***Sanicula arguta +***			I		

Native Status	Funct. Group	Scientific Name	CSS Seed Mix	CSS Shrub Recovery	CSS Seed. Recruit.	GL Seed Mix	GL Transects
Native	Forb	***Solidago velutina ssp. Californica +***			I		
Native	Forb	***Stachys species ^***					R
Native	Forb	***Uropappus lindleyi ^***					R
Non-native	Forb	*Brassica nigra*			RID		R
Non-native	Forb	*Centaurea melitensis*			R		R
Non-native	Forb	*Erodium cicutarium*			RID		R
Non-native	Forb	*Hirschfeldia incana*			RID		R
Non-native	Forb	*Lactuca serriola*			RD		
Non-native	Forb	*Malva parviflora*			D		R
Non-native	Forb	*Medicago polymorpha*			RID		R
Non-native	Forb	*Medicago species*			RI		
Non-native	Forb	*Senecio vulgaris*			RI		
Non-native	Forb	*Sonchus asper*			I		
Non-native	Forb	*Sonchus oleraceus*			RD		
Native	Grass	***Bromus carinatus ^***					R
Native	Grass	*Elymus condensatus*	R		I		
Native	Grass	***Melica imperfecta +***			I		
Native	Grass	*Stipa pulchra*	R		RD		R
Non-native	Grass	*Avena barbata*			D		
Non-native	Grass	*Avena fatua*			D		R
Non-native	Grass	*Avena species*			RID		R
Non-native	Grass	*Bromus diandrus*			RID		R
Non-native	Grass	*Bromus hordeaceus*			I		R
Non-native	Grass	*Bromus madritensis*			RI		R
Non-native	Grass	*Bromus species*			RD		R
Non-native	Grass	*Festuca myuros*			RD		R
Non-native	Grass	*Festuca perennis*			ID		R
Non-native	Grass	*Hordeum murinum*					R
Native	Shrub	*Artemisia californica*	R	RID	RI	R	R
Native	Shrub	*Encelia californica*	R	R	R	R	
Native	Shrub	***Ericameria palmeri * ^***			RI		R
Native	Shrub	*Eriogonum fasciculatum*	R	RI	I	R	
Native	Shrub	***Hesperoyucca whipplei +***		I			
Native	Shrub	***Heteromeles arbutifolia +***		I			
Native	Shrub	*Isocoma menziesii*				R	
Native	Shrub	***Malacothamnus fasciculatus +***		I			
Native	Shrub	***Malosma laurina * +***		RI			
Native	Shrub	*Salvia apiana*	R	RI		R	
Native	Shrub	*Salvia mellifera*	R	RI		R	

Table 3. Datasets for the Bee Flat Canyon Post-Fire Resilience Project.

Study	Data	Status	Source
CSS	Crown Spouting Shrubs	Collected (Nov/Dec 2021)	Capstone Team
	Maps of Bee Flat Canyon Restoration Polygons	Acquired	Priscilla Ta Robert Freese
Recruit	2021 Post-Fire Restoration Point-Intercept	Acquired	Priscilla Ta
	2021 Post-Fire Restoration Species List	Acquired	Priscilla Ta
	2022 Post-Fire Restoration Point-Intercept	Collected (Mar 2022)	Capstone Team Collaboratory
	2022 Post-Fire Restoration Species List	Collected (Mar 2022)	Capstone Team Collaboratory
Traits	IRC Seed Farm CSS Shrub Traits	Acquired	Sarah Kimball, Jennifer Funk, Travis Huxman, and Greg Vose
	Pre & Post-fire CSS Loma Ridge Global Change	Acquired	Sarah Kimball
Grassland	2011-2021 Bee Flat Grassland 50m Transects	Acquired	Robert Freese
	2022 Bee Flat Grassland 50m Transects	Collected (Mar 2022)	Capstone Team
	2014-2022 Bee Flat Canyon Temperature and Precipitation	Acquired	PRISM Climate Group
Misc.	Orange County Plant Species List	Acquired	Priscilla Ta
	Bee Flat Species Info	Acquired	Robert Freese
	Bee Flat Seed Mixes (Plant Palette)	Acquired	Robert Freese

Table 4. Results from the mixed-model ANOVAs on the effect of treatment (restored vs. intact) on different variables in the CSS shrub recovery study using polygon as a blocking factor. Asterisks (*) indicate statistical significance at p ≤ .05.

Dependent Variable	**Independent Variable**	**df**	**Sum sq**	**Mean sq**	**F**	**p**	
Recruitment Abundance	Treatment	1, 16	276.5	276.55	6.207	.024	*
Crown Sprout Abundance	Treatment	1, 17	144.8	144.79	5.551	.031	*
Per Species Abundance	Treatment	1, 13	1.1	1.07	0.041	.842	
Recruitment Shrub Size	Treatment	1, 16	6.5	6.49	0.795	.386	
Crown Sprout Shrub Size	Treatment	1, 16	7.1	7.14	3.680	.073	

Table 5. Results from the mixed-model ANOVAs on the effect of treatment (restored vs. intact) on the total cover of native and non-native forbs and grasses in the CSS seedling recruitment study. Asterisks (*) indicate statistical significance at p ≤ .05.

Functional Group	**Dependent Variable**	**Independent Variable**	**df**	**F**	**p**	
Native forbs	Total cover	Treatment	2, 65	3.41	.0391	*
Non-native forbs	Total cover	Treatment	2, 65	2.90	.0623	
Native grasses	Total cover	Treatment	2, 65	22.12	< .0001	*
Non-native grasses	Total cover	Treatment	2, 65	34.91	< .0001	*

Table 6. Pearson correlation coefficient values of CSS seedling recruitment species with each axis of ordination space. Values are represented by species vectors in Figure 10.

Species	**Axis 1**	**Axis 2**	**Axis 3**
ACMGLA	0.428	-0.298	0.052
AMBPSI	-0.182	-0.222	0.000
AMSMEN	-0.304	-0.156	-0.301
ANAVAR	0.249	0.023	0.022
ARTCAL	0.082	-0.013	0.054
AVEBAR	-0.328	-0.166	-0.059
AVEFAT	-0.436	-0.485	-0.043
AVESPP	-0.201	-0.041	-0.272
BRANIG	-0.276	0.461	0.143
BROCAT	-0.136	-0.125	0.092
BRODIA	-0.675	-0.382	0.142
BROHOR	0.191	-0.125	0.149
BROMAD	0.680	0.154	-0.165
BROSPP	-0.151	-0.265	-0.280
CALCAT	0.112	-0.121	0.151
CALCIL	0.097	-0.396	-0.205
CALMAC	0.417	-0.175	0.190
CAASPP	0.104	-0.036	-0.006
CAMEL	0.214	0.006	-0.254
CHAGLA	0.040	-0.030	-0.189

Species	**Axis 1**	**Axis 2**	**Axis 3**
CAASPP	0.122	0.128	-0.023
CIROC	-0.033	0.377	0.059
CLAPUR	0.293	-0.182	0.053
CRYINT	0.098	0.120	-0.191
DAUPUS	-0.081	-0.134	0.215
DELIAS	0.196	0.155	-0.786
DICCAP	0.246	-0.424	0.160
ELYCON	0.480	-0.076	0.315
EMMPEN	0.273	-0.215	0.199
ENACAL	0.000	0.449	-0.174
EPICAN	0.253	0.046	0.097
ERIELO	-0.019	0.016	0.198
ERIFAS	0.152	0.028	0.213
ERIPAL	0.141	0.108	0.254
EROCIC	0.366	-0.353	-0.192
EROMOS	-0.355	-0.117	0.033
EROSPP	0.040	-0.030	-0.189
ESCCAL	0.129	0.313	-0.003
EUCHRE	0.498	-0.409	0.131
FESMYU	-0.007	0.040	-0.151
FESPER	-0.112	-0.501	0.066
GALANG	0.258	-0.238	0.199
GALAPA	0.335	-0.278	0.001
GALSPP	0.132	0.056	0.140
GRICAM	-0.131	-0.072	-0.189
HIRINC	-0.015	-0.135	-0.310
HORMUR	0.009	0.044	0.115
ISOMEN	-0.163	-0.203	0.097
LASER	-0.126	-0.047	-0.237
LAMBIC	0.437	-0.404	-0.087
LUPUS	0.289	0.383	-0.063
MALFAS	0.357	-0.235	0.173
MALLAU	0.042	0.122	0.066
MALPAR	-0.150	-0.138	-0.018
MALSAX	0.067	0.435	0.442
MEDPOL	0.124	-0.221	-0.404
MEDSPP	0.216	0.168	-0.074
MELIMP	0.536	-0.420	0.281
MELINDA	0.212	-0.043	0.098

Species	Axis 1	Axis 2	Axis 3
MICLIN	0.042	-0.092	-0.055
MIRCAL	0.093	0.078	-0.133
MIRAGE	0.042	0.190	-0.064
PHACIC	-0.025	0.234	0.133
PHAPAR	0.074	0.174	0.373
RASCAL	0.064	0.037	0.099
SALAPI	0.081	0.118	0.131
SALCOL	0.248	0.317	-0.432
SALMEL	0.218	0.004	0.117
SANARG	0.153	-0.083	0.157
SENVOL	0.268	-0.093	-0.274
SOLVEL	0.229	-0.050	-0.015
SONASP	0.182	-0.016	0.003
SONOLE	0.121	0.031	-0.435
STAAJU	0.102	-0.114	-0.038
STAALB	0.170	-0.093	0.097
STIPUL	-0.115	-0.114	0.220
TIGRA	0.212	-0.043	0.098

Table 7. Results from the linear regressions run on plant functional traits and fire response values in the functional trait study.

