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Post-fire vegetation recovery and plant-pollinator interactions in southern California
ecosystems

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology & Evolutionary Biology

by

Xinyu Li

Dissertation Committee:
Professor Diane R. Campbell, Chair
Professor Travis E. Huxman
Professor Kailen A. Mooney
Associate Professor Sarah Kimball

2024

DEDICATION

To

My family, friends, mentors,

all those who have helped me along the way,

and

the conservationists of New Zealand,

who set me on this path.

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VITA

Xinyu Li

</div>

EDUCATION:
2024   Ph.D. Ecology & Evolutionary Biology, University of California, Irvine
2022   M.Sc. Biological Sciences, University of California, Irvine
2018   B.S. Biology, Duke University

PROFESSIONAL APPOINTMENTS
2018-2024   Teaching Assistant, School of Biological Science, UCI
2023-2024   Ed development scholar, Division of Teaching Excellence and
                 Innovation, UCI
2021-2022   Ridge2Reef NSF-NRT fellow
2019-2021   Writer, managing editor, The Loh Down on Science

PUBLICATIONS
(In review) **Li, X.,** Kimball, S., Ta, P., Schmidt, K.T., & Campbell, D. R. Understanding post-fire vegetation recovery in Southern California ecosystems with the aid of pre-fire observations from long-term monitoring.

Powers, J. M., Briggs, H. M., Dickson, R. G., **Li, X.,** & Campbell, D. R. (2021). Earlier snow melt and reduced summer precipitation alter floral traits important to pollination. *Global Change Biology*, 00, 1– 17. https://doi.org/10.1111/gcb.15908

SELECT PRESENTATIONS
2023   Ecological Society of America annual meeting, Portland, OR: *Flowers after fire: looking beyond vegetation recovery in coastal sage scrub*; talk
2023   OCCNPS (Orange County California Native Plant Society) meeting, Mission Viejo, CA: *Effects of post-fire age on vegetation recovery and flowering: A study of inland coastal sage scrub in Orange county;* talk
2022   Ecological Society of America annual meeting, Montreal, Canada: *Long-term monitoring before and after a fire in southern California elucidates changes in vegetative cover and composition*; poster

SELECT PROFESSIONAL DEVELOPMENT & CERTIFICATES
2022   Certificate in mentoring excellence
2020   Certificate in teaching excellence
2020   Certificate in course design
2019   Certificate in science communication

SELECT FELLOWSHIPS & AWARDS

2023	Senior Summer Scholar, UCI Division of Teaching Excellence and Innovation
2022	O'Neill grant, Orange County California Native Plant Society
2021	Pedagogical fellows, UCI Division of Teaching Excellence and Innovation
2021	Ridge2Reef fellowship, UCI
2020	Ridge2Reef fellowship, UCI
2018	UCI Graduate Fellowship Award
2018	UCI Graduate Dean's Recruitment Fellowship Award

ABSTRACT OF THE DISSERTATION

Post-fire vegetation recovery and plant-pollinator interactions in southern California

ecosystems

by

Xinyu Li

Doctor of Philosophy in Ecology & Evolutionary Biology

University of California, Irvine, 2024

Professor Diane R. Campbell, Chair

Post-fire recovery in terrestrial ecosystems is a complex, long-term process with outcomes that depend on the interaction of abiotic and biotic factors before and after fire. Understanding these processes helps to inform conservation efforts so that these natural ecosystems and the services they provide may be preserved. With anthropogenic activities changing fire regimes worldwide, there has been increasing interest in investigating the dynamics of recovery post fire. While comparisons of vegetation at different stages post fire are well documented, less is known about recovery in the form of comparisons of post-fire vegetation to pre-fire stands. Furthermore, recent fire history can not only affect vegetation cover, but also flowering and pollinator interactions. These effects on flowering and pollination should also be examined to better understand recovery patterns in the long-term.

The first chapter examines vegetation recovery in two southern California ecosystems through a long-term (15Y) monitoring dataset and compares pre- and post- fire

differences in plant community composition with chronosequence differences from the 2017 canyon 2 fire. Burned areas in coastal sage scrub had lower native shrub cover and greater forb cover, along with higher vegetation diversity from greater forb diversity, with changes in species composition persisting four years after fire. In contrast, vegetative cover recovered quickly in grasslands. The inclusion of pre-fire data allowed identification of a pre-existing difference in non-native grass composition between grassland field sites that would have otherwise been interpreted as a direct effect of fire. These results demonstrate the importance of long-term monitoring to allow for the separation of the effects of disturbance vs pre-existing differences.

The second and third chapters focus on flowering and pollination in coastal sage scrub. I sampled 22 transects with three burn statuses (recent = 0.5-1.5 y after fire, intermediate = 3.5-4.5 y after fire, and old burned = >10 y after fire) across two years. Chapter 2 explores how recent fire history affects flowering abundance, diversity, and flower size. Recent burn history increased flowering diversity and affected flowering community composition, but in a way that was mostly predicted by vegetation recovery rather than changes in flowering patterns, suggesting vegetation can serve to predict flowering diversity and composition. Flower abundances differed across the two sampling years rather than burn statuses, and most species showed no change in flowering intensity after fire.

The third chapter explores how recent fire history impacted flower visitation by pollinators and pollen deposition. Burn status alone had little effect on pollinator visits, with visits and number of visitors strongly associated with flower abundance per area observed. Differences across burn statuses and year did impact how pollinator visits

increased with flower count. Types of pollinators also differed, with *Apis mellifera*, the most common visitor, showing the greatest increase in visits in relation to flower count. Pollen deposition on five common flowering species (*Salvia mellifera, Gilia angelensis, Eucrypta chrysanthemifolia, Hirshfeldia incana, Erodium cicutarium*) was mostly not affected by burn status, expect for conspecific pollen deposition in *S. mellifera*, which was higher in intermediate burn sites.

Overall, we saw that while grasslands recovered quickly in both cover and composition, coastal sage scrub remained changed for longer after fire. Increased forb diversity in CSS after fire contributed to increased flowering diversity, and though effects of burn status on pollinator diversity were not directly detected, we did find an increase in pollinator diversity with increased flowering diversity at our sites. However, overall flowering abundances and their positive effects on pollinator visits were impacted by the annual changes in flower production in native forbs and shrubs, and less clearly associated with recent burn history. Combined, these chapters help to highlight facets of post-fire recovery beyond burned/unburned comparisons and vegetation recovery, including the importance of separating the effects of burn from pre-fire community differences, and impacts of flower number on pollinator visits.

INTRODUCTION

Wildfires are endemic disturbances in many ecosystems across the world. The resiliency of communities to wildfire disturbances depends on traits of individual species that allow them to survive or to re-establish in the same areas after fire (Keeley et al., 2011; Kimball et al., 2018; Nolan et al., 2021). Anthropogenic factors such as climate change (Fréjaville & Curt, 2015; Cary & Banks, 2000), increases in the urban-wildland interface (Syphard et al., 2007), and the introduction of invasive species (Brooks et al., 2004; Pausas & Keeley, 2014) can also alter fire regimes and subsequent post-fire dynamics (Keeley et al., 2005; Alba et al., 2015). Long-term recovery after burns is a complex process dependent on the interaction of abiotic (e.g. fire intensity, precipitation) and biotic factors (e.g. pre-fire communities, vegetation and animal interactions), the latter which includes the additional facet of species being differentially impacted by fire (Keeley et al., 2006; Carbone et al., 2019). To date, studies on the effects of fire in southern California ecosystems have mainly focused on vegetation recovery by looking at plant communities at different stages post fire, i.e. by using differences across space as a substitute for differences between time before and after fire. This dissertation aims to examine post-fire recovery in southern California ecosystems through the additional lens of pre-fire/post-fire comparisons (chapter 1), post-fire flowering (chapter 2), and interactions with pollinators (chapter 3).

The effect of recent fire history on vegetation cover and composition is well documented in studies across mediterranean-type ecosystems. Generally, fire removes woody species which dominate the canopies of mature vegetation stands, thus allowing for greater emergence of a variety of herbaceous annuals, including fire-following species

(Keeley et al., 1981). This process results in increased diversity but lower vegetation cover in the first years after fire, which persists until the slower growing woody species recover over time (Westman, 1981; Keeley et al., 2006). Grasslands recover vegetation cover rapidly, but the composition of species may change, especially with the presence of invasive grasses (Larios et al., 2013; Thomson et al., 2020). Many studies on this subject have relied on comparing vegetation cover and composition across sites at different post-fire stages. This kind of chronosequence comparison captures the temporal changes in environmental factors that can affect vegetation across different years, and recovery in these comparisons is assessed by high similarity of burned and unburned areas. Pre-post fire comparisons are rarer as the unpredictability of wildfires means that pre-fire data isn't usually available, unless long-term monitoring or other studies have been taking place in the same area. Comparisons of post-fire with prefire cover and compositions can better inform whether the vegetation has approached its pre-fire state, and whether observed differences between sites of different post fire ages are due to the effects of fire, or pre-existing differences. This is especially important for ecosystems which display high heterogeneity across the landscape, which include grassland and coastal sage scrub habitats.

Approximately 87% of flowering plants depend at least partially on animal visitors for pollination (Ollerton et al., 2011). For these species, attraction and competition with their neighboring species for pollinators plays a significant role in successful reproduction. Flowering abundances and composition can change after fire due to changes in plant community composition, but also from changes to flowering effort across different species (Wrobleski & Kauffman, 2003; Richardson et al., 2023). Changes in resource availability

after fire (Christensen & Muller., 1975; Debano & Conrad., 1978; Caon et al., 2014) could boost flowering and result in more flowers from the same plant cover in burned compared to unburned sites. Resource availability combined with differing resource allocation strategies selected through natural selection favoring growth and/or reproduction after disturbance can determine whether plants boost vegetation growth and flowering at the same time (resource matching) or switch allocation to favor one over the other (resource switching) (Borchert & Tyler, 2009). Metrics such as flower production per unit area (flowering intensity) and flower size could decrease (or increase) if species shift investment from flower production to recovering vegetative cover (or vice versa). Flowering may also be delayed in the immediate years after fire (Keeley & Keeley, 1984), so that the vegetation community of flowering plant species might not match with the actual flowers present. These factors affect whether vegetation recovery is directly predictive of flowering recovery in post-fire coastal sage scrub, and implications for attracting animal pollinators.

Pollinator visitation may be impacted by both direct and indirect effects of fire. Direct effects of fire on pollinator mortality (Cane & Neff, 2011) can remove species from localized areas, which would have a larger effect on the visits by species such as solitary bees that have short foraging ranges (Gathmann & Tscharntke, 2002). Indirect effects act through fire changing the availability of resources such as nesting substrate and floral rewards (Potts et al., 2003; Potts et al., 2005; Burkle et al., 2019). While increased flowering densities might increase overall visits to the flowering patch (Adedoja et al., 2022; Van Nuland et al., 2013), visitation rates can decrease as pollinators visit proportionally fewer flowers (Goulson, 2003). Visitation rates can also be affected by

pollinator choice, with more attractive flowering species successfully competing for more visits. However, greater visitation rates do not always translate directly into greater reproductive success. Movement of pollinators between flowers of different species can lead to heterospecific pollen transfer, which is often detrimental to seed set (Campbell & Motten, 1985; Morales & Traveset, 2008). Close proximity to high densities of heterospecifics can facilitate the number of visitors received by plants, but increase the chances of heterospecific pollen transfer (Bruckman & Campbell, 2016). Observing how pollinator visitation and pollen transfer are affected by time since fire can help us understand reproduction and recruitment of flowering species, which affects long- term recovery of these landscapes.

Chapter 1: Understanding post-fire vegetation recovery in Southern California ecosystems with the aid of pre-fire observations from long term monitoring. How vegetation recovers after fire is dependent on both pre-fire composition as well as post-fire variation in environmental factors. The most widely used method of studying post-fire recovery via chronosequences captures differences between communities at different stages after fire and accounts for annual environmental differences, but pre-existing heterogeneity in natural habitats can only be accounted for by comparisons to pre-burn observations. This chapter examined vegetation recovery in southern California coastal sage scrub and grasslands by comparing vegetation cover and composition between sites with different recent burn history and between pre-fire and post-fire observations of the same sites. Grassland and coastal sage scrub differed in their responses to fire. In coastal sage scrub, vegetation community composition differences between burned and unburned sites persisted four years after burn, with lower native shrub and greater forb cover

present in burned sites. Grassland vegetation cover recovered by the first season after fire though the species composition differed between burned and unburned sites. Comparisons with pre-burn observations determined that this was a pre-existing difference, and not due to the effects of burn.

Chapter 2: Effects of recent burn history on coastal sage scrub flowering. Post-fire flowering composition depends on both the assembly of vegetation in recovering habitats, as well as possible changes in flowering behavior of individual plants. The second chapter compared flowering metrics across coastal sage scrub at three different post fire stages by measuring flowering abundance and diversity, as well as flower size for common species. Flowering diversity was largely predicted by vegetation recovery, but flowering abundances differed between burn status in a different order between the two years of measurement: the most recently burned sites had the greatest flowering abundance the first year, but the least flowering in the second year compared to other burn statuses, due to an increase in flowering in high-flower producing species in both intermediate and old burned sites. Flower sizes for most of the most common species were not significantly affected by burn status, with *Salvia mellifera* in recently burned sites as an exception, having larger flower sizes in the second year after fire, after not flowering the first year.

Chapter 3: Flower visitation and pollination in post-fire coastal sage scrub. Post-fire pollinator visitation can be affected by direct effects of fire on pollinator presence in the local area, and by indirect effects on pollinators such as changes to floral community and availability. The total number of visits and identities of pollinators can affect the total amount of pollen being transferred, and the proportion made up by conspecific versus

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heterospecific pollen. Pollinator visits were relatively unaffected by burn status, but increased with greater flower number, with *Apis mellifera* visits increasing the most amongst pollinator groups showing that in our case, local flower abundance and the factors that impact flowering were more influential on pollinator visits than burn status. Pollen transfer metrics, including conspecific and heterospecific pollen deposition, were also not significantly affected by burn status for four out of five common flowering species sampled.

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CHAPTER 1

Understanding post-fire vegetation recovery in Southern California ecosystems with the aid of pre-fire observations from long term monitoring

INTRODUCTION

Wildfire disturbances are increasing in frequency and severity in many parts of the world due to anthropogenic factors, including climate change (Fréjaville & Curt, 2015; Cary & Banks, 2000). Fire disturbance in areas where fires are endemic can help maintain plant species diversity (Westman, 1981; Burkle et al., 2015; Ponisio et al., 2016), but too frequent fires can lead to vegetation-type conversion (Talluto & Suding, 2008; Syphard et al., 2007), as dominant functional groups shift from those that require more time to grow between fires to those that do not. Invasive species may also benefit from fires and further displace native species (Thomson et al, 2021).

Southern Californian ecosystems are subject to periodic fire, including the two native habitat types in our study: coastal sage scrub (CSS) and grassland (GL). Mature stands of native CSS consist of a dense native shrub cover with an understory of primarily annual forbs and grasses (Westman, 1981). Few native GL communities exist due to the prevalence of non-native invasive annual grasses and forbs that out-compete natives, but a mature native GL contains the native perennial bunchgrass, *Stipa pulchra*, along with a diverse mixture of native geophytes, annual forbs, and perennial forbs. Previous studies on post-fire recovery in southern California shrublands, which includes both chaparral (evergreen dominant) and CSS (drought-deciduous dominant), found a peak in vegetation

diversity in the first two years after fire, which gradually decreases as the community progresses towards a mature stand (Keeley et al., 2005; Whelan et al., 2002; Keeley & Fotheringham, 2003; Westman, 1981). This recovery pattern was observed in a 5-year post-burn observational study on southern Californian shrublands following fires in 1993 (Keeley et al., 2005; Keeley et al., 2006), and can be partially explained by differences in recovery strategies of vegetation groups. In contrast to shrublands, grasslands do not usually undergo short-term changes to their overall vegetation cover due to quick growth from grass and forb seed banks, but native perennial grasses are susceptible to replacement by non-native annuals, which are less seed-limited and faster growing (Menke, 1992; Cox & Allen, 2007; Larios et al., 2013). The recovery mechanisms of the species which were present in habitats before fire, such as seed banking and seed rain in forbs and grasses (Seabloom et al., 2003; Conlisk et al., 2016), and resprouting in woody shrubs (Malanson & Westman, 1985; Pausas & Keeley, 2014), are likely influential in the establishment of the initial post-fire community and subsequent recovery trajectory. These dynamics can change when there is low precipitation in the immediate years after fire (Kimball et al., 2014; Kimball et al., 2018). Crown-sprouting shrubs show increased mortality when confronted with drought after fire (Pratt et al., 2014). Experiments manipulating precipitation levels after fire confirm that a combination of burning and drought can facilitate conversion from native shrubland to non-native grassland communities (Kimball et al., 2014).