Trait	R^2	Adj R^2	p
Photosynthetic Rate	0.373	0.248	0.1452
Relative Growth Rate	0.003	-0.122	0.8864
Specific Leaf Area	5.324e-08	-0.125	0.9995
Nitrogen	0.005	-0.161	0.8724

Table 8. Type III repeated measures ANOVA results for the effect of the native status, functional group, and year, and the two and three-way interactions on absolute percent cover (number of hits/number of transect points*100) of functional groups in the grassland monitoring study. Asterisks (*) indicate statistical significance at p ≤ .05.

Dependent Variable	Independent Variable	df	F	p	
Percent Cover	Native Status	1, 20	0.021	.885	
Percent Cover	Funct. Group	1, 20	34.309	9.92E-06	*
Percent Cover	Year	4, 80	10.602	6.07E-07	*
Percent Cover	Native Status x Funct. Group	1, 20	0.724	.405	
Percent Cover	Native Status x Year	4, 80	5.510	5.71E-04	*
Percent Cover	Funct. Group x Year	4, 80	13.762	1.39E-08	*
Percent Cover	Native Status x Funct. Group x Year	4, 80	3.388	.013	*

Table 9. Significant post-hoc pairwise t-test results for the repeated measures ANOVA on differences in total cover by native status and functional group between years in the grassland monitoring study. Asterisks indicate statistical significance with a Bonferroni multiple testing correction at p ≤ .05. Non-significant values were omitted from the table for brevity. Asterisks (*) indicate statistical significance at p ≤ .05.

Native Status	Funct. Group	Dependent Variable	Group1	Group2	n1	n2	statistic	df	p adj	
Native	Forb	Percent Cover	2021	2022	6	6	-5.10	5	.038	*
Non-native	Forb	Percent Cover	2017	2022	6	6	-5.80	5	.021	*
Non-native	Grass	Percent Cover	2021	2022	6	6	-5.23	5	.034	*
Native	Grass	Percent Cover	2019	2021	6	6	7.05	5	.009	**
Native	Grass	Percent Cover	2019	2022	6	6	8.59	5	.004	**

Table 10. Multiple linear regression results to test growing season mean monthly temperature and total precipitation as predictors of percent cover of different functional groups in the grassland monitoring study.

Dependent Variable	Adj R^2	df_{reg}	df_{res}	F	p
Native forb	0.049	2	2	1.103	.476
Non-native forb	-0.495	2	2	0.338	.747
Native grass	0.373	2	2	2.191	.313
Non-native grass	-0.224	2	2	0.634	.612

Table 11. Correlation of grassland environmental variables with ordination of species space. Asterisks indicate significance at p ≤ .05 (*), .01 (**), .001 (***).

Variable	Axis 1	Axis 2	r^2	p	
Precipitation	0.87	0.50	0.09	.2798	
Temperature	0.35	-0.94	0.28	.0109	*
Native forb cover	-0.21	0.98	0.38	.0022	**
Native grass cover	0.97	0.25	0.84	.0001	***
Non-native forb cover	-0.47	0.89	0.51	.0004	***
Non-native grass cover	-0.93	0.36	0.66	.0001	***

Table 12. Correlation of grassland species with each axis of ordination space. Asterisks indicate significance at p ≤ .05 (*), .01 (**), .001 (***).

Species	**Axis 1**	**Axis 2**	**r^2**	**p**	
ACMGLA	-0.57	-0.82	0.23	.029	*
AMSMEN	0.13	0.99	0.15	.088	
AVEFAT	-0.98	-0.18	0.32	.010	**
AVESPP	-0.82	-0.57	0.28	.014	*
BRADIS	0.96	0.28	0.16	.077	
BRANIG	-0.24	0.97	0.46	.001	***
BROCAR	-0.16	0.99	0.22	.040	*
BROCAT	0.98	0.20	0.32	.007	**
BRODIA	-0.96	0.30	0.30	.006	**
BROHOR	0.30	-0.95	0.08	.315	
BROMAD	-0.90	-0.44	0.22	.030	*
BROSPP	-0.47	0.88	0.65	.001	***
CENMEL	-0.93	0.37	0.26	.025	*
CLAPUR	0.15	0.99	0.01	.887	
DEIFAS	-0.18	0.98	0.18	.082	
EMMPEN	-0.23	0.97	0.03	.627	
EROCIC	-0.95	-0.32	0.36	.003	**
ESCCAL	-0.01	1.00	0.20	.059	
FESMYU	-0.47	0.88	0.27	.017	*
FESPER	-0.87	-0.50	0.17	.084	
GRICAM	-0.42	0.91	0.01	.817	
HORMUR	-0.02	1.00	0.10	.217	
LUPMIC	0.92	0.39	0.02	.730	
LUPSUC	-0.62	0.78	0.35	.002	**
MALSAX	-0.28	0.96	0.08	.304	
MEDPOL	0.45	-0.89	0.00	.999	
PHACIC	-0.20	0.98	0.08	.296	
SONOLE	0.38	-0.92	0.02	.738	
STIPUL	0.97	0.23	0.84	.001	***

Figures

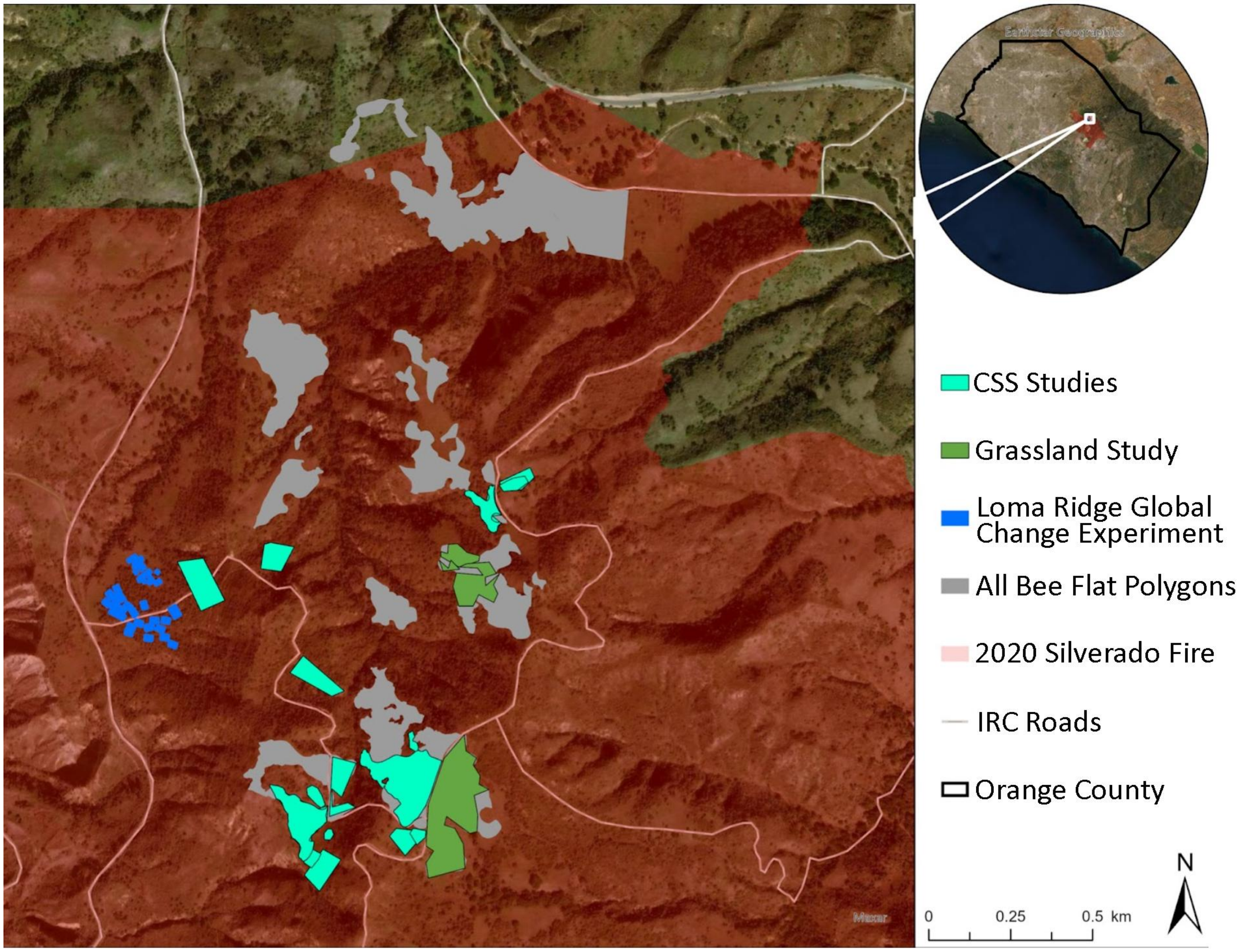

Figure 1. Full site map of Bee Flat Canyon showing the extent of all restoration polygons and locations where data were collected for the post-fire resilience studies. CSS studies include the fall 2021 crown-sprout and shrub recruitment survey in shrub restored strips and the spring 2021/2022 seedling recruitment survey in forb restored areas. Vegetation cover data were collected on established long-term monitoring transects in the grassland study. Physiological trait data were correlated with pre- and post-fire CSS species abundance data from the Loma Ridge Global Change experiment.