Long-term vegetation monitoring in fire-prone areas is needed to accurately assess post-fire recovery. Such monitoring allows the use of a Before-After-Control-Intervention design

rather than simply Control-Impact comparisons. Currently, most studies of natural systems rely only on comparing controls and impacted sites with data collected post-fire, as the location and timing of wildfire burns is not determinable before the fact. A few studies which estimated pre-fire species presence in southern California shrublands used the skeletons of shrubs to characterize the "Before" condition (Keeley et al., 2008), but this method misses the presence of herbaceous species, which usually have their above-ground cover eliminated by fire. For studies where the interest is determining community differences between fire ages, in the absence of pre-fire data, chronosequences of sites at different years post fire have been used to make comparisons across a landscape scale (Potts et al., 2003; Keeley & Brennan, 2012; Capitanio & Carcaillet, 2008). These comparisons are useful as we can use them to contrast sites with different fire histories under the same temporal changes in climate and other environmental factors. The chronosequence approach assumes that the only difference between sites is time since fire, whereas in reality, it is likely that biotic and abiotic factors vary across space (Johnson & Miyanishi, 2008; Pickett, 1989). Thus using a BACI design to examine whether the difference between control and impact sites is different after fire than it is prior to fire provides a stronger design for analyzing the impact of fire (Christie et al. 2019). Furthermore, while previous studies have revealed much about the recovery of different types of vegetation types over time after fire, less attention has been paid to individual species. This existing variation in vegetation prior to fire is likely to contribute to community composition after fire and can be addressed with the inclusion of detailed pre-fire data from long-term monitoring projects.

In this study, we answer the following questions: (1) How did a major wildfire change the vegetation cover of native vs. non-native species, as well as the cover of species with different growth forms in GL and CSS?, (2) Did diversity and community composition in the burned sites return to the pre-fire state by four years after fire – and was this recovery different in timescale for different growth forms or species? Question (2) has rarely been explored (but see Thomson, 2020 on grassland recovery). In this study we take advantage of a 15 year dataset that allows for detailed comparisons in community composition and cover of not only burned and unburned locations, but also the same locations before and after fire (BACI design). It focuses on the Canyon 2 fire which burned an area ~3700 hectares in October 2017 to characterize the recovery of specific forbs, grasses, and shrubs in CSS and grassland in Orange County, CA, USA. Long term monitoring data capturing pre-fire and unburned observations allows us to perform two types of analyses: (1) comparing burned against unburned sites at the same point in time, and (2) comparing burned sites post fire to burned sites pre-fire. The former method has the advantage of controlling for other factors besides fire that may vary temporally (e.g. annual precipitation), but the disadvantage that the burned and unburned sites may have differed in composition pre-fire. The latter method has the advantage of controlling for geographic variation, but the disadvantage is that post-fire years may also differ from pre-fire years in environmental variables. As many studies of fire disturbance have used the first method only, our study aims to address if the two methods lead to similar conclusions to each other in our study, and to previous studies of the same ecosystems in this region.

MATERIALS AND METHODS

Study Sites

The data in this study come from a long-term transect monitoring program of vegetation across Orange County, California, USA collected by the Center for Environmental Biology at UC Irvine (UCI-CEB) in partnership with The Nature Conservancy and the Natural Communities Coalition, with the goal of tracking changes in native and non-native plant presence in Orange County over time. Kimball et al. (2018) report on the first 10 years of data, prior to the 2017 Canyon 2 fire that we focus on (map in Appendix S1.1). The monitoring sites are spread across the ~200 km² Nature Reserve of Orange County, with transects being added and retired starting in 2007. 50-m transects were selected using a semi-random design (Kimball et al. 2018) and marked with permanent rebar stakes at the start and end points upon establishment. Ecosystem type was visually assessed in the field and determined by the dominant vegetation type on the transect (drought-deciduous shrubs for CSS and grasses and forbs for GL). The beginning and end points of the transects were located 30-300 m from an accessible road, and the transect lines ran across inclines that were under 35% slope (Kimball et al., 2018). Monitoring took place annually in the spring, usually between mid-March and June to coincide with the time of year when most annual plants are growing. Not all transects were sampled every year, with annual plot selection made through a rotating panel design to allow for spatial coverage over the area given constraints on time and personnel (schedule in Appendix S1.2).

A total of 97 CSS and GL transects were established between 2007 - 2021, including some where fires occurred after transect establishment (Appendix S1.3). Two other fires occurred during monitoring, one in 2007 at the start of the monitoring period and a smaller

fire in 2020. Seven transects that burned in 2007 were monitored in 2008, but unmonitored in 2009 and 2010 before returning to the regular monitoring schedule. Following conclusions drawn in Kimball et al. (2018), data from the monitoring of burned sites in 2008 were omitted from this analysis as they differed significantly in cover compared to unburned areas. For the same reasons, post-fire observations of sites burned in the 2020 fires were also removed. Of the transects included in the analysis, 58 are CSS, and 39 are GL (Table 1.1).

Data collection

To determine vegetation composition for a transect during a year, species presence and percent cover were determined along the transect lines. Pairs of observers were trained on a common protocol and drew a 50-m measuring tape between the beginning and end points upon each visit to the transect, with each observer performing one of the following two sampling methods.

Method 1: Point intercept

Vegetation cover values were calculated from data collected through the point intercept method, which allows for better coverage of the transect than does quadrat sampling. In this protocol, points were observed at 1-m intervals along the transect line starting at 0 m for a total of 50 points per transect. All vegetation that came into contact with a vertical 1.3 cm-diameter dowel dropped at each meter interval was identified to species level. Because sampling continued as vegetation was senescing, recently senesced vegetation was included.

Species percent cover was calculated as the number of contacts by individual species at the 1-m intervals divided by the number of intervals (50), following the same methods as Kimball et al. (2018). Intercept data were collected from 2007- 2021.

Method 2: Quadrat sampling

We used quadrat sampling data for species richness and diversity, as this method is better able to detect smaller and rarer species compared to the intercept method. Quadrat data were collected in ten 1-m² quadrats alternating left and right of the transect every 5 m. The cover of each individual species in each quadrat was visually estimated to the nearest 1%. We summed species richness and calculated diversity metrics across all quadrats for the transect. As both intercept and quadrat data included all species found on location, the summed vegetation cover of each quadrat or all points sometimes exceeded 100% due to overlapping species cover. Quadrat data were collected from 2014 - 2021. The number of species in each dataset is shown in Table 2.

Analyses

We categorized the species found in the data using the Calflora database (https://www.calflora.org/) into different groups based on combinations of the following factors (Appendix S1.4): (1) native and non-native species, (2) functional group (forbs, shrubs, grasses). Vegetation cover of each category was calculated by summing the species covers within each category across the transect. Transect was treated as the unit of replication. One limitation is that transects could be spatially correlated and thus not

statistically independent, as we had no control over where the fire had burned. Spatial

autocorrelation is addressed in Appendix S1.5.

Changes in vegetation cover

To describe changes in vegetation cover, we used two types of cover estimates as response

variables: (1) absolute cover and (2) relative cover. Absolute cover values are the direct

calculations of cover from point intercept data, and are used to determine whether a

category of vegetation increased or decreased. Relative cover values are calculated as the

percentage of a specific vegetation category out of the sum of all categories and address

how cover changed relative to other types of vegetation in the same community, since total

cover may change from year to year. Six vegetation cover categories (total native plant

cover, native forb cover, non-native forb cover, native grass cover, non-native grass cover,

and native shrub cover) are included. Non-native shrubs are uncommon in the sites and

therefore omitted.

Linear mixed effects models (lme function, R version 4.2.1 nlme package) were used to take

into account repeated measures of transect sites over the years, by including transect as a

random effect. Two tests were done for each community type to examine the effects of the

fire disturbance. The first test compared burned and unburned sites by taking all data from

all sites after 2017 (i.e. post-burn only), and modeling each functional group cover with two

explanatory factors - burned status and year. The effect of each factor tells us whether

cover changes can be attributed to 1) sites being burned, 2) variation across years, and 3)

interaction between burn status and yearly variation. An interaction can be produced

either by an effect of fire on the response to an environmental variable (such as precipitation) that varies from year to year or by recovery of the site. For example, burned and unburned transects might be very different shortly after fire but converge over a longer period of time.

A second test compared cover each year after fire to pre-fire cover for transects that were burned in the Canyon 2 fire only. All pre-fire data points for a given transect were grouped together as "pre-fire" regardless of the year, which allowed inclusion of transects that were not sampled immediately prior to the fire. This analysis also used a linear mixed effects model with year category as the explanatory factor (pre-fire, 2018, 2019, 2020, 2021) and included transect as a random effect.

Since the two tests were performed separately for multiple vegetation categories over the same sites, a Bonferroni correction for multiple comparisons was applied within each test.

Diversity

Quadrat data were used to determine both alpha species richness and diversity. Species richness was assessed as the total number of unique species in all quadrats along the transect. Species diversity was assessed using Shannon's index, which is a metric that includes evenness and richness (Magurran, 1988). The effects of burn status and year after fire on species diversity and richness were also assessed using the same statistical models as method 1 in the vegetation cover analyses. Analysis comparing species richness and diversity each year after 2017 with pre-2017 values was conducted through t-tests of each

of the post-2017 yearly means with the pooled pre-2017 means in each of the four

burn/habitat categories (burned and unburned CSS, burned and unburned GL).

Community species composition

We used canonical analysis of principal coordinates (CAP), implemented in the capscale

function (R vegan package) to analyze species composition based on absolute cover. The

CAP collapsed the highly multivariate data into explanatory axes based on Bray-Curtis

dissimilarity, that best separated the groups incorporated into the model (Anderson &

Willis, 2003). We looked at the first two axes which usually explain the most variation. CAP

analyses were performed separately for CSS and GL communities.

We first used CAP to compare the burned vs. unburned sites, crossed with year as a

categorical variable, using only the post-burn data. Second, to see whether community

compositions returned to their average pre-fire state, we performed a second CAP analysis

using only the sites that were burned in the Canyon 2 Fire. The analysis was constrained by

time: pre-fire ("before") and each subsequent year (2018, 2019, 2020, and 2021) after fire.

We used the anova.cca function to test for significant effects of factors in the model.

Differences in species cover among groups were determined by examining their

distribution on the CAP axes, and through the envfit function (R vegan) which tests for the

significance of correlations between each species and the ordination axis.

Finally, we performed a third CAP ordination to compare burned vs. unburned sites before

and after fire. This analysis made full use of the BACI design and allowed us to examine if

community composition differed initially between sites that burned vs. those that did not, and if that impacted the differences we see between burned and unburned sites the first year after fire. An effect of the site factor unburned vs. burned would show that the compositions of the two groups of sites are different, while an effect of the time factor pre-burn vs. post-burn would indicate that the compositions were different in the year before and up to 2017 compared with the first year after fire in 2018. A significant interaction effect would show that the compositions for the two groups of sites (burned and unburned) changed in different ways from pre-burn to post-burn.

Precipitation and spatial autocorrelation

We performed additional analyses to examine whether spatial autocorrelation (Appendix S1.5) or annual precipitation level (Appendix S1.6) helped to explain changes in vegetation.

RESULTS

How did the Canyon 2 fire change the vegetation cover?

After fire, burned and unburned sites differed in many aspects of vegetation. Year and burn status both influenced the total absolute cover of native plants, and burn influenced relative cover of native plants in CSS (Fig. 1, Appendix S1.7, $P < 0.05$; Appendix S1.8). The burn effects are likely driven by native shrub cover, as shrub cover in burned sites dropped drastically after the fire in 2017 and has since remained lower than the cover of unburned sites for the 14 years of monitoring that we analyzed (Fig. 1.1, Appendix S1.8). Another group of interest is the native forbs, for which there is a significant interaction effect between burn and year on absolute cover, indicating that there is an effect of burn on how

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the native forb cover changes from year to year (Appendix S1.8). In the time-series of CSS, absolute and relative cover of native and non-native forbs and non-native grasses were higher in burned than unburned sites starting the second year after fire (Fig.1.1, Appendix S1.7).

Looking only at sites that burned in 2017 (method 2), CSS showed significant differences in cover for the years post fire compared to pre-fire cover (Appendix S1.9). The overall native plant cover decreased significantly in the first year after fire (differences in absolute cover: -48.84%, relative cover: -21.4%) compared to averages pre-fire, and the significantly lower relative cover was maintained through 2021. As in the comparisons between burned and unburned sites, native shrub cover was the likely driver of lowered native plant cover, as there are strong decreases in all years after fire in both absolute and relative covers of that vegetation type (Fig. 1.1, Appendix S1.8). Native grasses generally had a small decrease in cover, while non-native grasses generally increased compared to pre-fire cover (Fig. 1.1, Appendix S1.8, S1.9). Native and non-native forbs increased in cover after fire (Fig. 1.1, Appendix S1.8, S1.9).

In GL sites, burned and unburned transects (method 1) were not statistically distinguishable in absolute cover for any of the vegetation types after 2017, nor for interactions between burn status and year (Appendix S1.10). Absolute cover of native plants, non-native grasses, and native forbs did differ greatly across years (all $p < 0.01$, Appendix S1.10), which we could observe in time-series, where values dipped in 2018

followed by a peak in 2019 that is most drastic for native and non-native forbs (Fig. 1.1). The relative proportions of different vegetation types, however, remained relatively consistent across years (P > 0.05, Appendix S1.10), with the exception of native forbs, which increased in proportion sharply in 2019 in both burned and unburned sites (p = 0.0005; Appendix S1.7).

Comparing pre-fire and post fire data in burned GL (method 2), revealed that total native plant cover decreased in the first year after fire (effect for absolute cover = -20.96%, relative cover = -8.68%), but few significant effects of fire were observed for functional group covers. Native and non-native forbs increased in 2019 (two years after fire) compared to pre-fire levels, and non-native grasses decreased in relative cover in 2019 (Appendix S1.11).

Precipitation

After 2017 higher cumulative precipitation corresponded to higher cover that year for all native functional groups and non-native forbs in both burned and unburned CSS (Appendix S1.6). In GL, native forb absolute cover increased while non-native grasses did not change in relation to precipitation level (Appendix S1.6). Both non-native forb and native grass cover were at their highest in a low rainfall year in unburned GL while in burned sites they increased with precipitation (Appendix S1.6).

Did diversity and community composition in these burned sites return to the pre-fire state?

Species richness and diversity

In a model for CSS with year and burn status, only year and the interaction between year and burn status significantly influenced species richness (Appendix S1.12). Species richness was higher in burned CSS than in unburned areas in 2021 (Fig. 1.2A). Burn status, but not year, strongly influenced the diversity index in CSS (p = 0.00379), with higher average diversity in burned areas than unburned areas (Fig. 1.2B), especially in the first year after fire (mean of H = 1.94 vs. 1.60, Appendix S1.13). In CSS, unburned transects changed significantly in richness and diversity from pre-2017 values for more functional groups than was the case for burned transects (Appendix S1.13). Although mean species richness in burned CSS dropped in 2018 (from 27.0 to 22.5, p=0.0059), a similar drop was seen in unburned CSS (from 26.1 to 20.2, p=0.0132), along with two other significant changes compared to pre-2017 values in 2019 (increase to 31.8) and 2021 (drop to 16) that were present in the unburned, but not burned CSS data. Species diversity was significantly lower than pre-fire averages in both burned and unburned CSS in 2020, but unburned CSS had a significant drop in diversity in 2018 and 2021 as well, which was not observed in burned CSS (Appendix S1.13).

Burned GL did not change significantly in species richness and diversity from pre-burn values in any of the monitored post-burn years. The only significant change in GL was for unburned sites in 2018 (H = 1.38 to 0.769, p=0.014; Appendix S1.13).

Community composition burned vs. unburned

Ordinations comparing communities in burned and unburned sites after fire (method 1) showed how these two groups of sites shifted yearly after 2017, during which the burned sites were recovering from the Canyon 2 fire. The CSS sites were significantly different depending on burn status ($p < 0.001$), year after burn ($p < 0.001$), and also the interaction between the two factors ($p = 0.03$). The first CAP axis separated burned and unburned sites (Fig. 1.3). This separation was driven by high native shrub cover in unburned sites, and high non-native grass and forb cover in burned sites, along with the native fire-following perennial forb *Acmispon glaber* in later years (Fig. 1.3). The second CAP axis mainly separated years. High presence of the invasive grasses *Avena* and *Bromus* and the non-native forb *Erodium cicutarium* defined 2018 for burned sites, while later years had increased invasives (forbs *Centaurea melitensis* and *Hirschfeldia incana,* and grasses from the *Bromus, Festuca,* and *Avena* genera) and increased native *Acmispon glaber* (Fig. 1.3). The variation of community composition in 2018 (first year after the Canyon fire) for both burned and unburned sites was greater compared to other years in the same site category (Fig. 1.3). GL community composition differed between burned and unburned sites ($p < 0.001$) but did not differ by year ($p = 0.065$) or have a significant interaction between burn and year ($p = 0.545$). The CAP1 axis separated burned and unburned sites (Appendix S1.14). The main species presences driving this separation were *Avena fatua* in the unburned sites, and *Bromus diandrus* in the burned sites (Appendix S1.14).

Community composition of burned sites before and after fire
The ordination of transect data that only included sites that were burned in the 2017 fire (method 2) showed us how community composition in these particular sites shifted from

before fire to each subsequent year after fire (Fig. 1.4 and Appendix S1.15). In CSS (Fig. 1.4) the species composition differed significantly across years (p < 0.001). Community composition before fire included mainly native shrubs, but in the first year after fire shifted positively on CAP1 and negatively on CAP2, with increased presence of non-native grasses in the *Avena* (envfit function: p = 0.003) and *Bromus* (p = 0.001) genera. However, 2019, 2020, and 2021 showed shifts to more positive values of both CAP1 and CAP2, corresponding to loadings for a variety of non-native grasses, some non-native forbs including *Hirschfeldia incana* (p=0.001) and *Centaurea melitensis* (p=0.01), but also *Acmispon glaber* (p=0.001) and other native forbs. The 2021 and pre-burn compositions differed despite four years of post fire growth (p=0.001), with greater presence of the fire-following native forb *Acmispon glaber* (p=0.001) and non-native grass *Bromus madritensis* (p=0.001) in burned sites, and lower covers of native shrubs such as *Eriogonum fasciculatum* (p=0.001), *Salvia mellifera* (p=0.006), and *Artemisia californica* (p=0.008). Community composition of burned GL sites (Appendix S1.15) did not differ by year (p=0.218) or between pre-burn and 2021 (p=0.189).

Community composition of burned and unburned sites before and after fire

Our final analyses revealed differences in community composition between burned and unburned transects even prior to fire in the GL, but not CSS, habitats. In the ordinations of CSS (Fig. 1.5, Appendix S1.16), the transects before fire are overlapping in ordination space, indicating that sites that would be burned in 2017 had been similar to unburned sites prior to fire. In the first year after fire (Fig. 1.5) the burned sites shifted to a higher presence of non-native grasses such as *Bromus* and *Avena*, and non-native forbs such as *Erodium*. On

the other hand, the unburned sites in 2018 shifted towards *Artemisia californica* and *Salvia mellifera* which are native shrubs, and towards the native forb *Oxalis albicans* among others. There were significant burn, before/after, and interaction effects in this model (Table 1.3). The interaction effect is of particular interest as that indicates that the burned and unburned site compositions have changed after fire, but in different ways according to whether the transect was burned or not.

Ordinations of the GL transects (Fig. 1.6, Appendix S1.17) showed significant effects of before/after (Table 1.3) and burned/unburned, but no interaction between these two factors and thus no evidence for a direct effect of fire. Instead the differences between the burned and unburned sites were due to differences in community composition that already existed in these sites before fire. CAP 1 separates data points by burn status, driven by the three *Avena* species in the unburned sites and *Bromus diandrus* in the burned sites (Fig. 1.6). A calculation of Moran's I on the cover of these particular species showed little autocorrelation due to spatial proximity of sites (Appendix S1.5). Transects moved through time along the CAP 2 axis. Overlapping with species ordinations in Fig. 1.6, CAP2 seems to show an overall shift with gradual loss of the native grass *Stipa lepida* and increased presence of the invasive forb *Brassica nigra.*

DISCUSSION

Our study led to two major conclusions. First, the two habitat types we studied differed in responses to fire. Vegetation community composition showed persistent decreased native shrubs and increased all other functional groups four years after fire in coastal sage scrub.

In contrast, grasslands showed reduced native perennial grass cover post-fire but were otherwise indistinguishable from unburned grasslands by the first growing season after fire. Second, pre-fire data informed our analysis of recovery, showing how community composition in CSS changed over the four years since fire. It also identified pre-existing differences between burned and unburned grassland site compositions that could have led to an erroneous conclusion of fire-driven conversion from *Avena fatua* to *Bromus diandrus* domination if only post-burn data had been available.

Comparisons of burned and unburned sites after the 2017 Canyon 2 Fire

As most studies of wildfire impacts rely on post-fire data only, we first compare our results for post-fire data with those from other studies in these southern California habitats. Post-fire vegetation cover was affected differently in grassland vs. CSS communities. If we rely on post-fire data only, grassland cover would appear relatively unaffected by fire disturbance, with non-significant differences between burned and unburned sites for the absolute cover of all vegetation types. In contrast, burned CSS had lower native plant cover than did unburned sites, and increased presence of native and non-native forbs relative to overall cover, which also included shrubs. Many of these differences persisted four years after the Canyon 2 fire, with one of the most notable effects being the slow recovery of native shrubs. In mature stands of CSS, native shrubs including *Artemisia californica, Salvia mellifera,* and *Eriogonum fasciculatum* are defining dominant species that use both resprouting and new seedling recruitment to regain vegetation cover after fire disturbance (Keeley et al., 2006; Pausas & Keeley, 2014). Woody shrub cover is also an important factor in preventing invasion from non-native grasses and forbs (Keeley et al., 2005), therefore

extended periods of low native shrub cover are cause for concern for the long-term maintenance of native CSS communities. We observed the same decrease in native shrub cover immediately after fire as observed in many other studies (Kimball et al., 2014; Kimball et al., 2018; Westman, 1981; Keeley & Keeley, 1984). In contrast with these previous studies, however, we found that native shrub cover was still lower than it had been pre-fire after four years. This difference from previous studies was largely a consequence of our classification of *Acmispon glaber (= Lotus scoparius)* as a native forb. We made that classification following its grouping as a perennial herb on Calflora, its recovery strategy as a re-seeder/facultative resprouter, and its initial herbaceous state (Montalvo et al., 2017) which separates it from the crown-sprouting woody shrubs. Similar to our findings, despite concluding that native shrub cover had recovered by four years after the 2007 Santiago fire, Kimball et al. (2018) also documented a shift from *Artemisia californica* to *Acmispon glaber.* As an important dominant native species in the intermediate successional stages after fire, *Acmispon glaber* might help prevent the encroachment of non-natives before the final succession of woody native shrub species in mature CSS, however this relationship needs to be tested directly. Looking at specific species compositions rather than broadly defined categories of vegetation cover allows us to examine recovery based on the return of species previously present, which would yield different conclusions if for example, vegetation was replaced by a different plant species of the same vegetation category.

Comparisons of reseeding forbs and grasses in burned and unburned sites were also mostly consistent with previous literature. A post-fire initial increase in forbs due to

increased seedling recruitment is well documented in shrublands (Keeley et al., 1981; Westman, 1981; Keeley & Keeley, 1984), and was previously observed in grasslands as well (Thomson et al., 2020). Our observations of post-fire CSS forb cover were consistent with these patterns, with higher native and non-native cover in burned sites compared to unburned sites starting in the second year after fire. Although we did not see an effect of burn on the absolute cover of either native or non-native forbs in grasslands, the relative cover of non-native forbs did increase.

There are conflicting accounts on native vs. non-native grass recovery after fire in the literature. Non-native species decline initially in some cases (Thomson et al., 2020), while increasing in others (Larios et al., 2013). The results of our study seem to follow the latter pattern, in which native grasses are not able to recover fully after burn and are replaced by non-native species. Both CSS and grassland transects had low levels of native grass cover after fire, while non-native grass cover was higher in burned compared to unburned CSS starting the second year after fire. One caveat of our study is that we treated each transect as an independent unit of replication, which required us to assume a lack of spatial autocorrelation at the landscape scale. We did test for and find no significant spatial autocorrelation for the two dominant invasive grass genera that defined the later burned and unburned sites in ordination space.

We explored the possibility that year to year changes in cover post-fire could be explained by changes in annual precipitation. Previous studies have shown that non-native plant cover and richness in CSS is correlated with precipitation (Keeley et al., 2006), but high

rainfall also benefited the recovery of native species when invasives were removed in both CSS and grassland (Thomson et al., 2021; Cox et al., 2011). In grasslands, greater cumulative rainfall from the previous year generally led to increased cover for most of the functional groups in both burned and unburned sites in the four years after the Canyon 2 fire, and that could explain some of the year effects observed in time series and detected in the year x burn models for absolute cover. In comparison, precipitation patterns in CSS post fire did not explain the changes in native shrub cover. A lack of a strong response from the native shrubs to precipitation is corroborated in Kimball et al. (2018), but a previous drought experiment showed that extended periods of low water availability does slow shrub recovery after a burn (Kimball et al., 2014). Ultimately, factoring in precipitation helped to explain some of the variation across years, but additional subtleties such as the effect of precipitation before fire on the local fire regime should also be considered (Smith et al., 2019). To fully test this relationship in natural settings we would need data following multiple different burns which occurred in different years from the same ecosystem and region, each with a different post-fire precipitation pattern.

The utility of pre-fire data on vegetation composition

While we found many similarities with previous studies utilizing post-fire data (Keeley et al., 2005; Whelan et al., 2002; Westman, 1981), our pre-fire data, including our rare data on species composition of forbs as well as shrubs, showed that the response to fire was more complicated than indicated by the post-fire data only.

With the inclusion of pre-fire data, post-fire recovery can be defined by two standards: how similar the post-fire community composition is to pre-fire values or how similar burned sites are to unburned sites. The pre-fire community plays an important role in determining the make-up of the post-fire community, from directly contributing seed banks and crown sprouting *in situ* to more indirect effects such as impacting fire severity during the burn (Keeley et al., 2005; Keeley et al., 2008). Comparison with unburned sites post-fire is only informative if burned and unburned sites were similar prior to the fire, which cannot be ascertained without pre-fire data. At the same time, communities are not static, and are prone to slow change over time in response to other environmental variables besides fire. For example, low precipitation for a few years post fire could prevent recovery to the pre-fire condition even when burned sites do converge upon unburned sites that are similarly impacted by low water. A combination of the two comparisons can be especially effective. In our analysis of the grassland data, pre-fire differences in composition contributed to differences between burned and unburned sites after 2017, and post-fire there was a steady shift over time towards less native grass and more non-native forbs irrespective of burn status. In CSS our results from comparing the composition of burned and unburned CSS were consistent with our pre-burn/post-burn comparisons, showing that burned sites four years after fire were still different from both their pre-fire condition and unburned sites. Combining the two comparisons revealed an interaction effect between burn and pre/post-2017 status. The compositions of the groups of burned and unburned sites overlapped each other before the fire in 2017, and while it was expected that the composition of burned sites changed after disturbance, the unburned sites also shifted in composition after 2017. In this case, since we confirmed that the burned and unburned

communities were similar before fire, there is a possibility of attributing the difference between burned and unburned sites to the burn disturbance. Subsequent vegetation recovery can now be compared to the current conditions of unburned sites.

An important use of pre-fire data is the identification of pre-existing differences among sites. As we cannot predict which sites will be affected by fire beforehand, we cannot control for uniform compositions when originally choosing sites for long term monitoring. The compositions of burned and unburned grassland sites differed after fire, mainly due to two non-native grass species: unburned sites having a higher cover of *Avena fatua* and burned sites more *Bromus diandrus*. Without knowledge of pre-fire compositions, this difference may suggest a shift from *Avena fatua* dominated grassland to *Bromus diandrus* after fire, which is the opposite of observations from a previous study in a similar system (Thomson et al., 2020). In reality, comparing the composition of burned sites before and after fire showed a higher cover of the native grass *Stipa lepida* pre-fire, and increases in both *Avena fatua and Bromus diandrus* post-fire, along with non-native forbs such as *Brassica nigra, Hirschfeldia incana,* and *Erodium* species. When we combined burned/unburned and pre-fire/post-fire comparisons we could see that *Stipa lepida* cover was higher before the fire in both burned and unburned sites, with increases in similar non-native species in both burned and unburned sites after the fire event. The differences in *Avena* and *Bromus* presence between burned and unburned sites existed prior to the burn and so were not attributable to the effects of the burn. Due to the continuous nature of wildfire, burned sites were spatially distributed in one area within the fire perimeter, which may mean that proximity led to similar initial community compositions. However

this kind of spatial blocking was unlikely: the study from Larios et al. (2013) which took place within the same area in southern California followed geographically close paired sites of native vs. non-native grass dominated grassland, lending evidence that variation in grassland communities likely exists at a fine scale within the Canyon 2 fire perimeter as well. Our calculations of Moran's I for *Avena* and *Bromus* species cover showed no spatial autocorrelation, which confirmed that there was no clustering pattern of distribution for these species across the landscape.

Combining post-fire observations with our rare instance of pre-fire monitoring data allowed us to confirm pre-existing differences between burned and unburned sites. Looking at community composition rather than functional groups also allowed us to identify the species that drive these recovery patterns. Other studies which include pre/post-fire comparisons exist in two main categories: prescribed fires and remote monitoring. Prescribed fires allow for predictability over sample sizes of burned and unburned sites, and control over the composition of pre-fire conditions. However, prescribed fires and wildfires can elicit different responses from native vs. non-native species (Alba et al., 2015), so extrapolating results from prescribed fire to wildfire effects needs to be further evaluated. Remote sensing studies are able to make use of historical images taken pre-fire and have been used to study the effects of fire severity (Diaz-Delgado et al., 2003), pre-fire heterogeneity (Lee et al., 2014), and even the susceptibility of sites to burn due to pre-fire vegetation composition and subsequent effects on post-fire recovery (Barker et al., 2019). While remote sensing offers advantages of data availability and landscape coverage, it is more difficult to get species-level composition information,

especially on forbs (but see Barker et al. (2019). Ultimately, more long-term field records in fire-prone regions will be necessary to obtain detailed community composition data through time, and to 'catch' more instances of wildfire and post-fire recovery under different environmental conditions so we may clarify the effects of pre-fire composition and other abiotic factors on post-fire recovery.

CONCLUSION

Our results add to the expanding literature on vegetation recovery after fire and highlight the importance of having long-term, large-scale monitoring efforts to ensure the existence of pre-fire data when a wildfire occurs. We were able to examine the recovery of not only shrubs but also specific species of forbs and grasses after a fire with our long-term monitoring data set and make better informed conclusions on recovery by pulling out pre-fire differences in community composition. Many more long-term studies which capture both the pre-fire community and post-fire recovery trajectories of independent wildfires will be necessary to understand how post-fire recovery is altered by accompanying environmental factors.

TABLES

Table 1.1. Sample size of unique CSS and grassland transects monitored as of the end of July 2021 and analyzed in this study. Burn status indicates whether sites were burned in the 2017 Canyon 2 Fire.

Habitat	Burn status	Number of transects
CSS (58)	Unburned	36
	Burned	22
Grassland (39)	Unburned	26
	Burned	13

Table 1.2. Number of taxa in each vegetation subcategory recorded in intercept and quadrat data sets. Non-native shrubs are not listed as they are not present in this dataset. In most cases taxa were identified to species, but 46 (intercept) and 48 (quadrat) taxa are listed at the genus level because of constraints during monitoring resulting in late season identification of dried vegetation matter.

Vegetation Type	Intercept Data	Quadrat Data
Native Forb	152	182
Non-native Forb	44	55
Native Grass	14	17
Non-native Grass	23	21
Native Shrub	57	49
Total	290	324

Table 1.3. Results of canonical analysis of principal coordinates (CAP) analysis of the community compositions of CSS and GL sites. The CAP model included whether the site was burned in 2017 and before/after fire as factors. Bold font: P < 0.05.

Community type	Factor	Df	p-value
CSS	Burned/unburned	1	**0.003**
	Before/after	1	**0.001**
	Interaction	1	**0.001**
GL	Burned/unburned	1	**0.001**
	Before/after	1	**0.013**
	Interaction	1	0.256

Figure 1.1. Absolute cover of growth forms over time. Panels on the left are for coastal sage scrub (CSS), and panels on the right are for grasslands (GL). Error bars represent standard error. The orange box shows years after the 2017 Canyon 2 Fire. Data from sites that were burned in 2017 are shown in red (label Y) while those that were unburnt are shown in blue (N). A: native plants. B: native shrubs. C: Native forbs. D: Non-native forbs. E: Native grasses. F: Non-native grasses.