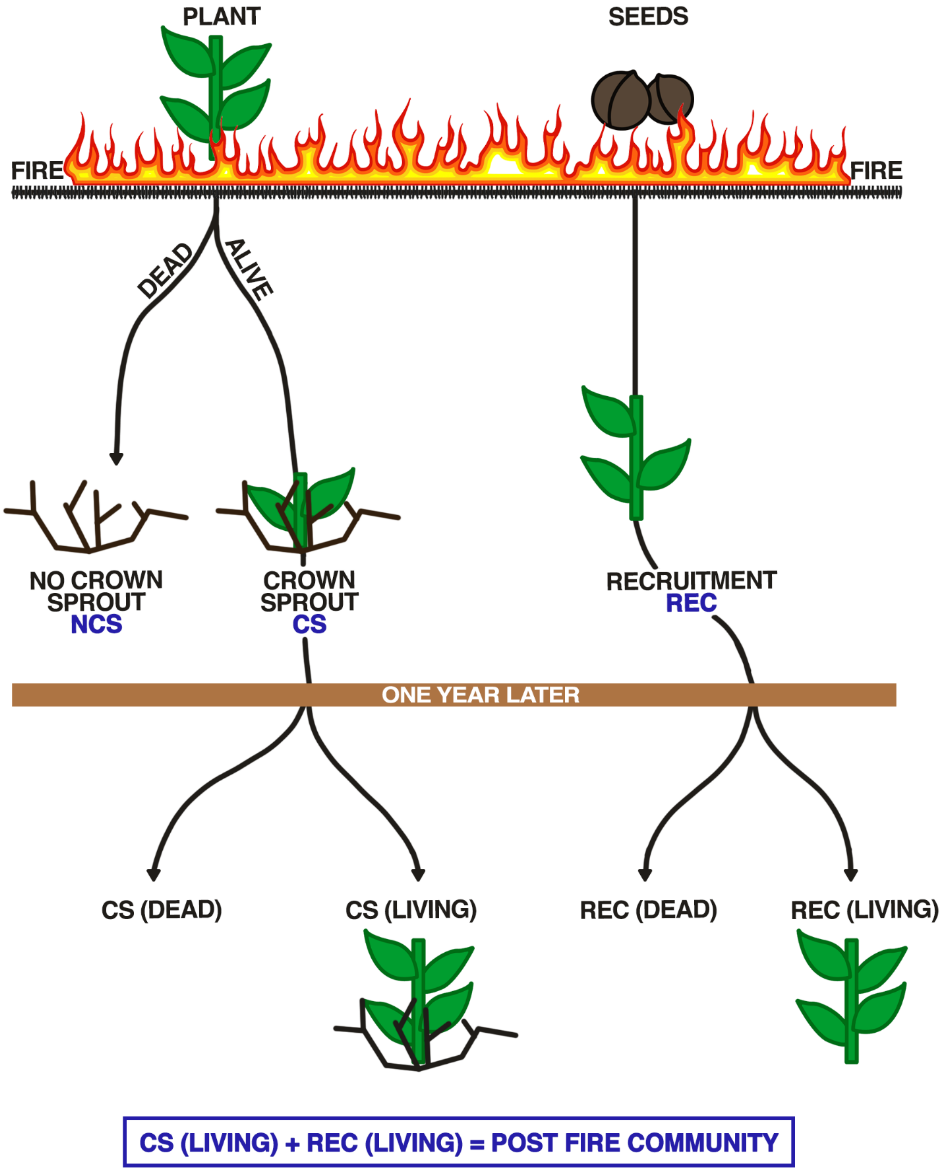

Figure 2. Diagram of the crown sprout and seedling recruitment growth types of shrubs at Bee Flat Canyon after the Silverado Fire and drought one year later. After fire, established shrubs will either die or survive with a crown sprout and seeds may germinate into a recruitment seedling. After one year of drought, the crown sprouted shrubs and recruited seedlings will either die or survive.

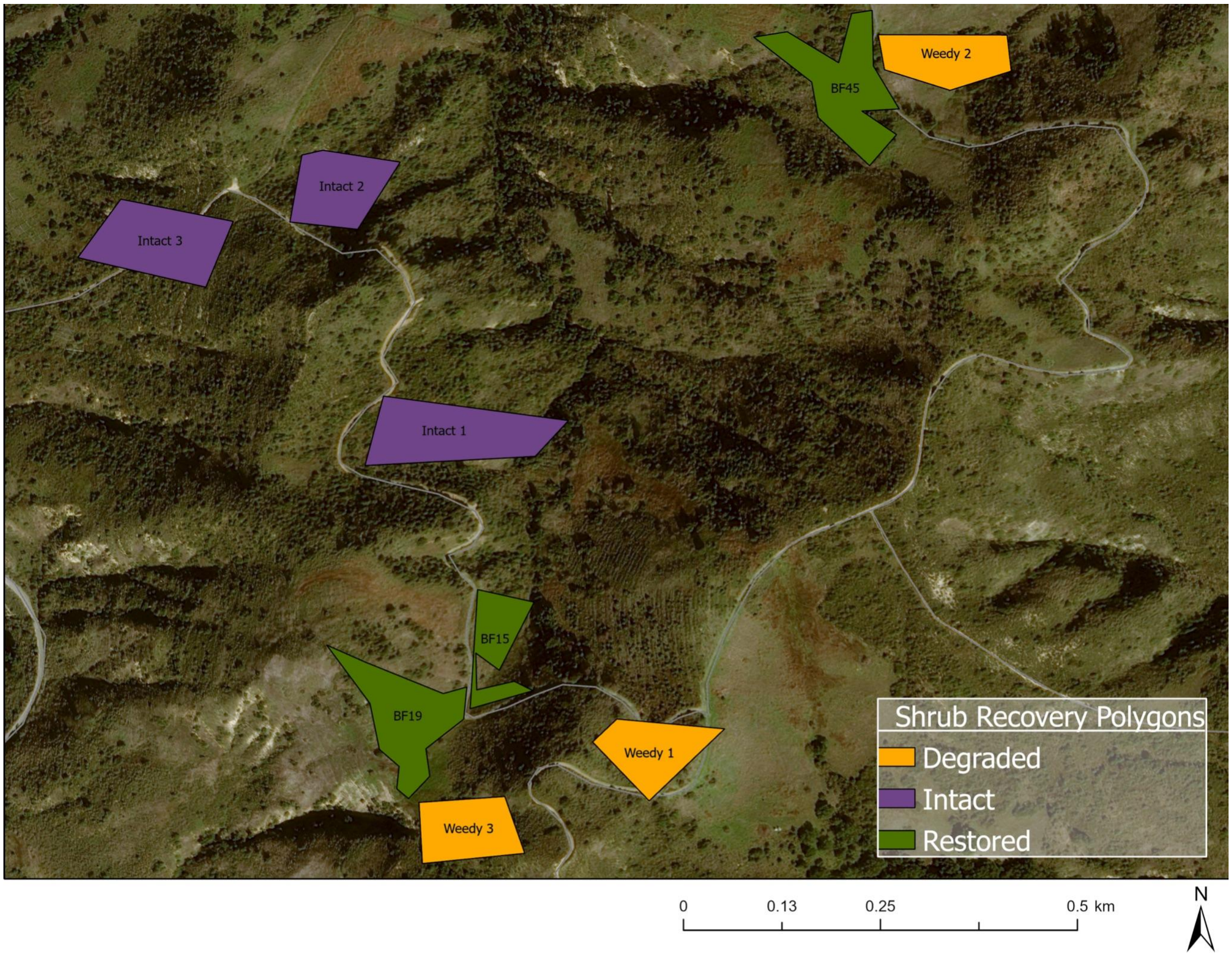

Figure 3. Map of the shrub recovery study sites in Bee Flat Canyon. Crown sprout and seedling recruitment data were collected from fully restored polygons (BF45, BF15 and BF19) and adjacent degraded and intact areas.