A
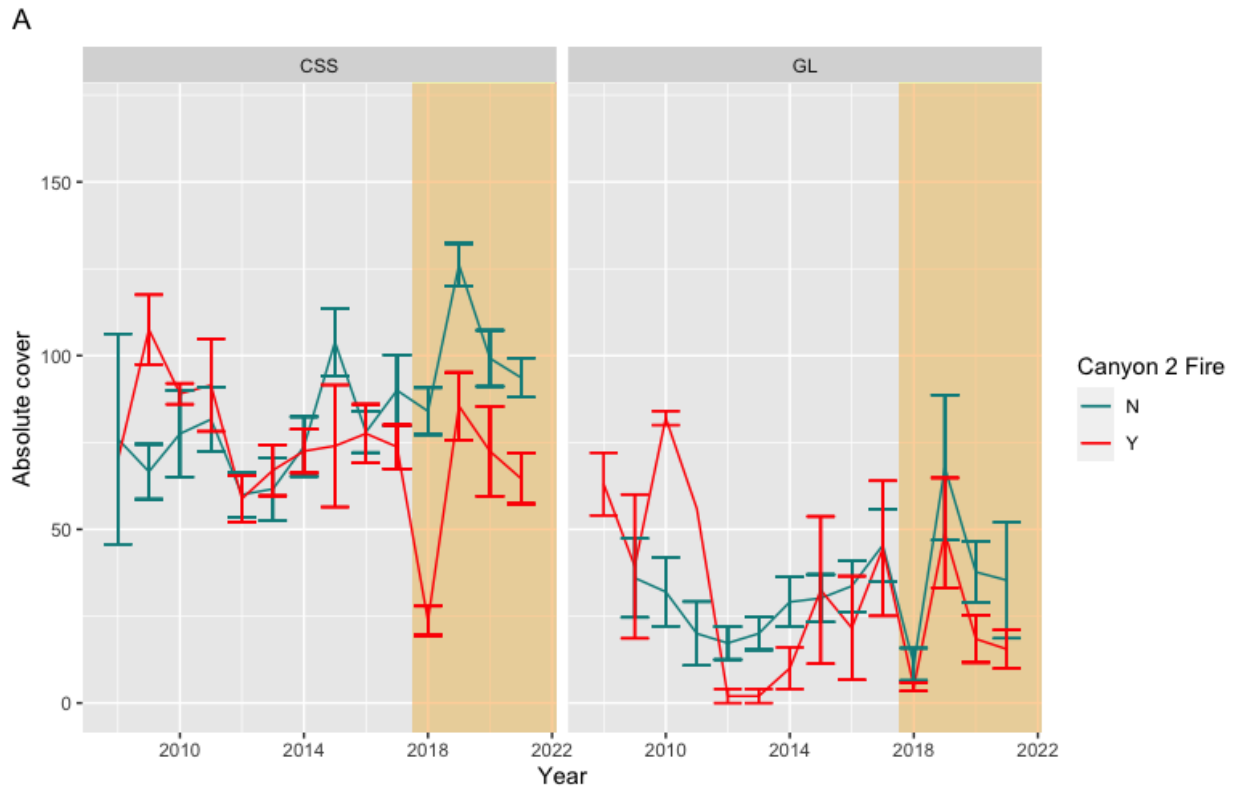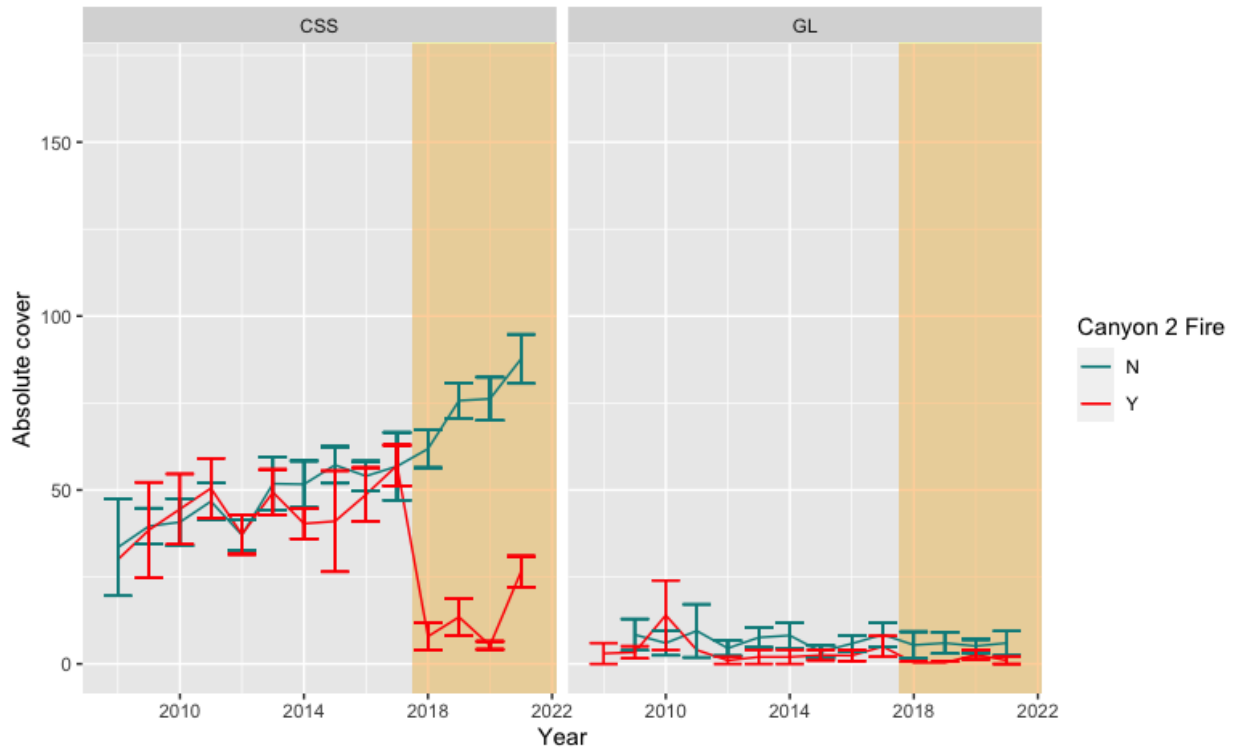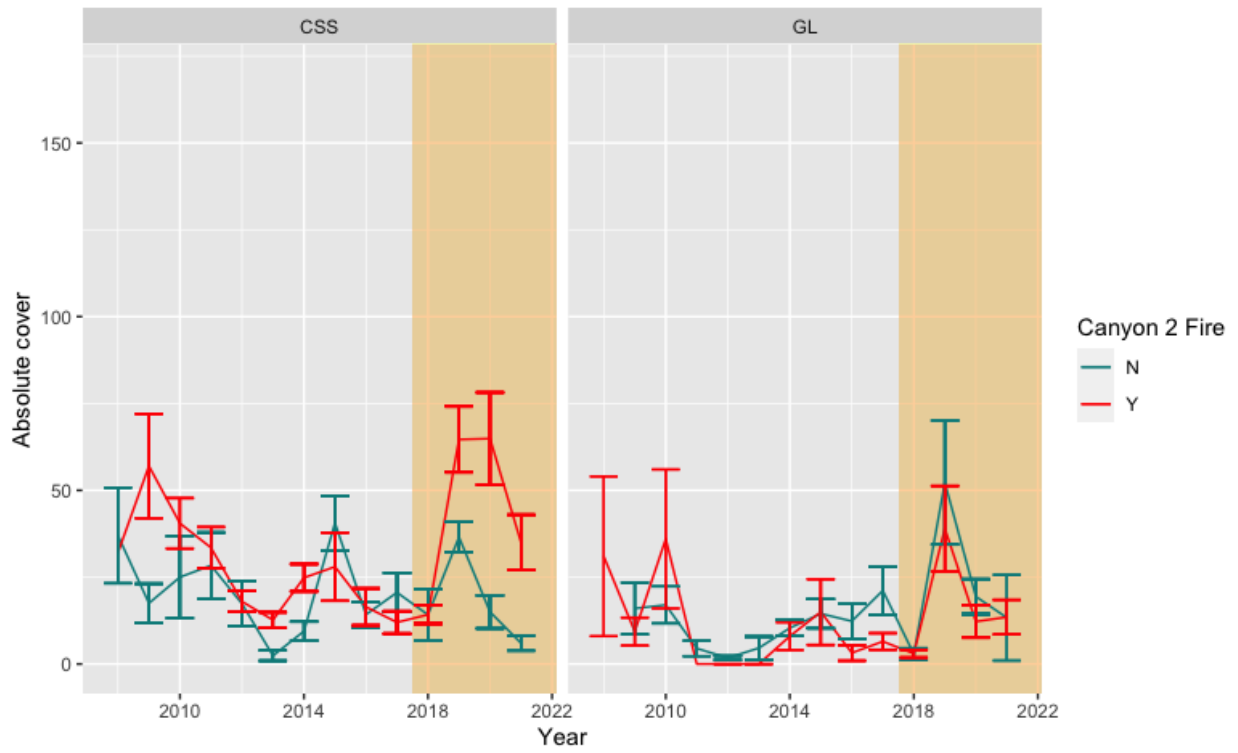
D
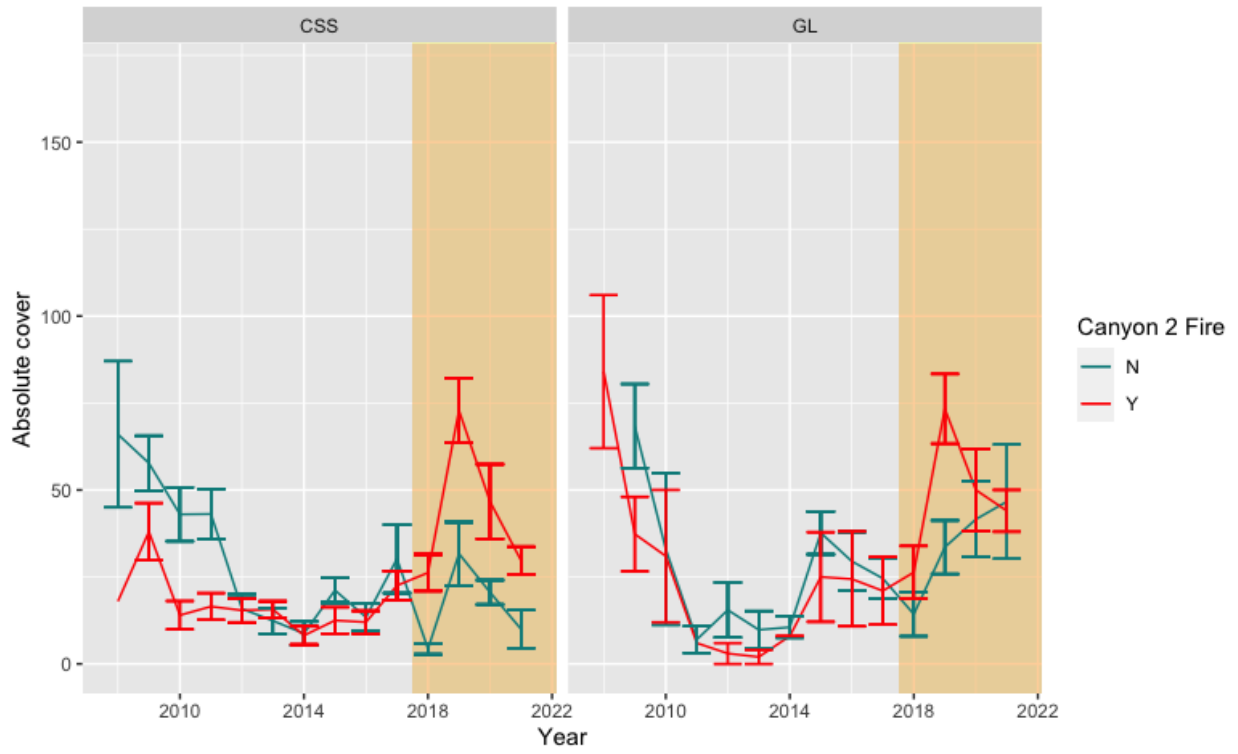
E
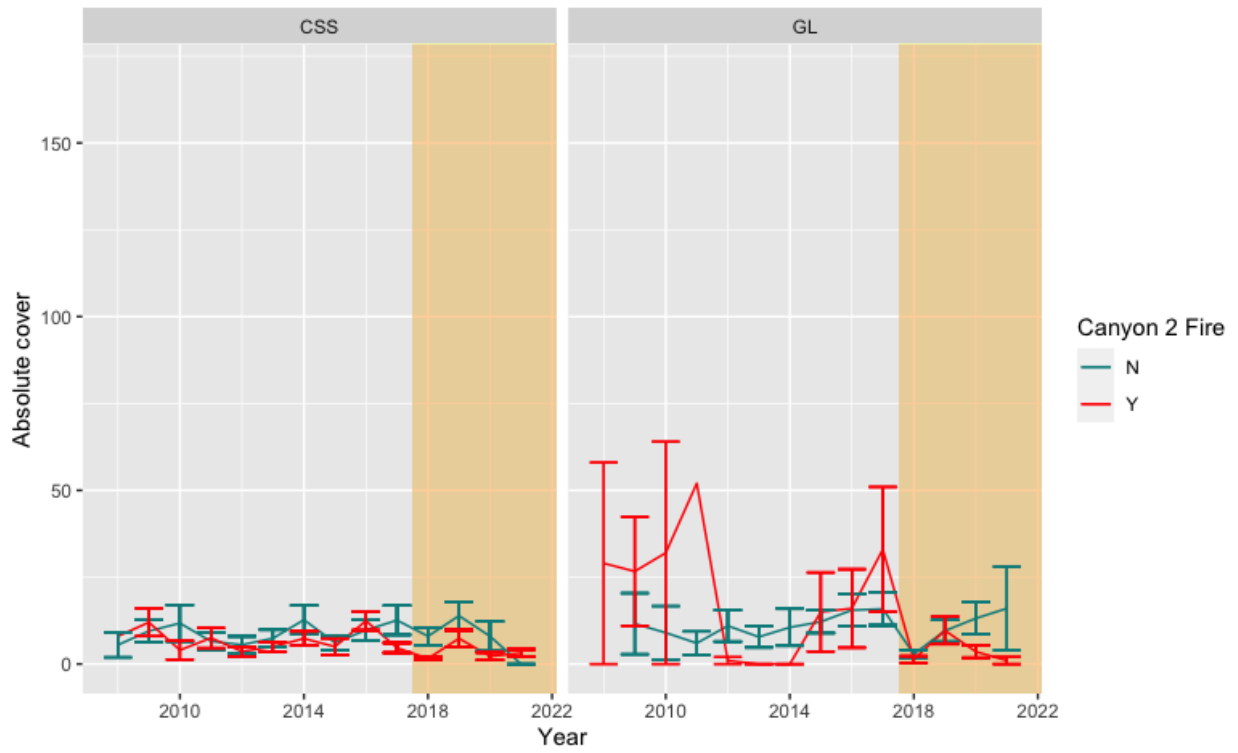
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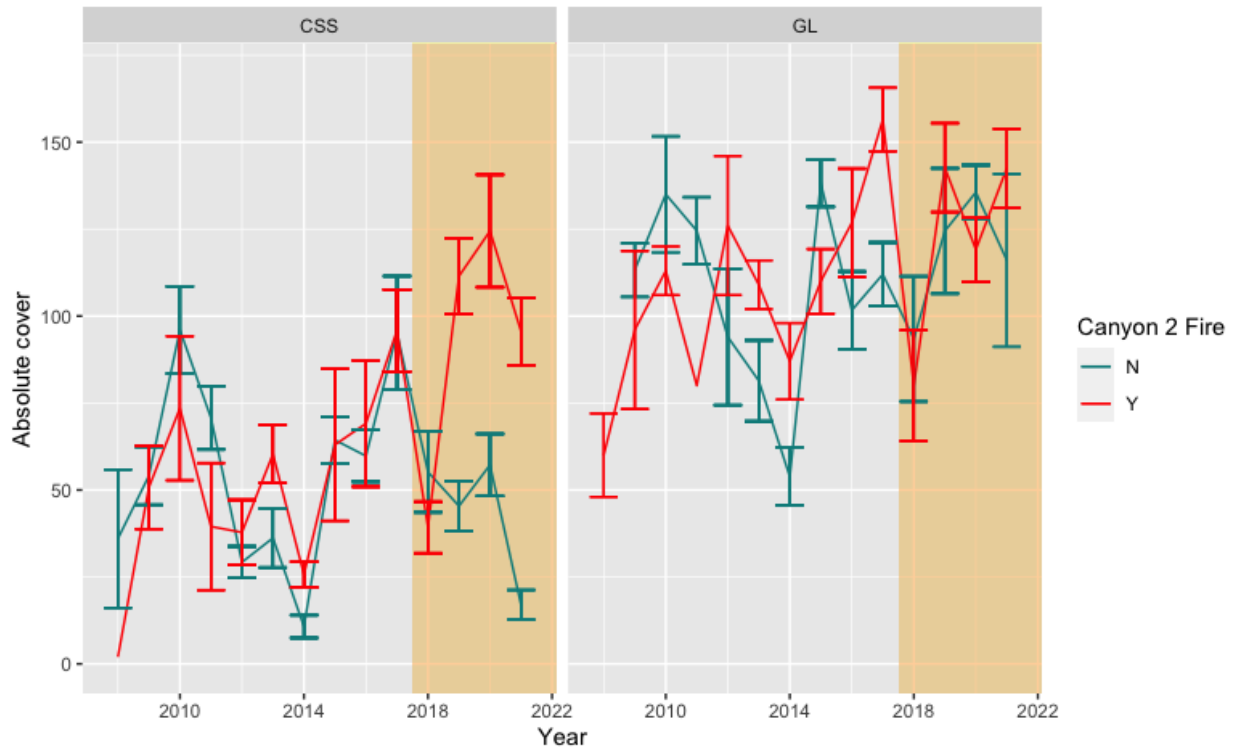
Figure 1.2. Changes in mean a) species richness and b) Shannon diversity index across the years with CSS (left) compared to GL (right) quadrat data. The orange box shows years after 2017. Data from sites that were burned in 2017 are shown in red (label Y) while those that were unburnt are shown in blue (N). Error bars represent standard error.
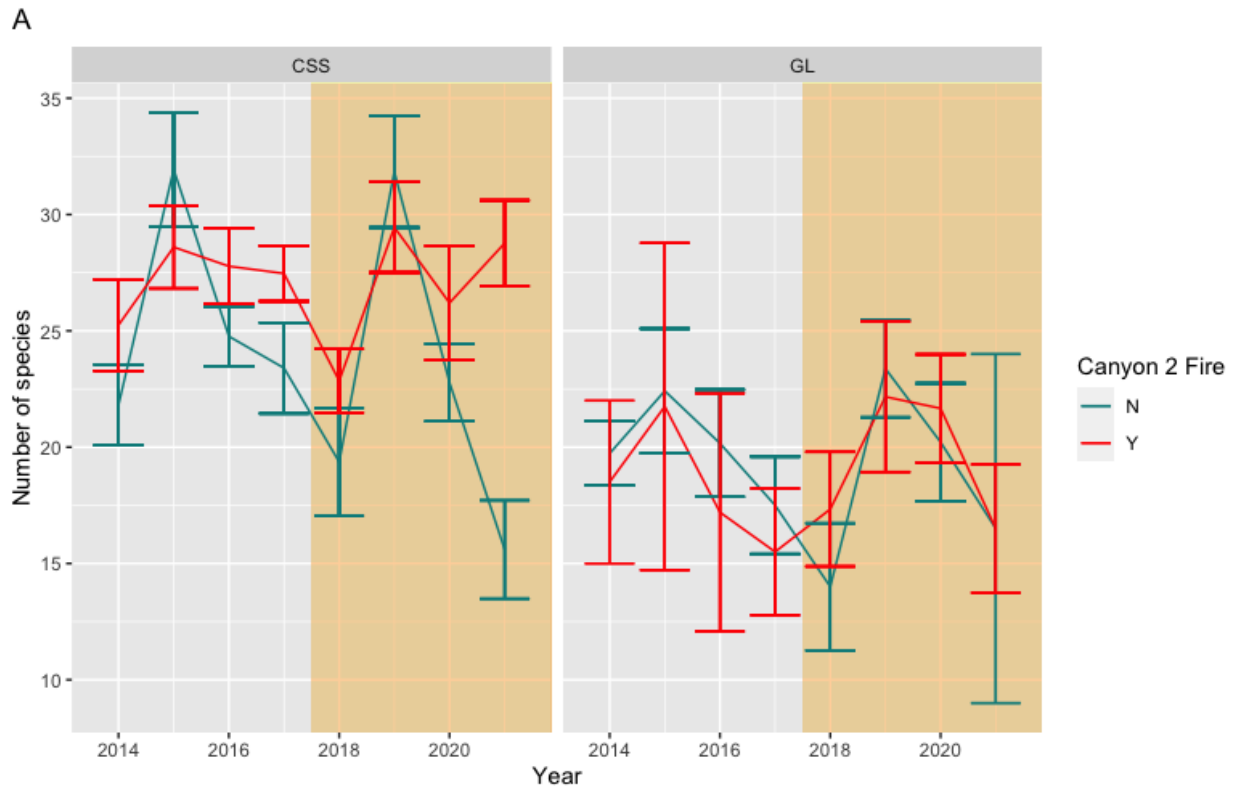
B
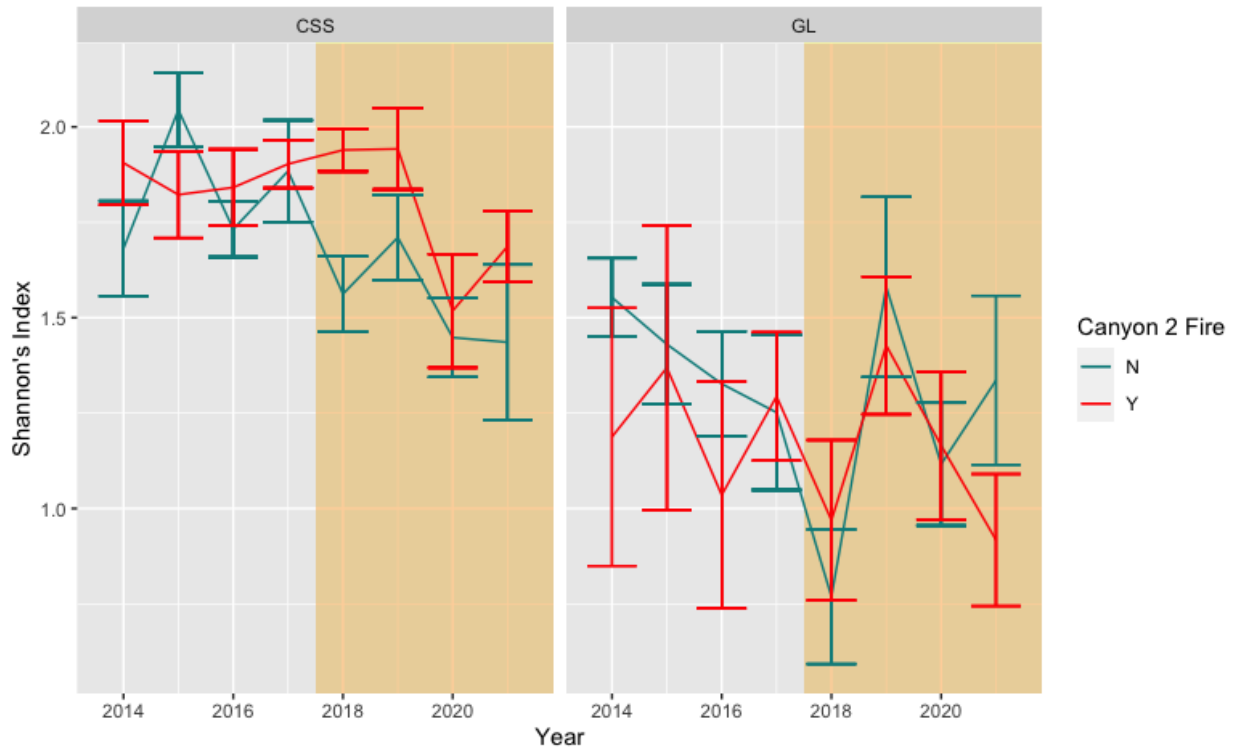
Figure 1.3. CAP analysis of vegetation community composition in burned and unburned CSS sites after the Canyon 2 fires. Total observations = 100, unique transects = 30. The points visualize individual observations of transects, with paths connecting different years' observations from a unique transect. Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Full species names are in Appendix S1.4. Ellipses show the burn/year combination groups with 95% confidence level.
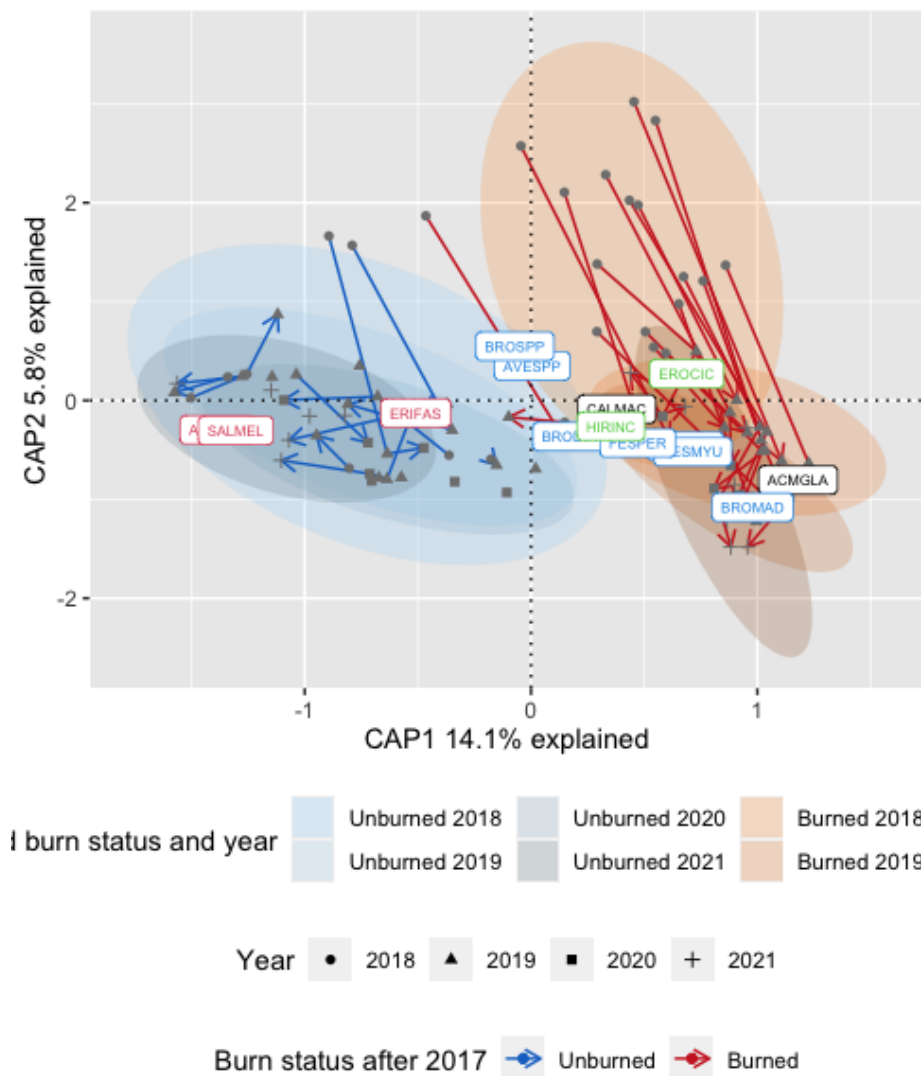
Figure 1.4. CAP analysis of vegetation community composition in the 22 CSS sites that burned in 2017, comparing pre-fire and each subsequent year after fire. Points are connected for each unique transect, showing its trajectory through time. N = 120. Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Full species names are in Appendix S1.4. Ellipses show the burn/year combination groups with 95% confidence level.
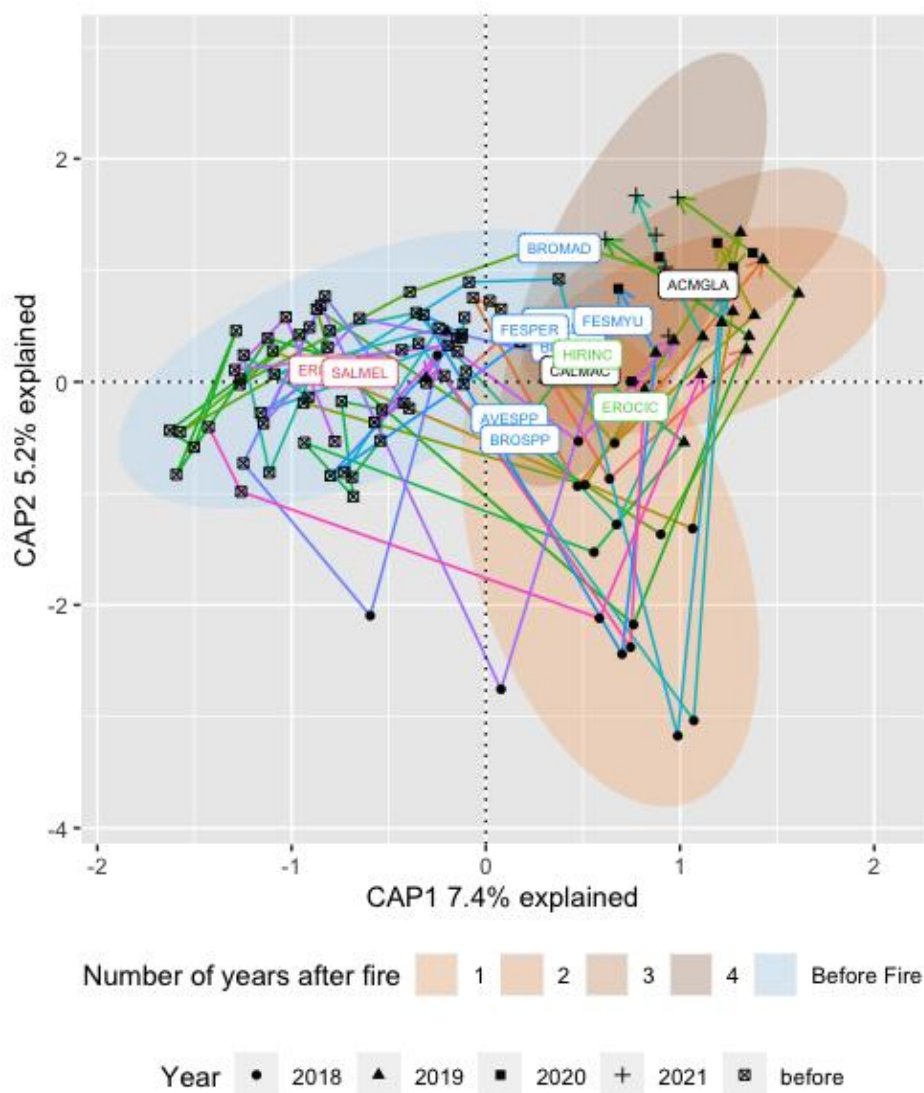
Figure 1.5. CAP analysis of vegetation community composition in burned and unburned CSS sites, before and the first year after the canyon II fires. Unique transects = 47. N=200. Points visualize individual observations of transects and paths connect different years' observations from a unique transect: transects that were burned in 2017 are represented by a red arrow (Y) and unburned blue (N). Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Full species names are in Appendix S1.4. Ellipses show the burn/year combination groups with 95% confidence level.
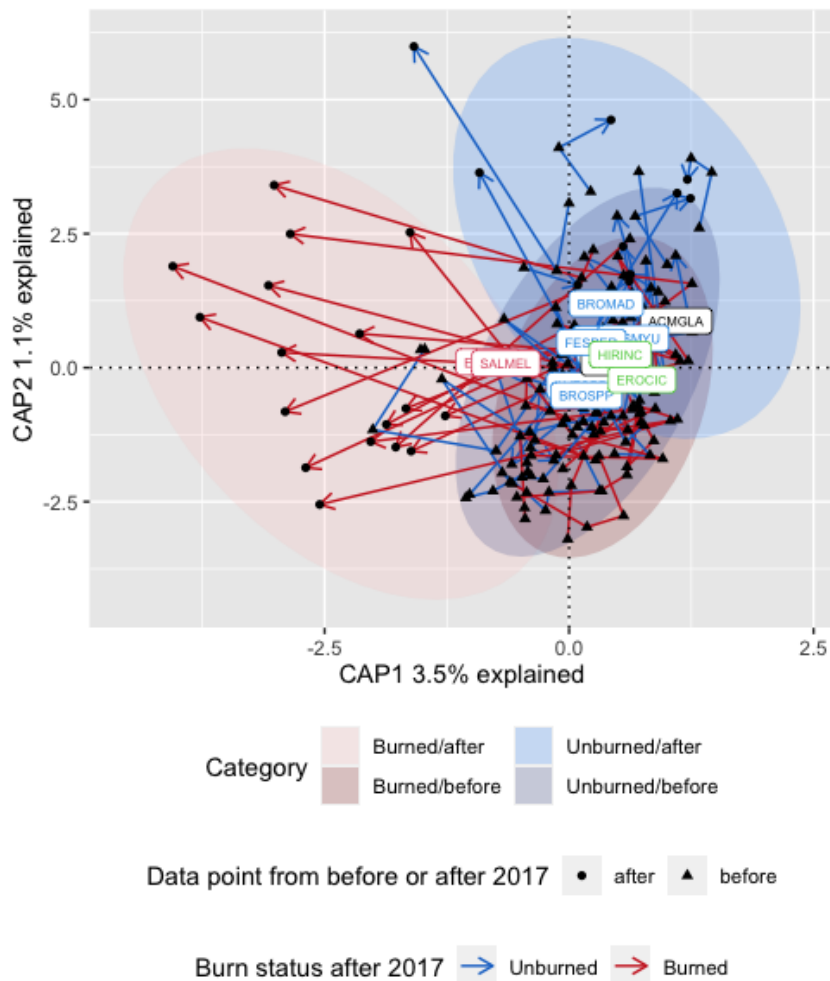
Figure 1.6. CAP analysis of vegetation community composition in burned and unburned GL