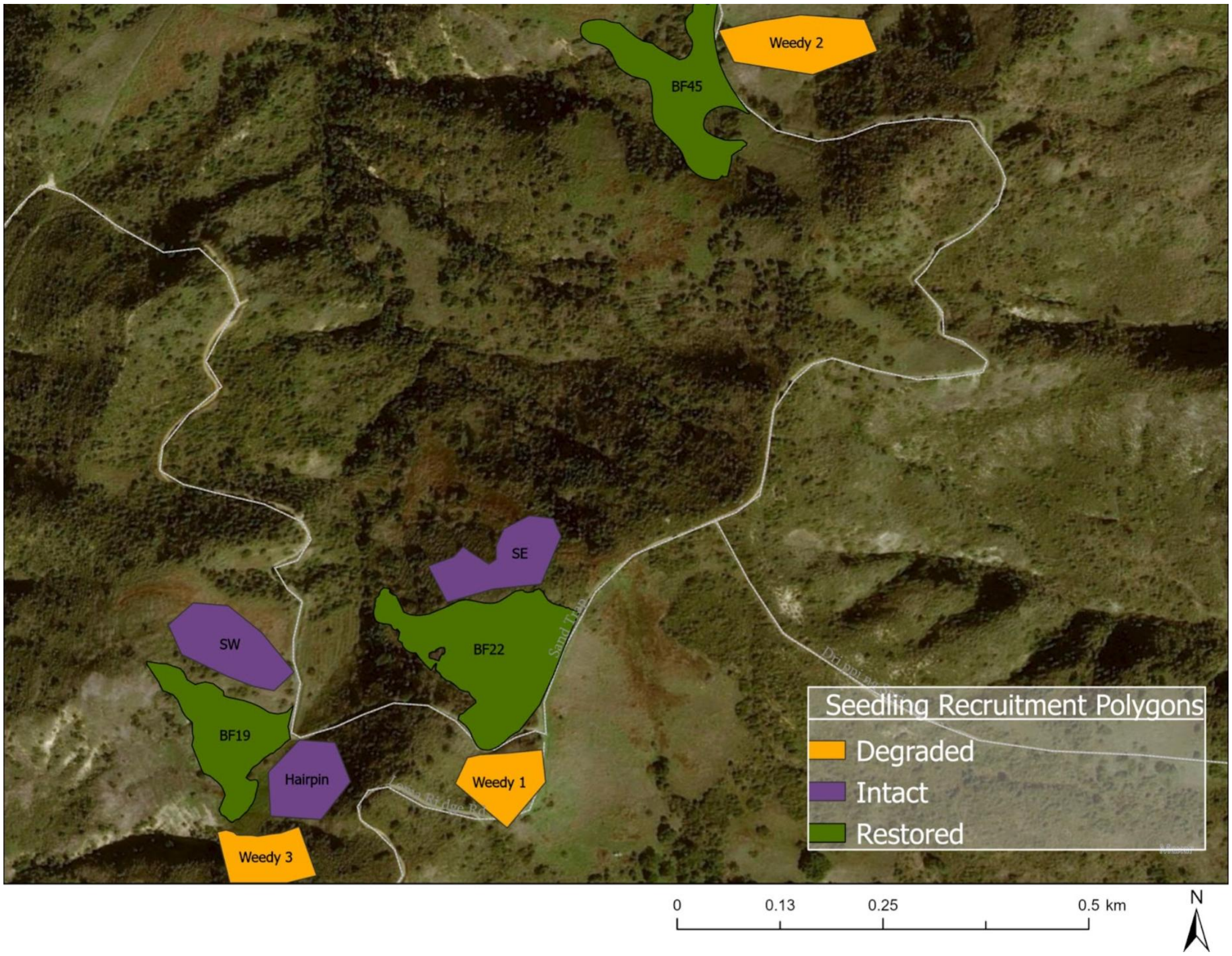

Figure 4. Map of the seedling recruitment study sites in Bee Flat Canyon. Vegetation cover of CSS seedling recruitment in restored forb areas were collected from fully restored polygons (BF19, BF 22, BF45) and adjacent degraded and intact areas.

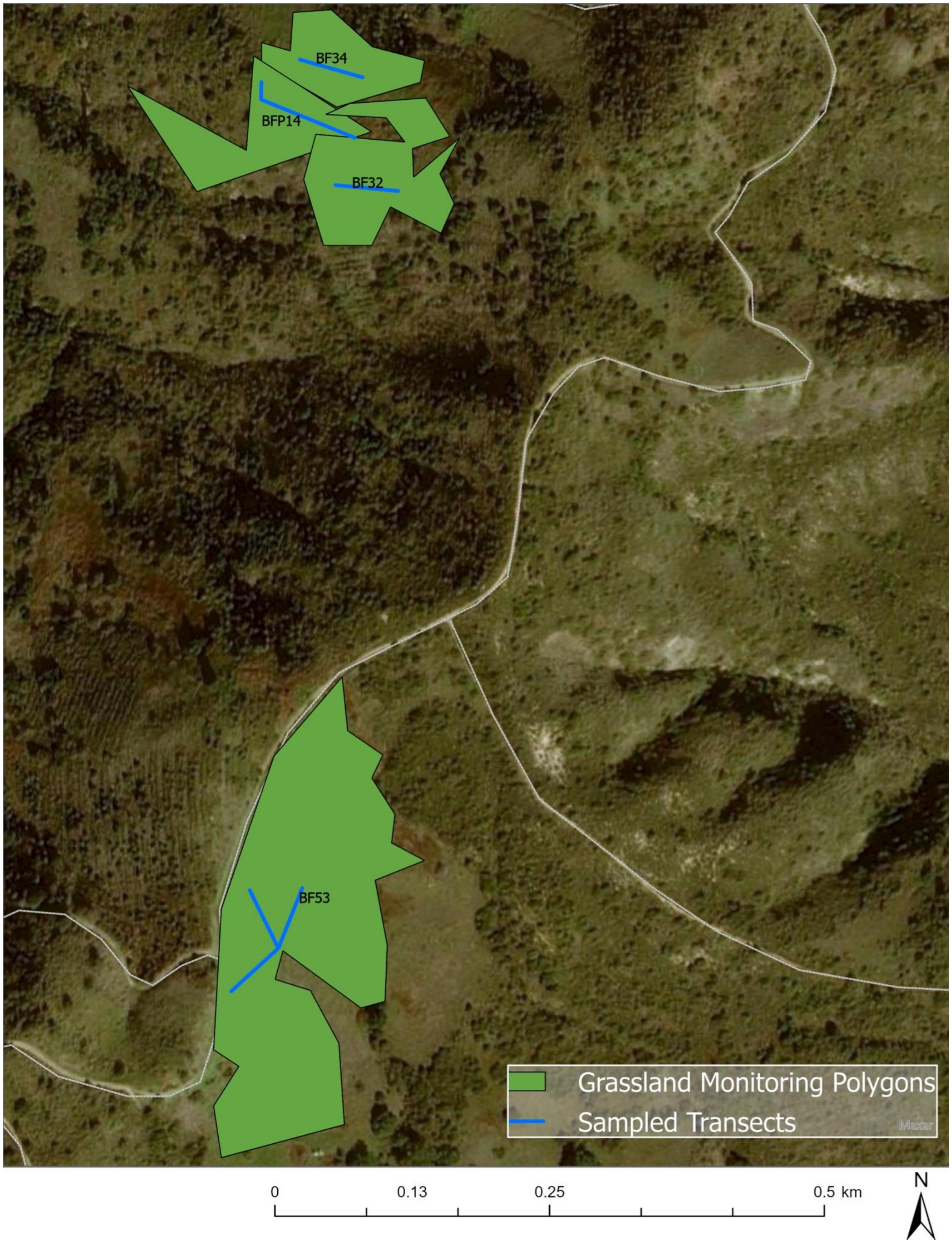

Figure 5. Map of the long-term monitoring transects in the southeastern portion of Bee Flat Canyon. Vegetation cover data for the grassland study were collected on six 50 m transects in four restored polygons (BFp14, BF32, BF34, BF53).

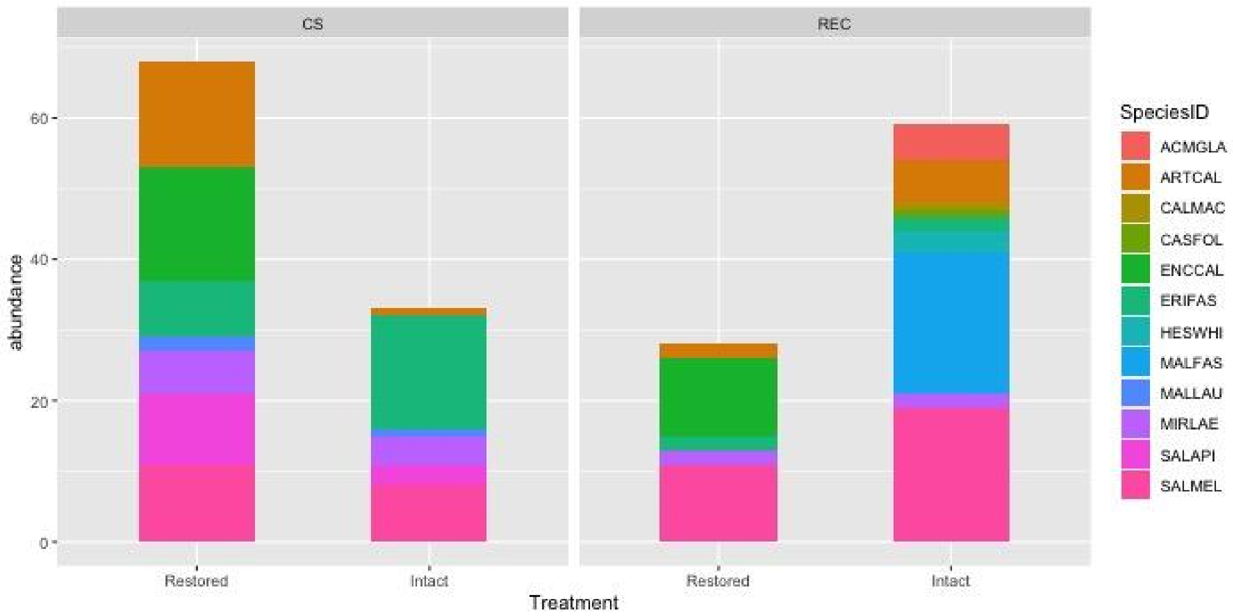

Figure 6. Crown sprout abundance (living + dead) and seedling recruitment abundance (living + dead) with species identification by treatment.

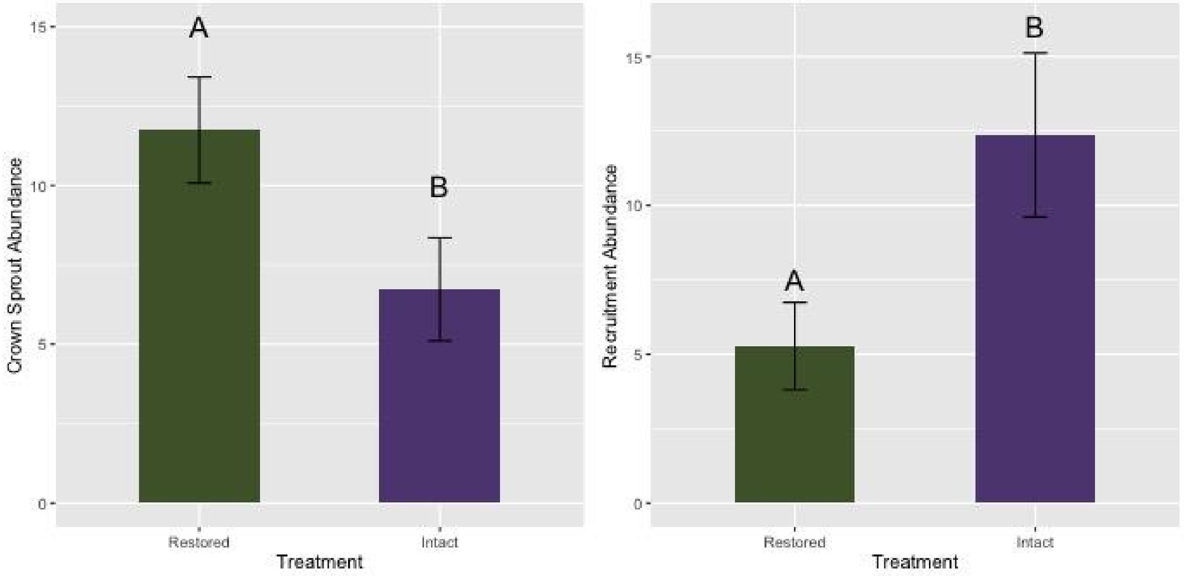

Figure 7. Average (mean) crown sprout abundance (living + dead) and seedling recruitment abundance (living + dead) by treatment (+/- SEM).

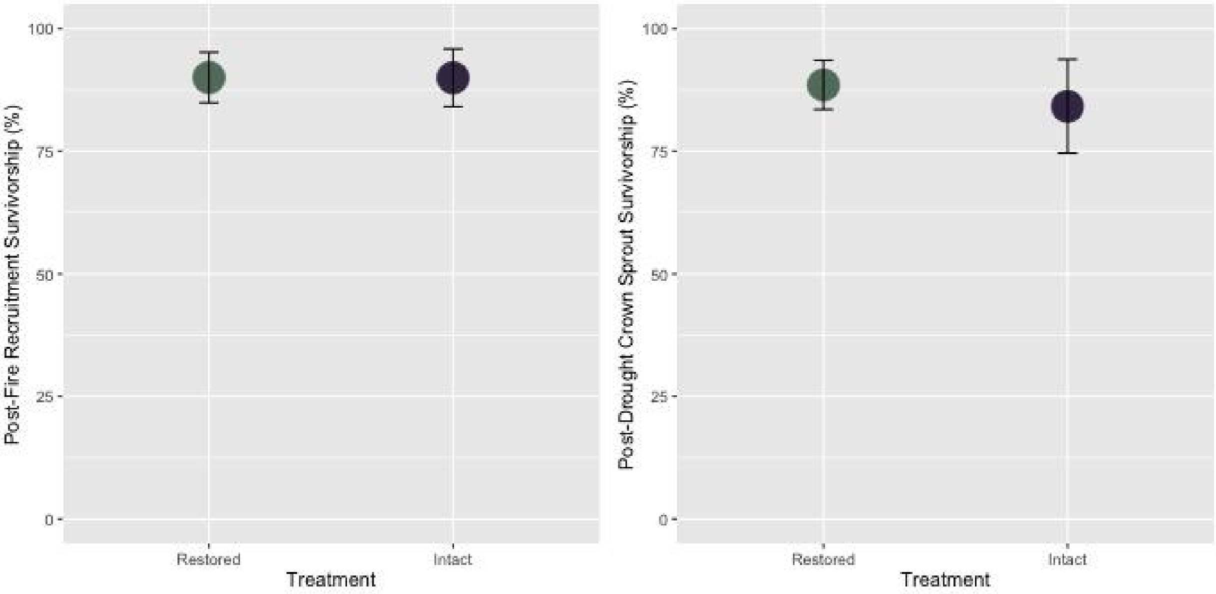

Figure 8. Post fire seedling recruitment survivorship and post-drought crown sprout survivorship between restored and intact treatments. Results showed no significant difference in post-fire recruitment survivorship between treatments ($z < 0$, $p = 0.924$) or post-drought CS survivorship between treatments ($z < 0$, $p = 0.449$). Average values show both recruitment survivorship and crown sprout survivorship is high (~85 - ~90%) in both treatments.