sites, before and the first year after the canyon II fires. Unique transects = 35. N=120.

Points visualize individual observations of transects and paths connect different years'

observations from a unique transect: transects that were burned in 2017 are represented

by a red arrow (Y) and unburned blue (N). Species values are overlaid on the same CAP

axes, with labels categorized based on growth form and native status (native shrub = red,

native forb = black, non-native forb = green, non-native grass = blue). Only species with

CAP absolute values greater than 0.3 are shown. Ellipses show the burn/year combination

groups with 95% confidence level.

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CHAPTER 2

Effects of recent burn history on coastal sage scrub flowering

INTRODUCTION

Wildfire is an endemic disturbance in many ecosystems around the world, but many fire regimes are changing in frequency and intensity, affected by climate change (Fréjaville & Curt, 2015; Cary & Banks, 2000). Persistence of local plant species despite fire depends on both initial emergence after fire and subsequent successful reproduction. Initial emergent vegetation associations after fire are a result of species resprouting from surviving burned or below ground structures in pre-fire stands, and germination from seed banks, including the emergence of fire-following species which are rare in more mature stands (Seabloom et al., 2003; Conlisk et al., 2016, Malanson & Westman, 1985; Pausas & Keeley, 2014). Long term recovery of these communities is then affected by the growth and reproduction of this initial stand.

For the approximately 87% of flowering plants that rely on animal pollination (Ollerton et al. 2011), successful reproduction depends on a multi-step process: flower production, attraction of animal visitors to flowers, successful pollen transfer to conspecifics by those visitors, fertilization of ovules by that pollen, and sufficient resources to mature seeds. Perturbations from wildfire to any step of the process can affect reproductive outcomes. In this study we focus on the first step: changes in flower abundance after wildfire. We also include flower size because it, along with other individual floral traits, can affect the next step of attraction of potential pollinators to the plant.

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Flowering can be affected by changes in resource availability. Fire releases resources via burning of above ground biomass, increasing spatial availability, light availability to low-growing species, and nutrient availability in the soil (Christensen & Muller., 1975; Debano & Conrad., 1978; Caon et al., 2014). However, greater investment of resources into flowering can also incur trade-offs with survival, especially after recent disturbance (Brys et al., 2011). Burned sites could differ in reproductive output in the form of flowers per unit area, from either a greater number of flowering individuals or higher flower production per individual. High-flower producing species could draw in more visitors, but also attract pollinators away from less prevalent heterospecifics (Steven et al., 2003), and affect the identity of pollinator visitors (Hung et al., 2019). Previous studies which were focused on small numbers of species have approached the question of reproductive output by counting the number of flowers per individual plant (LoPresti et al., 2018; Borchert & Tyler, 2007, Wrobleski & Kauffman, 2003), but we can also assess these differences through a metric of flowers per vegetative cover, as in Wrobleski & Kauffman (2003). Different outcomes can arise from different resource allocation strategies employed by plants after fire. Vegetative growth and flowering production can both increase with the availability of fire-released resources (resource matching), or resources can be allocated more to vegetation growth or flowering (resource switching) (Borchert & Tyler, 2009). With resource matching, flower number for a given species increases or decreases in proportion with the change in vegetative cover. While burn status still influences flower abundance in this case, the change is directly predictable from the size of vegetative cover compared to undisturbed individuals and has less to do with changes to the species' investment in flowering post-fire. With resource switching, we expect to observe flowers per area of vegetative cover to

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increase or decrease in recently burn sites in a way such that flowering patterns are not directly predictable from comparing the size of vegetative cover with unburned sites.

Changes to flower traits such as flower size could also be indicative of changes in reproductive patterns post fire. Aspects of flowering, such as increased flowering abundances, flower sizes, and greater nectar reward can increase the attractiveness of the plant to potential pollinators (Conner & Rush, 1996; Campbell et al., 1991; Gallagher & Campbell, 2017; Parachnowitsch et al., 2019), which may eventually lead to greater reproductive fitness. However, the identity of the local floral neighborhood, relative abundances and the attractiveness of neighboring heterospecifics can also have competitive and/or facilitative effects on pollinator visitation (Bruckman & Campbell, 2016; Campbell & Motten, 1985, Morales & Traveset, 2008). It is less clear whether individual flowers in large displays receive greater visitation and whether individual flower size influences visitation rate, with some evidence of increased attractiveness to pollinators (Bell, 1985; Eckhart, 1991; Connor & Rush, 1996). Higher investment to produce larger flowers could also incur tradeoffs with the number of flowers produced (Sargent et al., 2007**).** Observations of changes in flowering investment, such as fewer flowers produced per vegetative area post-fire, could be offset by larger flowers produced, and vice versa.

In this study, we examine flowering within coastal sage scrub (CSS) ecosystems at various post-fire stages in southern California. Mature stands of southern California CSS are characterized by dense canopies of native perennial shrubs, such as *Salvia mellifera* and

Artemisia californica, and an understory of mostly annual forbs and grasses (Westman., 1981). Previous studies on post-fire vegetation succession have identified an initial increase in diversity of plants the first few years after fire, followed by a decline back to the shrub dominated mature stands (Keeley et al., 2005; Whelan et al., 2002; Keeley & Fotheringham, 2003; Westman, 1981). The increased post-fire diversity is a result of a combination of factors, including the increased presence of many forb species which were previously suppressed by dominant shrub canopies, and emergence of species which require fire as a trigger for germination (Zirondi et al. 2021). The first few growing seasons after fire could be an important window of opportunity for increased reproductive output and seed banking for these flowering forbs, before the more dormant period of suppression by shrub returns. Fire-stimulated flowering has been observed in many species in Mediterranean-climate ecosystems across the world (Zirondi et al., 2021; Pyke, 2017; Lamont & Downes, 2011; Keeley, 1987), contributing to increased presence of these species in the first few years after fire (Keeley & Keeley, 1984). Post-fire changes to flowering phenology, including increased synchrony and extended flowering seasons (Richardson & Wagenius, 2021; Wagenius et al. 2020; Mola & Williams, 2018) could also alter the community composition at different points across the flowering. In chaparral and coastal sage scrub, studies of fire impacts on flowering are rare. Although one study on post-fire seedling recruitment and above ground biomass included observations on initial flowering in the first years after fire (Keeley & Keeley, 1984), the focus was not on the abundance of flowers nor on flower sizes.

Using flowering data collected during the peak blooming periods of 2021 and 2022 from transects featuring three different burn histories, we address the following questions related to fire history: (1) How does recent fire history impact coastal sage scrub flowering diversity and community composition? (2) What influence does it exert on flowering abundance? (3) How does it affect flower size in individual species? For metrics related to flower abundance, we also examine effects on flowering intensity using the metric of flowers per vegetative area, to see whether changes in flowering can be attributed to genuine shifts in flowering efforts or are merely proportional to changes in vegetation cover.

Materials and Methods

Study Sites

We collected flowering and vegetation data from 22 transects spread across an area of ~20km2 in Orange County, California, USA in the spring of 2021 and 2022. The transects are a subset of those previously established as a part of a long-term vegetation monitoring project by the Center for Environmental Biology at UC Irvine in partnership with The Nature Conservancy and the Natural Communities Coalition (Kimball et al. 2018). The sites were classified as coastal sage scrub based on an initial visual assessment of the dominant vegetation types in the field at first establishment. Recent fire history of the sites fell into three categories: recently burned (7 sites, burned in fall 2020), intermediate burned (4 sites, burned in fall 2017), and old burned (11 sites, over 10 years unburned). We changed our burn status terminology from chapter 1 (burned/unburned) as ch1 deals with burned vs unburned comparisons of one fire, while ch2 and ch3 look at multiple fire histories.

Data Collection

Data collection occurred from mid-March to late May, corresponding to the peak flowering season in the area. To account for changes in flowering across the season, all transects were visited three times in consecutive rounds, except for three sites in 2021 when one recent burn site was observed only in the first round and one intermediate and one old burn site were observed only in the second and third rounds. Each transect consisted of a 50m linear line marked by two permanent rebars marking the start and end points, and 1x1m quadrats distributed in 5m intervals alternating left and right of the transect line, drawn by a 50m measuring tape. To account for flowering species richness and diversity at the transect, all species with open flowers within 1m of the transect line were identified and recorded. Flower abundances were recorded for all quadrats, counting the total number of open flowers for each species in bloom or estimating high blooming species by counting the average number of open flowers on 10 randomly selected inflorescences and multiplying by the number of flowering inflorescences. Photos were taken above each quadrat to allow us to estimate vegetative cover of common species, and photos of open flowers were taken next to a ruler for up to 10 individuals per species per quadrat, and flower length and area were measured using ImageJ (version 2.3.0), using the ruler in the photo for calibration. The plane at which flowers were photographed varied between species, with consideration to which plane would yield consistency in measurements. Once chosen, the plane of photography for the individual species was kept consistent to allow for within-species comparison. For example, *Salvia mellifera* were photographed from the top, where the bilateral symmetry of the flower was visible, while *Acmispon glaber* was

photographed from the side due to the individual curvature of flowers, which would alter top-down measurements depending on the extent of curvature.

Analyses

Plant species were categorized into native vs non-native species and flowering shrubs vs forbs using the Calflora database (https://www.calflora.org/). All analyses were conducted in R version 4.2.3. A total of 74 different flowering species were recorded over the course of two flowering seasons. However, as many species were rare, and some were only present on one burn category of transects, only four common species with high vegetation cover were selected for analysis of flowering intensity. We also created a subset of 8 of the more common flowering species for size analyses based on the following criteria: (1) observed in more than one burn category, (2) observed in two or more transects per burn category, (3) each observation included more than 2 flowers counted.

Diversity

To compare the flowering alpha species richness (S, total number of species) and diversity (H, Shannon's Index) between different burn status, we used two methods of calculating diversity metrics (1) season average, and (2) season total. Season averages were calculated by averaging richness and diversity metrics calculated from individual visits to the transects (3 per year), and therefore better capture the average state of the sites across the season. Season total metrics were created by first aggregating all data from the transect across the season, and then performing the calculations for species richness and diversity. This second method accounts for all species seen on the site across the season, and

compared to the season average calculations, doesn't include repeated observations of species with extended flowering times across multiple visits. Statistical tests comparing species richness and diversity between transects of different burn statuses and accounting for observation year were performed using linear mixed effect models (LME function, R nlme package 3.1) with burn status and year as interacting factors and transect as random factor accounting for repeated observations. Post-hoc Tukey tests through the glht function (R multcomp) were applied after linear models to determine which pairs of burn categories differed.

Flowering abundance and intensity

We calculated average flowering abundance through summing all species' flower counts from all quadrats in each single observation and then averaging the values of all visits across the season for each transect. We averaged quadrat numbers before averaging across transects to better account for the high heterogeneity in flower counts from quadrat to quadrat across our transects. Average flowering abundance was then compared between the different burn statuses with a linear mixed effects model, using year and burn status as interacting fixed effects and transect as a random effect, due to each transect having two replicates representing the two years of observations.

To further pull apart whether differences in flowering abundances were simply due to correlation between plant size and flower number, or whether there were changes in the number of flowers produced per unit vegetation area, we calculated flowering intensity for four selected species by first dividing the flowering abundance of individual species in each

quadrat by their corresponding vegetation cover. Whereas vegetation cover does not capture possible variation in plant height that could also contribute to plant size, we wished to see how well that commonly used metric predicted flower density. Vegetation cover values were determined by looking at top-down quadrat photos and estimating species' cover as a % of the 1x1m square. Species which were present but had less than ~1% cover were designated a cover value of 0.1%. Transect averages were calculated for each species by averaging all quadrat values. We performed a Mantel test between the flower count and vegetation cover matrices and analyzed flowering intensity for each of the four species using linear mixed effect models with burn status and year as interacting factors and transect as random factor accounting for repeated observations.

Flower size

We obtained both length and area measurements for each flower image taken in the field using ImageJ. We calibrated the size by first setting the image scale through drawing a known length along the closest edge of the ruler used in the photo to the open flower and then measured the area. Measurement methods were kept consistent within species but sometimes differed between species with different morphologies. For example, the opening of the *Calystegia macrostegia* corolla (Convolvulaceae) could vary greatly depending on its blooming stage, so the flattened side profile was photographed and measured instead. For each flowering species present per transect visit, we calculated averages of flower area over the quadrat and then averaged the quadrat values for that transect visit for each individual species. We analyzed flower measurements for each species individually, using

linear mixed effect models with burn status and year as interacting factors and transect as random factor accounting for repeated observations.

Composition

We used canonical analysis of principal coordinates (CAP) implemented through the capscale function (R vegan 2.6) to analyze composition of flower abundance and flowering intensity. CAP is a constrained ordination which allowed us to collapse the multivariate data from the community of flowering species into explanatory axes which best expressed the species variation separated into the groups incorporated into the model based on Bray-Curtis dissimilarity (Anderson & Willis, 2003). We analyzed flowering abundances (all species) with CAP models, using year crossed with burn status as categorical variables. We used the anova.cca function to test for significant effects of the factors in the model and examined the differences among groups by their separation on the first two CAP axes, which usually explains most of the variation among groups.

RESULTS

Diversity

Total flowering richness across the season was affected by burn status, (Fig 2.1, Table 2.1, p=0.0269, p<0.05) and year (p=0.00305), but not the interaction between year and burn (p=0.188), with higher richness in 2022 compared to 2021, and recent burned and intermediate sites compared to old burned sites. Average season richness across the multiple samplings was influenced by both burn status (Appendix S2.1, p=1.51e-06, p<0.05) and year (p=0.00123, p<0.05) but not interaction between year and burn

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(p=0.074), with the highest richness in recently burned sites, followed by intermediate, and lowest in old burned sites. Average flowering richness also increased in the 2022 season compared to 2021.

Shannon diversity was impacted by burn status (fig 2.2, p=0.0305, p<0.05), year (p=0.014), and the interaction between burn status and year (p=0.000162, p<0.05) for the seasons as a whole, with higher diversity in recent burned sites compared to old burned sites, while intermediate sites were closer in value to recent burned sites in 2021 and to old burned sites in 2022. Burned sites had the highest season averages of Shannon diversity (Appendix S2.2). Burn status (p=0.0416), year (p=0.0013), and the interaction between burn status and year (p=0.0056) were all significant in this analysis based on season averages.

Abundance and intensity

Cumulative flower count of all sites was higher in the 2022 growing season compared to the 2021 growing season for all burn statuses, particularly for the intermediate sites and the recently burned sites (fig. 2.3), which had large increases in flowering of two mass flowering species: the native forb *Acmispon glaber* in intermediate sites and the native shrub *Salvia mellifera* in old burned sites. Average transect flower counts were also higher in 2022 compared to 2021 (p= 0.00037) but burn status (p=0.539) and the interaction of burn status with year (p=0.21) did not have a significant effect.

Flowering intensity was calculated for four high flower-producing, abundant species: the native shrub *Salvia mellifera,* subshrub *Acmispon glaber,* and the non-native forbs *Hirschfeldia incana,* and *Brassica nigra* (fig. 2.5). These species were chosen because they

were present in sites across different burn statuses, and had large enough vegetation covers for visual estimations. Mixed models analyzing transect intensity averages with burn status and year as fixed effects and transects as random effects showed only a significant effect of year for *Salvia mellifera* with higher flowering intensity in 2022 compared to 2021(p=0.0039), and a significant interaction between year and burn status for *Acmispon glaber* in which flowering intensity was highest in intermediate burn sites in 2022 but showed no significant differences among burn statuses in 2021 (p=0.0112).

Flower size

Out of the 8 species analyzed, only the native shrub *Salvia mellifera* and native forb *Gilia angelensis* showed any significant differences in flower size amongst the different burn categories. In recently burned sites, *S.mellifera* did not produce any flowers in the first year after fire in 2021 (fig 2.6), but in 2022 produced larger flowers (mean of area = 33.4mm2) compared to intermediate (29.2mm2, p=0.028), and old burned sites (25.3mm2, p=0.0001). *Gilia angelensis* flower areas were significantly affected by burn status (p=0.01391), where flowers in burned sites (27.5mm2) were significantly larger than in intermediate sites (18.6mm2, p = 0.022), but not old burned sites (24.3mm2, p=0.15).