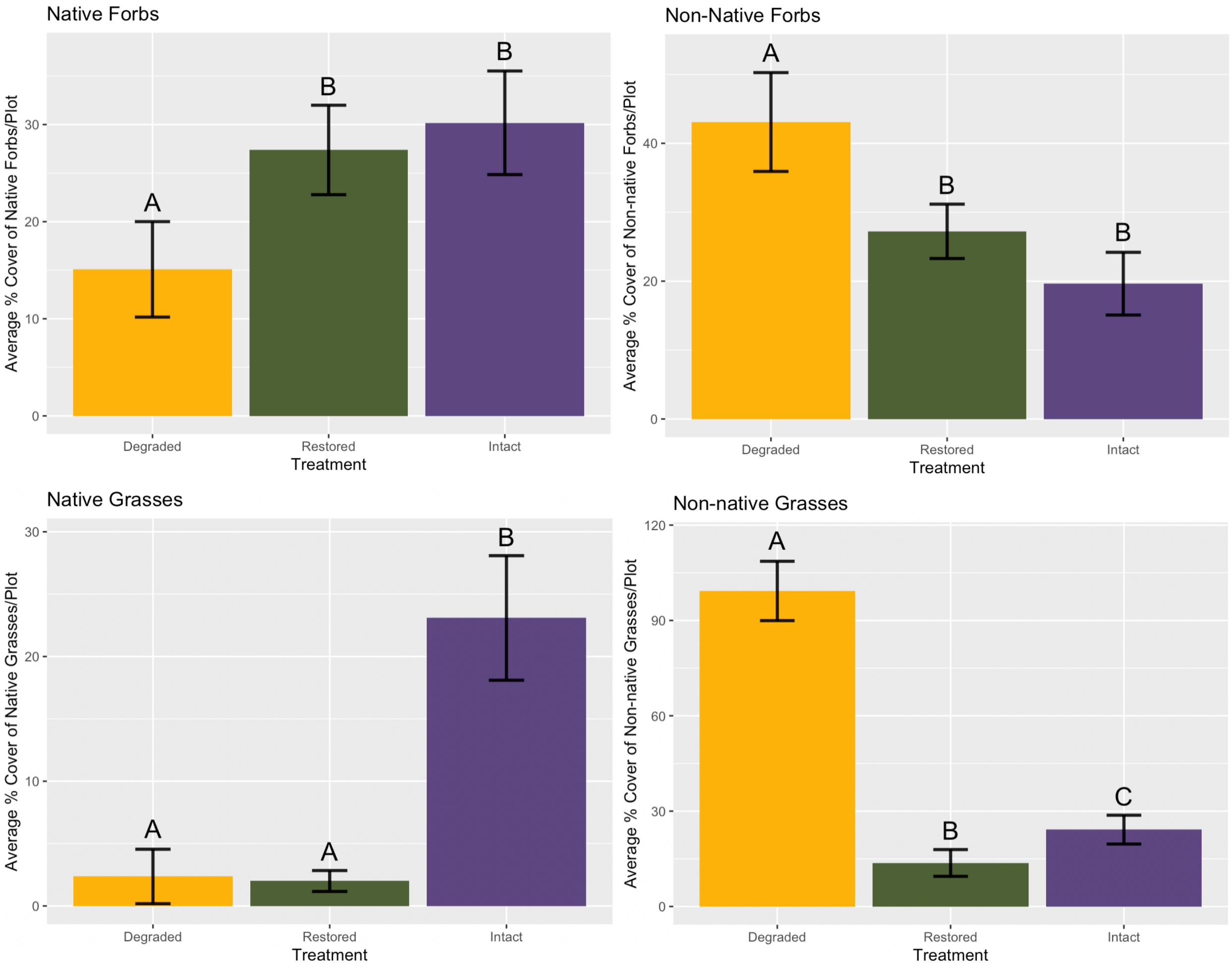

Figure 9. Bar plots of ANOVA recruitment study displaying two different functional groups (forbs and grasses) with native and non-native counterparts observed at Bee Flat Canyon. Shared letters indicate no sig diff (*p* > 0.05).

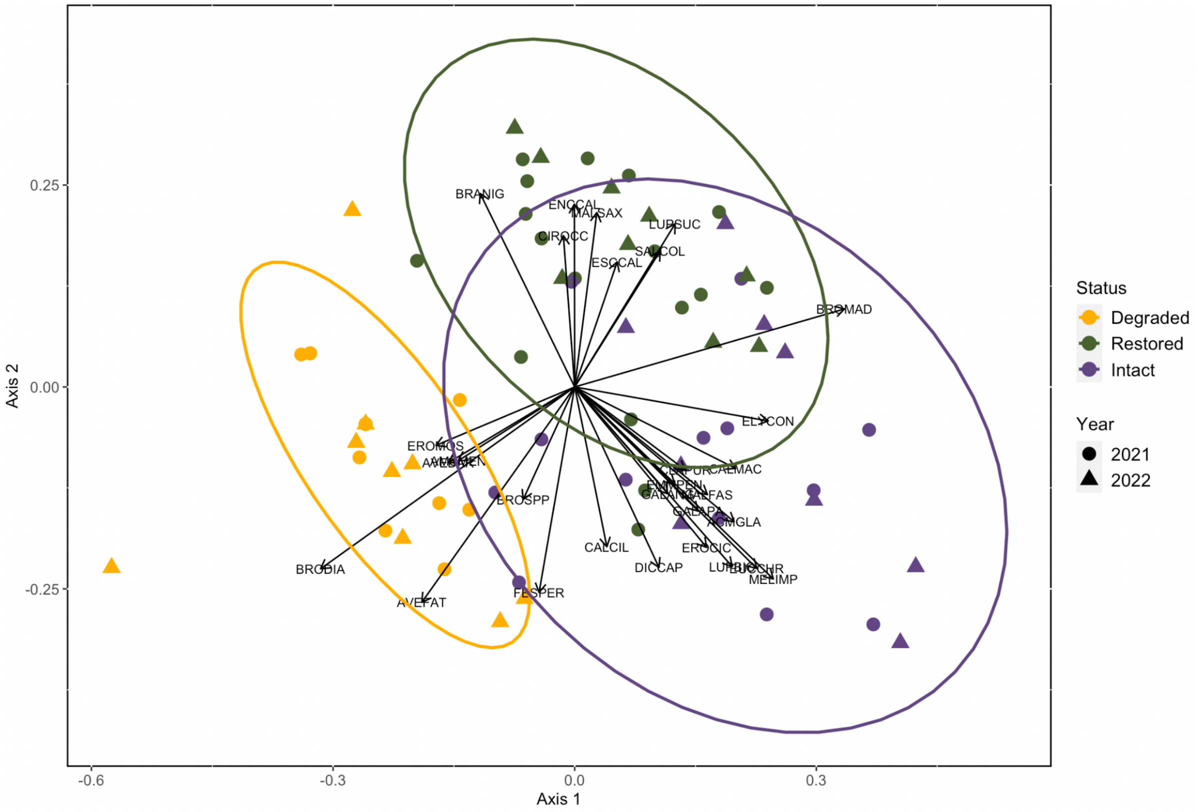

Figure 10. NMDS plot showing how sites are sorted out in species space. The symbols represent each year-point-intercept sample. Vectors are shown for all species that are significantly related in ordination space. Treatment sites are arranged according to their dissimilarities of species composition. Sites that are closer together are more similar and sites further apart are more dissimilar (stress = 0.167). See Table 6 for all correlation values of species with each axis.

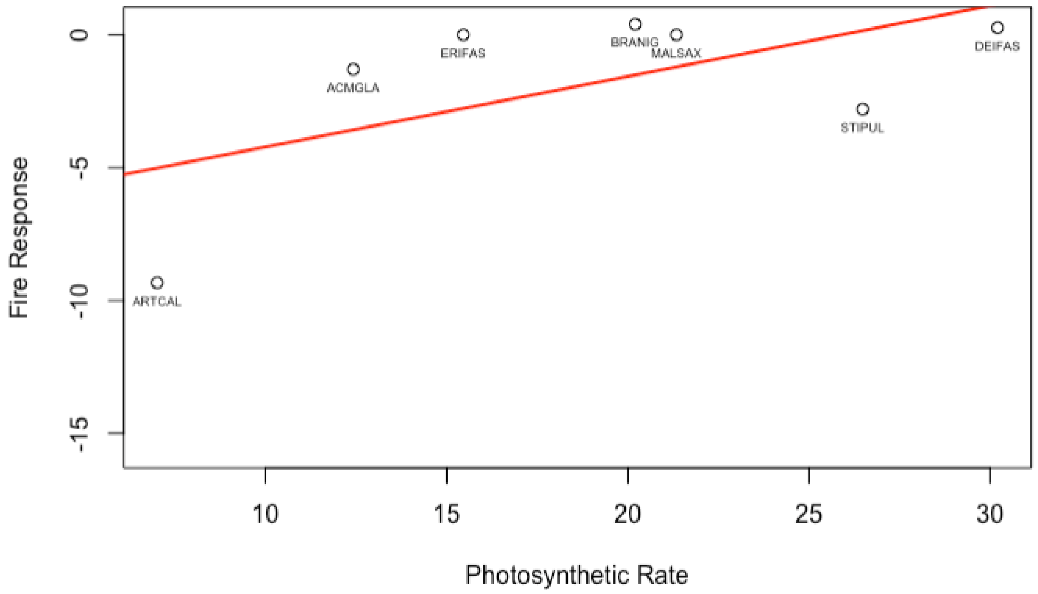

Figure 11. Scatter plot showing the relationship between species' fire response value and photosynthetic rate. Each point represents a specific species as indicated by the six letter species code. A negative fire response value indicated that the species was not seen after the Silverado Fire, while a positive value indicates that the species was seen post-fire. Results indicate that there is no correlation between fire response and photosynthetic rate.