Composition

Using constrained ordination with all counted species included, we observed separation of the composition of the three burn categories and between the two years. Recently burned sites and old burned sites overlapped very little, but intermediate sites overlapped with both others along the CAP1 axis (fig 2.7. p = 0.001 (ANOVA.cca), 5.3% of variance

explained), corresponding with higher flowering abundances of native shrubs towards intermediate and old burned sites, and more native and non-native flowering forbs, including known native fire followers such as *Phacelia parryi* and *Emmenanthe penduliflora* in recently burned sites. Intermediate sites differed the most from recent burned and old burned sites along the CAP2 axis (p=0.001, 4.2% of variance explained), with increased *Acmispon glaber* presence in intermediate sites in 2022, and the presence of native forbs such as *Calandrinia menziesii* and *Uropappus lindleyi* in intermediate sites in 2021. Intermediate sites had the least overlap between the two years of observations, and 2022 intermediate site compositions were more similar to old burned sites in the same year than they were to themselves the previous year. Composition based on flowering was correlated with composition based on vegetative area (Mantel correlation = 0.093, p = 0.01), but the relatively low correlation indicates that other unexplained variables influence flowering intensity.

DISCUSSION

The impacts of recent fire on vegetation recovery is historically well studied in coastal sage scrub (Westman, 1981; Keeley & Keeley, 1984; Keeley et al., 2005), with less known about how flowering of the entire community, including shrubs, is affected. We found that recent fire history increased flowering diversity and affected community composition, but largely in a way predicted by vegetation recovery patterns found in previous studies. Flower size was similar across burn statuses for most species. *Salvia mellifera* was an exception; it did not flower the first year and had larger flowers than in old burned sites the second year after fire. However, we found no evidence to support differences in *Salvia mellifera*

flowering intensity across burn categories, with the same holding true for two other species tested (*Brassica nigra,* and *Hirschfeldia incana*), with the exception that *Acmispon glaber* increased flowering intensity (flowers per unit area) in intermediate burned sites over other burn categories in one of two years. Our results suggest that general patterns of post-fire flowering in southern California CSS can be accounted for through association with vegetation composition without needing to consider alterations in flowering intensity, although there are a few species-specific differences that could be important.

How does recent fire history impact coastal sage scrub flowering diversity and community composition?

Vegetation covers of coastal sage scrub at different post-fire stages may directly explain our observed patterns in floral diversity and composition. Our results indicate a higher flowering diversity in recently burned stands, with compositions that favor more flowering forbs compared to shrubs in older burned areas. Mature stands of CSS consist of a dominant canopy of native shrub, with forbs and grasses limited to grow below the cover and/or within canopy gaps (Gray 1982). Fire disturbance changes this dynamic by clearing above ground vegetation, opening spatial resources and contact with sunlight for a few growing seasons as the perennial shrubs resprout or germinate from seed regrow their vegetation cover. Fast-growing herbaceous annuals can take advantage of these gaps by sprouting from seedbanks, including fire followers which appear more frequently, after recent burns. For example, *Emmananthe penduliflora* was observed to be in flower only in our recently burned sites and contributed both to vegetation and flowering community compositions. As a result, there are higher levels of vegetation species richness and

diversity observed in the first few years after fire, and community composition differs from mature stands through lower shrub and higher herb presence (Keeley & Keeley, 1984; Westman, 1981). Looking across studies of different Mediterranean ecosystems, a few circumstances could result in differences in flowering diversity and composition compared to vegetation presence. For example, fire stimulated flowering, where species do not flower unless there has been recent fire disturbance (Lamont & Downes, 2011; Zirondi et al, 2021) could increase flowering diversity after fire. Conversely, delayed reproduction/flowering in some resprouting perennials while vegetation is recovering (Keeley & Keeley, 1984) could decrease flowering diversity more so than vegetation diversity. In our study we did find delayed flowering in *Salvia mellifera,* but the relatively few perennials compared to the increase in presence of flowering annuals meant that there was still an overall increase in flowering diversity following fire.

How does recent fire impact flowering abundances?

The overall lack of significant differences among burn statuses in average flowering abundances and intensity suggest that floral production may not have been strongly affected by recent burn in coastal sage scrub. Species can vary in how fire impacts flower production; for example, there is evidence of increased head counts in some prairie asters but no effect on others (Richardson et al., 2023) after recent burn. Higher flower production in the first years after fire has been observed in a herbaceous species in southern California chaparral (Borchert & Tyler, 2009), and speculated to be due to higher light and nutrient availability immediately after fire allowing for resource matching of leaf growth and flower production, while this is later replaced by resource switching with

alternating flowering years as sites recover and resources are more scarce. In contrast, woody re-sprouters can allocate more resources to vegetative structures that enhance long term survival after fire (Knox & Clarke, 2005), which could mean lowered investment to reproduction. In our study, total cumulative flower count of all sites in each burn status category differed greatly between the two years, but the counts were heavily influenced by mass flowering species *Acmispon glaber* and *Salvia mellifera* which had high presence in intermediate and old burn sites, respectively, and had low flowering in 2021 followed by high flowering in 2022. Variation in other environmental factors such as annual precipitation could cause these year-by-year differences in flowering (Inouye et al., 2003), and as our study only encompasses two years of observations and the effects of two burns, we were not able to reliably separate the effects of burn and other environmental effects on flower count.

We included flowering intensity as a measure of flowering effort that distinguishes whether increased flowering simply reflects increased vegetative growth, or not. In northern California chaparral, *Trichostema laxum* with larger flower displays were found in recently burned areas, but they corresponded with larger individuals rather than more flowers produced per vegetative area (LoPresti et al. 2018). Changes in flowering intensity were not observed in the four large, abundant flowering species we selected, and burn status did not impact the number of flowers produced relative to the size of the plant for the four species we analyzed. Amongst our four species, only *Salvia mellifera* is a post-fire resprouter, whilst the others develop from seed after fire disturbance. Differences between a resprouting vs seeding species post fire have previously been observed in a transition site

between pine forest and chaparral in southern California, with increased flowering intensity in the seeding species (Fulton & Carpenter, 1979). Our measure of vegetation size is based on a birds-eye view of quadrats and doesn't consider the number of individuals or the height of plants. The lack of information on individual plants means we could not calculate intensity for smaller forbs, where the total vegetation area was less than 1% of our quadrats, and information on plant height, particularly for larger species, would have given a better overview on the size of the plant.

How does recent fire affect flower size?

Out of all the common species observed, we only found significantly larger flowers in *Salvia mellifera* in recently burned sites in the second year after fire, following one year of non-flowering. Few studies have looked at changes to flower morphology and size after recent fire disturbance, but there is reason to speculate that there is high variability depending on flowering species as well as the effects of other compounding environmental factors such as light availability (Aizen & Vazquez., 2006). Effects of recent burn on overall community flower sizes appear to vary when comparing different paired burned and unburned localities across a landscape, though comparisons where only common species were included found the same overall lack of difference that we saw in our study (Burkle et al., 2019). Measurements of flower size following other types of disturbance such as drought also suggest that the cost of producing larger flowers can vary even within species (Galen 2000). There are also possibly tradeoffs with other flowering traits such as abundance (Sargent et al., 2007), or investment into nectar production (Lamont 1985; Ne'eman & Dafni, 1999; Potts 2003).

Implications for reproduction

Post fire flowering in coastal sage scrub, as well as subsequent pollination and seed set, is less well studied compared to in other Mediterranean regions. We observed patterns of flower density that were similar to those for vegetation recovery drawn from previous studies in the same region, with higher richness resulting from more forbs on the landscape immediately after fire, along with higher evenness due to a lack of dominant, high-flowering species which appear later in post-fire succession.

Ultimately, flower production is one of many-steps that lead to successful reproduction. Increased flowering effort after fire could play a part in increasing successful pollination by attracting more pollinator visits through higher flowering densities (Mola & Williams, 2018) or display sizes (LoPresti et al. 2018, Kuppler et al., 2021; Eckhart 1991). Other plant traits that we did not account for, such as increased nectar production (Fulton & Carpenter, 1979, Potts et al., 2003) and increased flowering synchrony and season length (Mola & Williams, 2018) can also increase pollinator visitation and could have been changed by fire. The next step will be evaluating whether recent burn influences the chance of a flower being visited by a pollinator, a metric that could respond not only to effects of plant traits, such as the flower size measured here, but also to independent effects on pollinator abundances due to nesting resources (Burkle et al. 2019), which are largely unknown for coastal sage scrub. Gaining more information on the post-fire dynamics of flowering and subsequent pollination can allow us to better understand the process of post-fire recovery beyond that of vegetation presence.

TABLES

Table 2.1. P values from mixed-model ANOVAs on the effect of year (2021 vs. 2022), burn status (recent, intermediate, old burned), and year by burn interaction on season average and season total transect metrics of flowering species richness and diversity

	df	Species richness (S)		Species diversity (H)	
		Season avg	Season total	Season avg	Season total
Year	1	**1.51e-06*****	**0.00305****	**0.0416***	**0.0305***
Status	2	**0.00123****	**0.0269***	**0.00128***	**0.014***
Year x Status	2	0.0744	0.188	**0.00562****	**0.000162*****