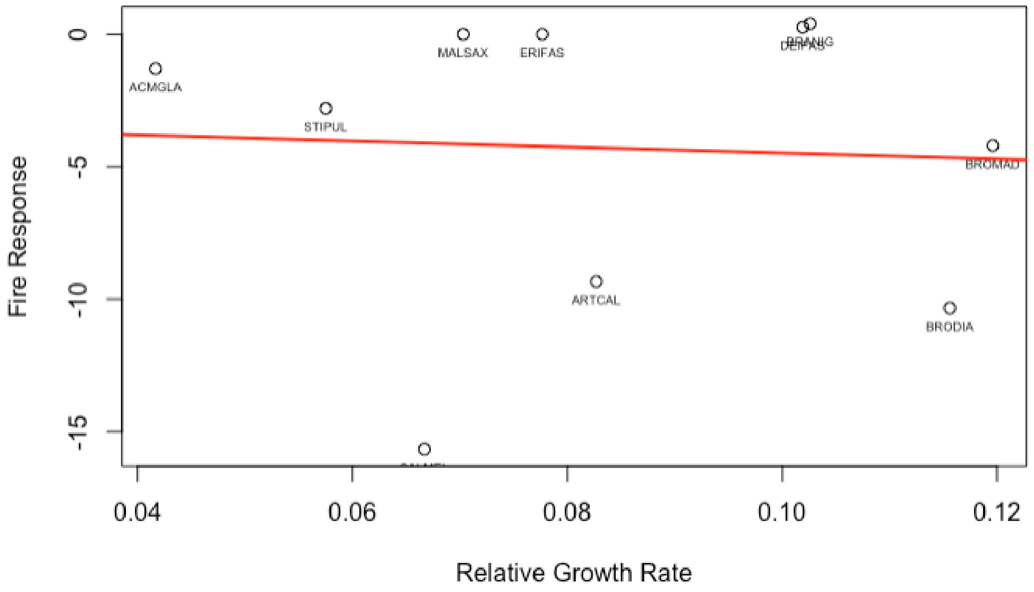

Figure 12. Scatter plot showing the relationship between species' fire response value and relative growth rate. Each point represents a specific species as indicated by the six letter species code. A negative fire response value indicated that the species was not seen after the Silverado Fire, while a positive value indicates that the species was seen post-fire. Results indicate that there is no correlation between fire response and relative growth rate.

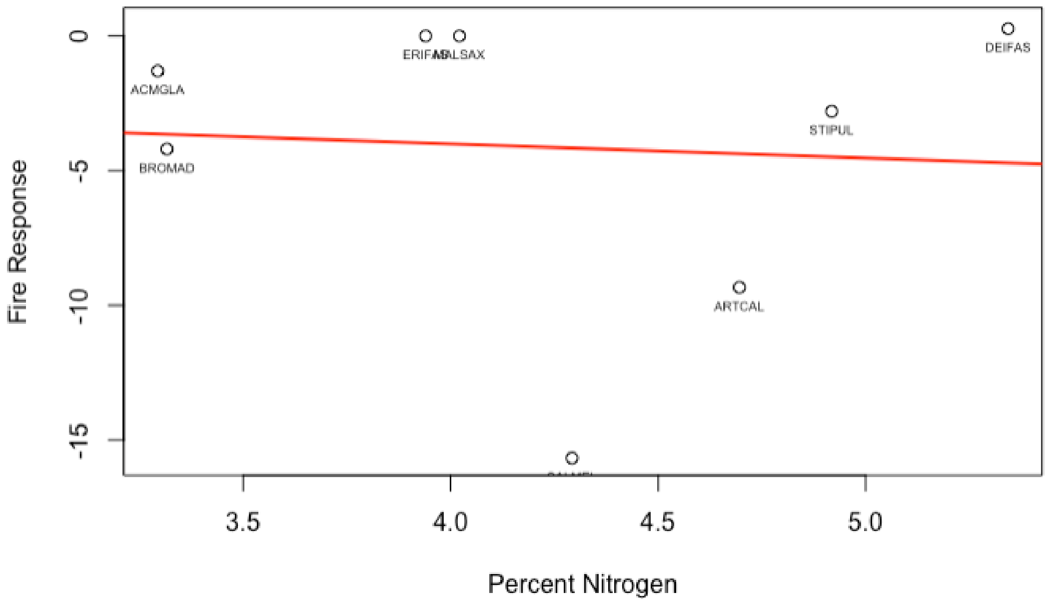

Figure 13. Scatter plot showing the relationship between species' fire response value and percent nitrogen. Each point represents a specific species as indicated by the six letter species code. A negative fire response value indicated that the species was not seen after the Silverado Fire, while a positive value indicates that the species was seen post-fire. Results indicate that there is no correlation between fire response and percent nitrogen.

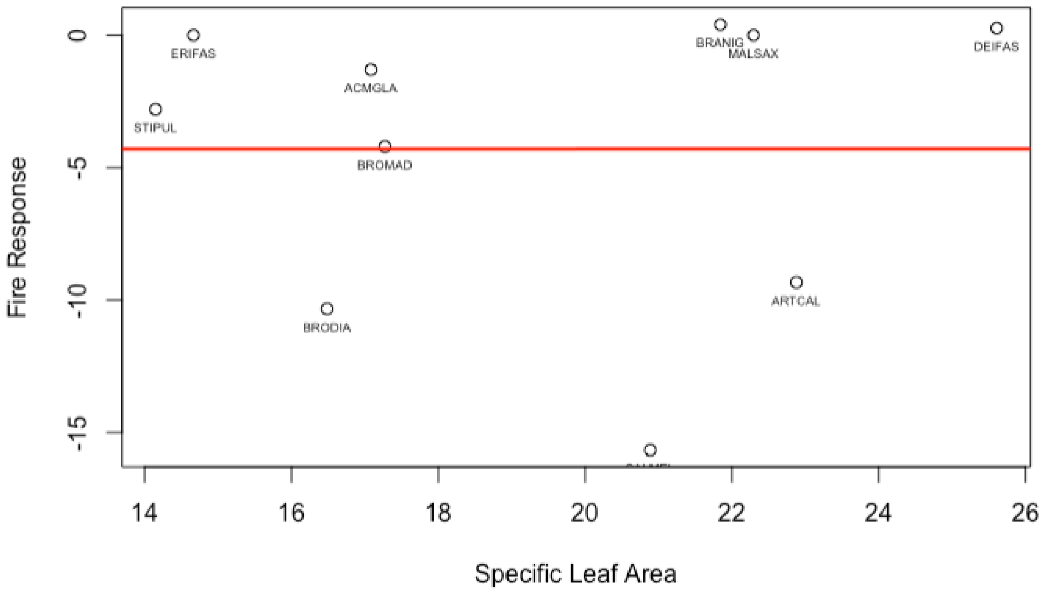

Figure 14. Scatter plot showing the relationship between species' fire response value and specific leaf area. Each point represents a specific species as indicated by the six letter species code. A negative fire response value indicated that the species was not seen after the Silverado Fire, while a positive value indicates that the species was seen post-fire. Results indicate that there is no correlation between fire response and specific leaf area.

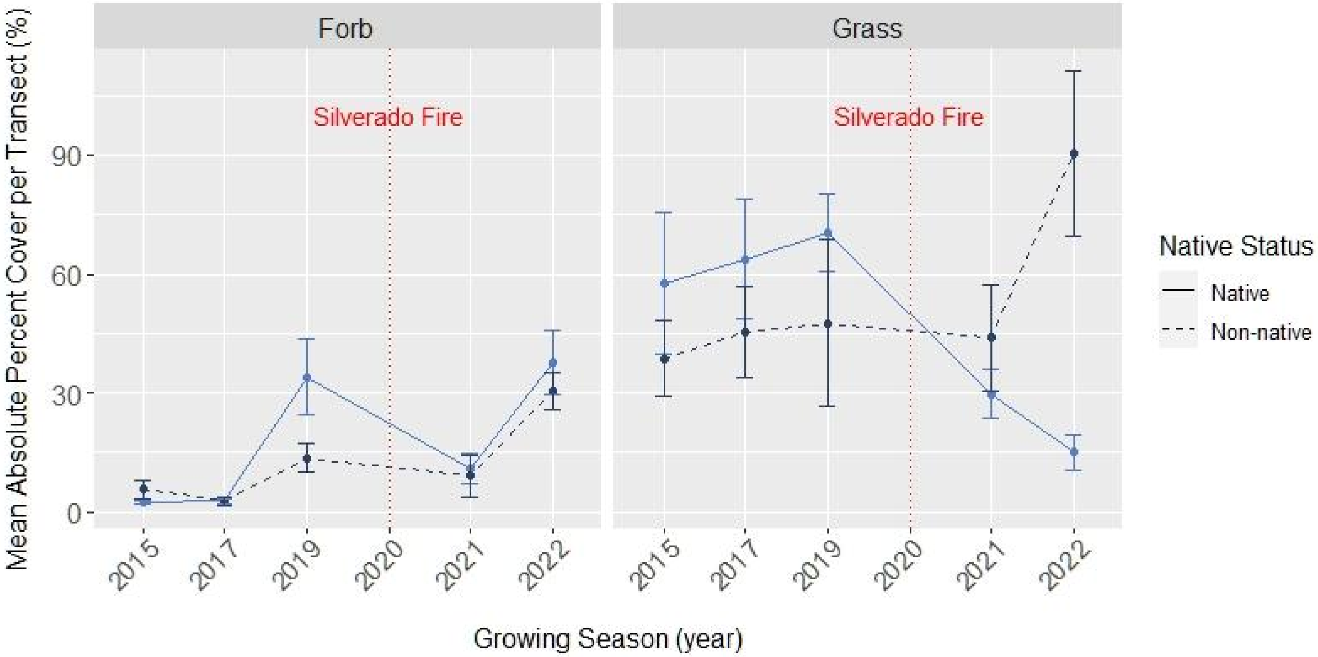

Figure 15. Line graph showing the mean absolute percent cover of each grassland functional group each year. The light blue solid lines represent natives species, and the dark blue dashed lines represent non-native species. The Silverado Fire is represented as the red dotted line.

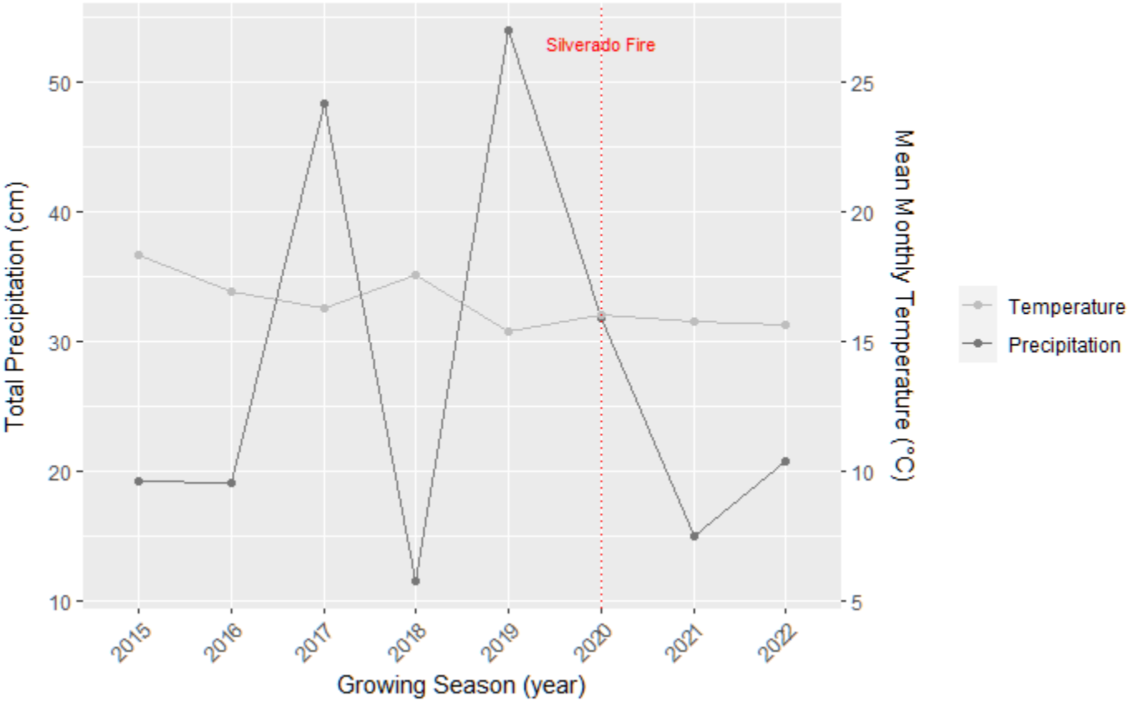

Figure 16. Line graph showing the total precipitation (cm) and mean monthly temperature (°C) during the growing season (October to March) at Bee Flat Canyon in Irvine, California.

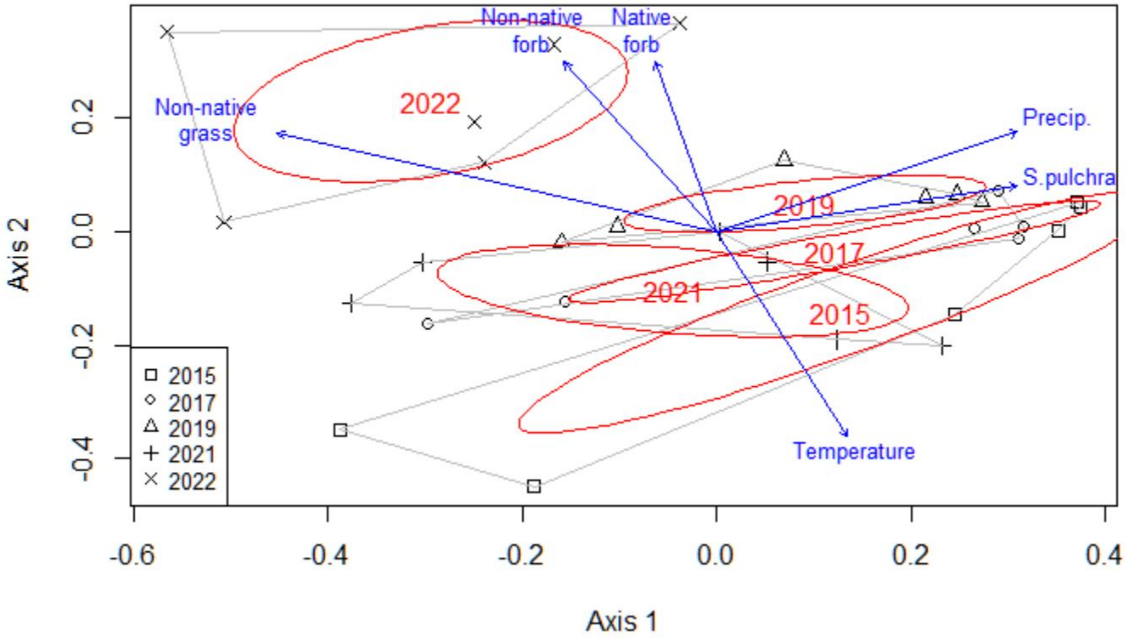

Figure 17. NMDS ordination of grassland transects plotted in species space to show changes in species composition over time. Stress = 0.140. The symbols represent each year-transect sample and the distance between samples relates to the degree of dissimilarity in species composition. Red ellipses represent transects grouped by year at a 95% confidence interval.

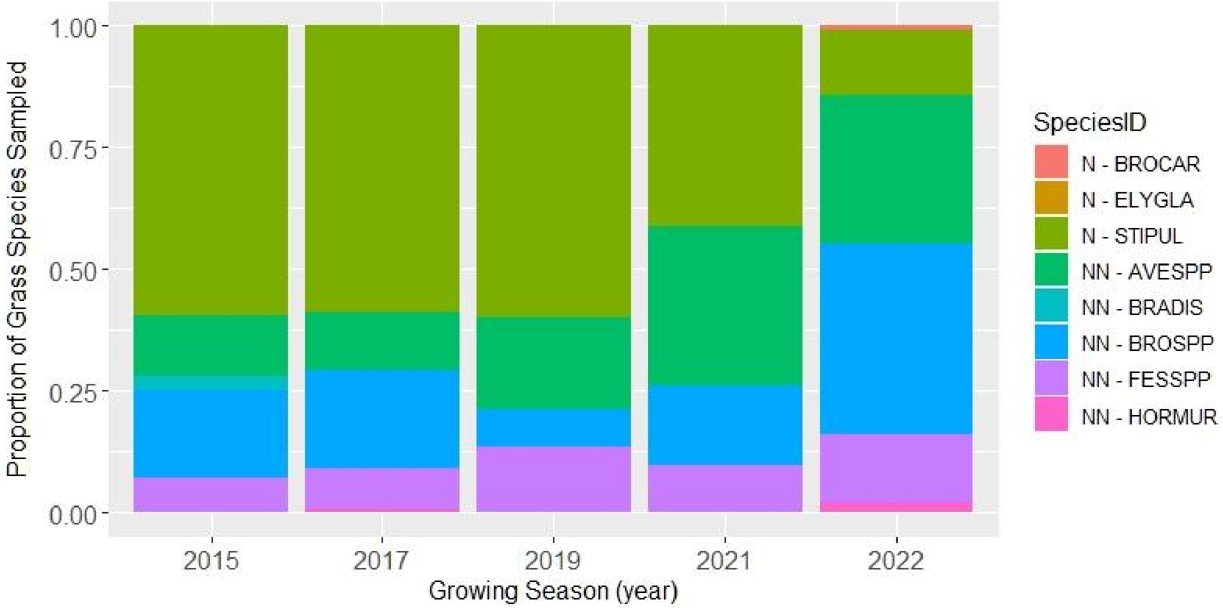

Figure 18. Stacked bar graph showing the relative proportion of all grass species sampled each year. The species are ordered by native status. N indicates a native species and NN indicates non-native. Some specific species in AVESPP, BROSPP, and FESSPP were identified in the original data but were combined for clarity for this graphic.