* P < 0.05. ** P < 0.01. ***P < 0.001

FIGURES

Figure 2.1. Boxplots of total season flowering richness for transects per year. Observations are separated by burn status across the different panels.
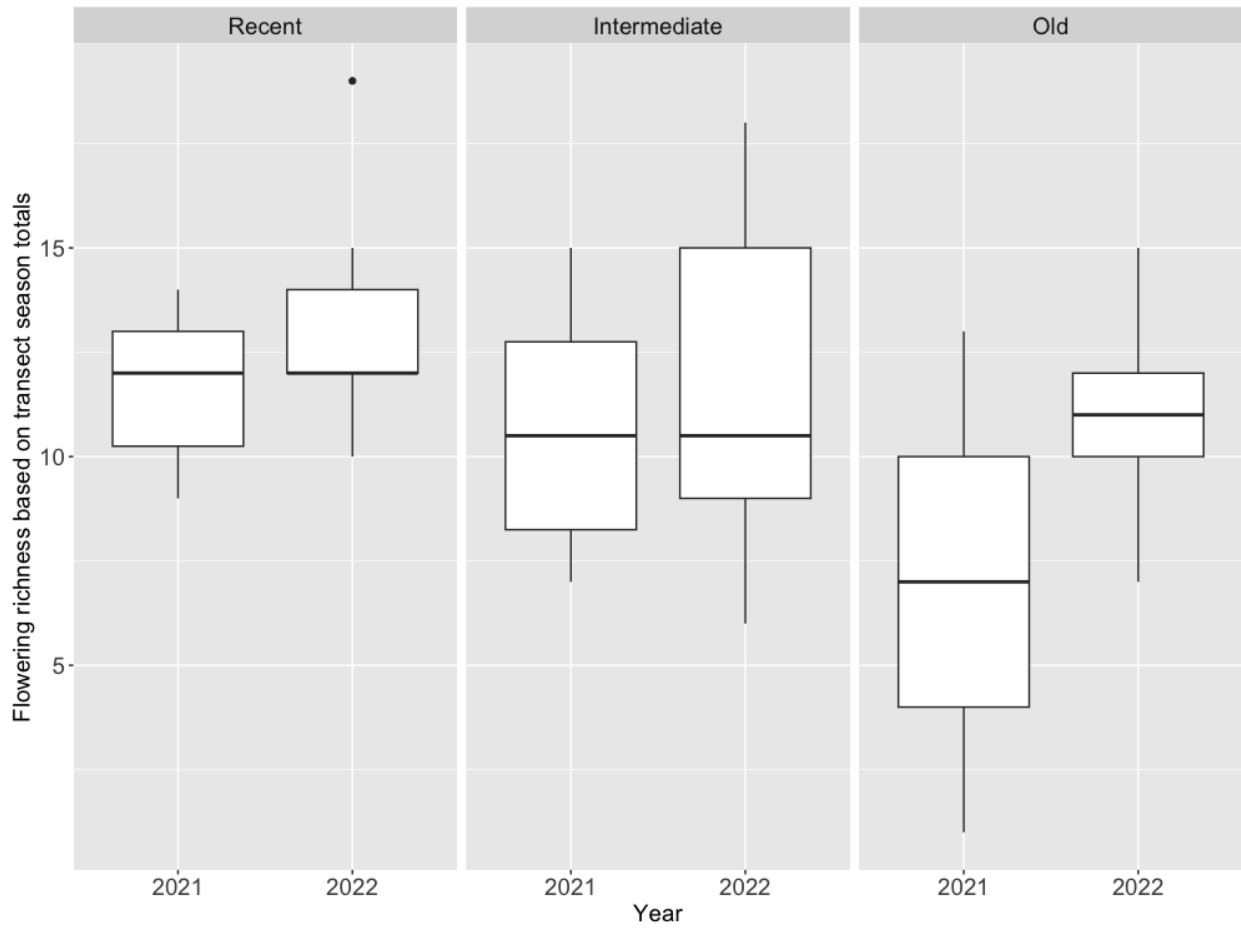
Figure 2.2. Boxplots of season flowering diversity for transects per year. Observations are separated by burn status across the different panels.
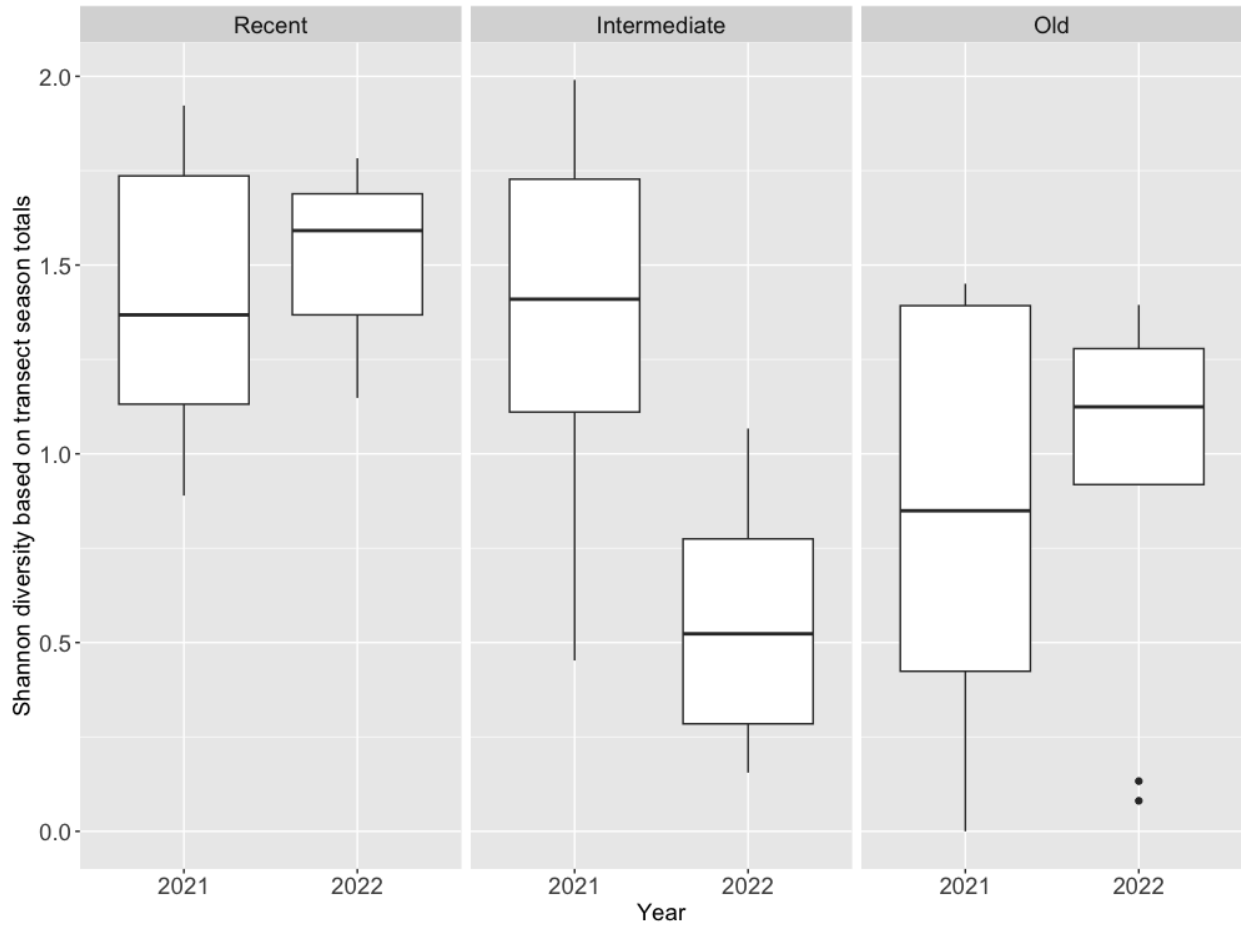
Figure 2.3. Total flowering abundances of all species from all transects in both years of data collection, separated by burn status and year. Flowering counts are categorized by species classification as non-native forb (NN_Forb), native shrub, and native forbs.
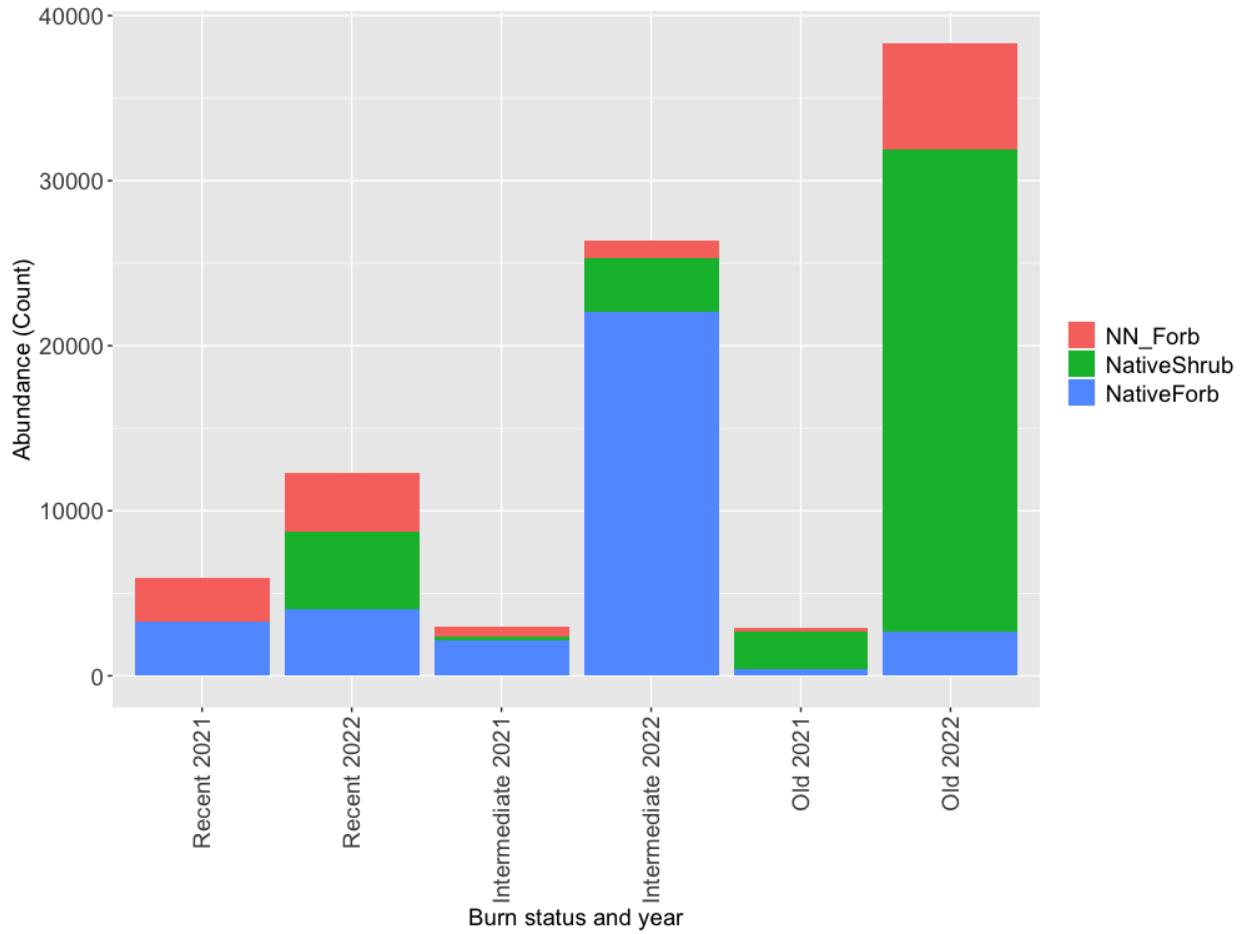
Figure 2.4. Boxplots of average flower counts of each transect per year. Each point represents the flowering count of all species for a transect in the year indicated on the x axis, averaged across the three observations per year, and each line joins the two points representing the same transect between the two years. Observations are separated by burn status across the different panels.
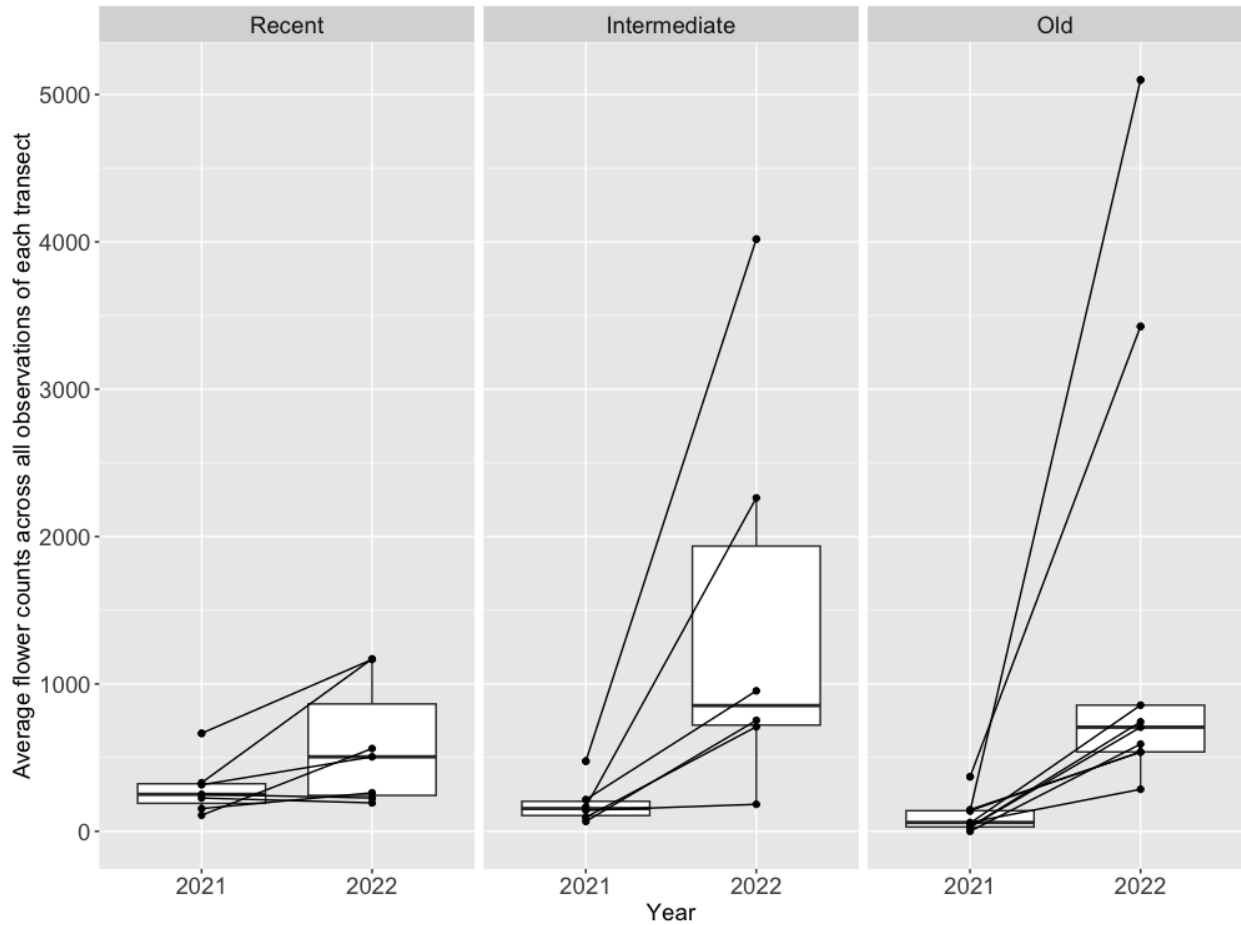
Figure 2.5. Boxplots of flowering intensity for four abundant flowering species (ACMGLA = *Acmispon glaber*, BRANIG = *Brassica nigra*, HIRINC = *Hirschfeldia incana*, SALMEL = *Salvia mellifera*), calculated as the transect average of flower counts for each species divided by vegetation cover, calculated at the quadrat level. The panels from left to right show burn status. Whiskers displayed are 1.5x the interquartile range. Each species is in a different row. Linear-mixed models testing for differences in intensity for each species between different burn statuses interacting with year and transect identity as random factor revealed no significant effects, except for year on SALMEL (p=0.00652), and interaction between year and burn status for ACMGLA (p=0.0112).
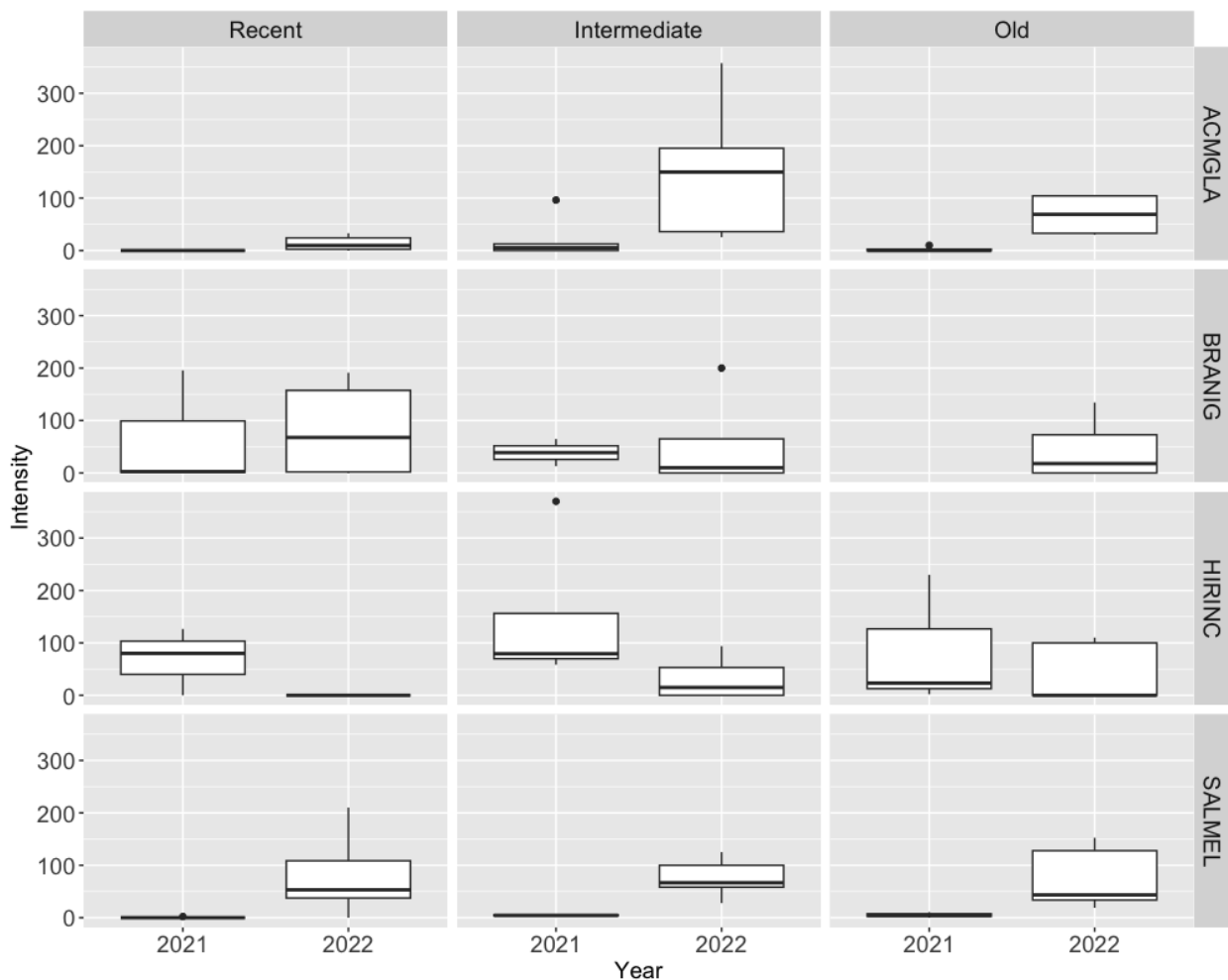
Figure 2.6 Relative difference in measured flower area for individual species in 2021 (top) and 2022 (bottom). Transects are grouped by burn status while the selected commonly observed flowering species are grouped by growth habit and native status. Each colored square is a positive representation of species presence within the corresponding transect. Color represents the relative difference, calculated by dividing the difference between individual transect averages and the average of all old burned sites by the average of all old burned sites. Full species names are in Appendix S1.4.
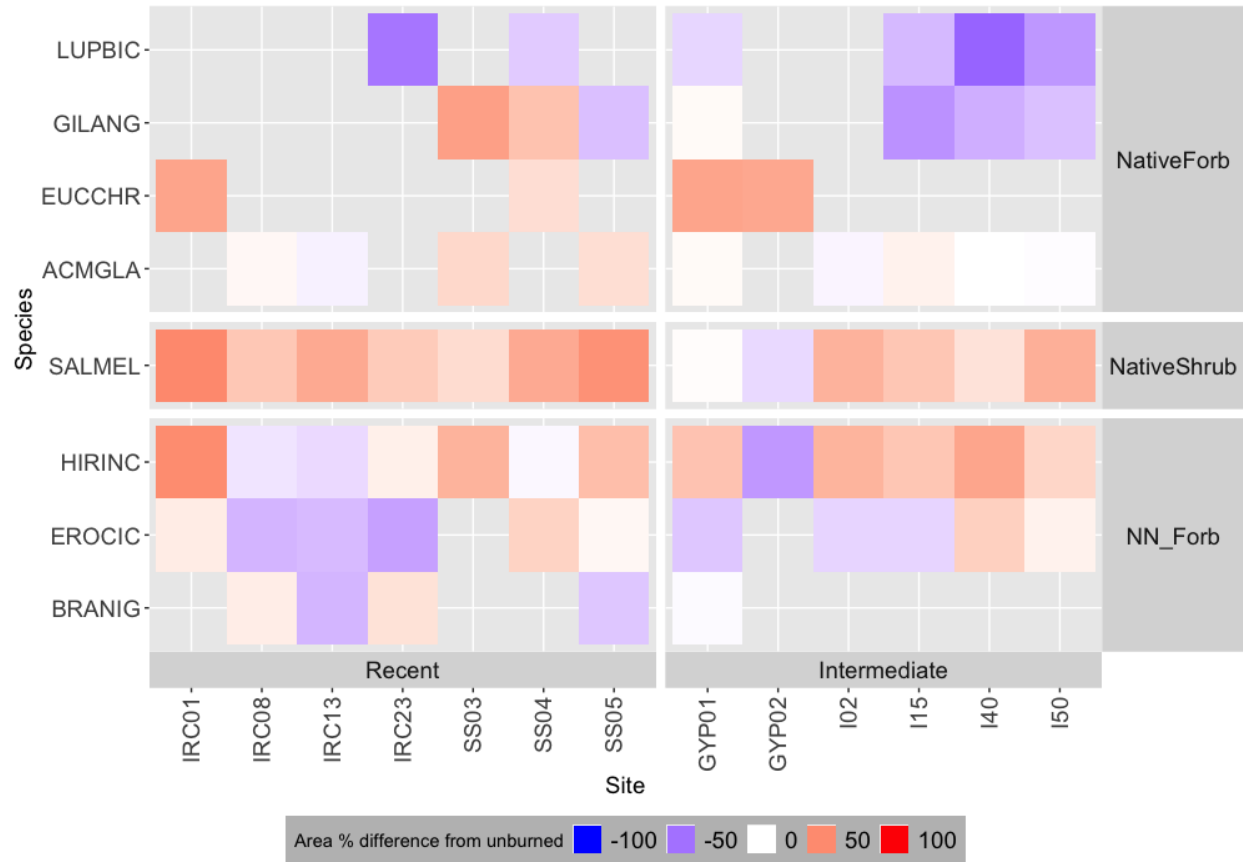
Figure 2.7 CAP analysis of vegetation community composition with sites of all burn statuses (unique sites = 22) and both years of observations included. Top: The points show individual observations of transects. Bottom: Species values are overlaid on the same CAP axes and marked with species name labels. They are categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green). Only species with CAP absolute values greater than 0.3 are shown. Full species names are in Appendix S1.4. Ellipses show the burn/year combination groups with 95% confidence level.
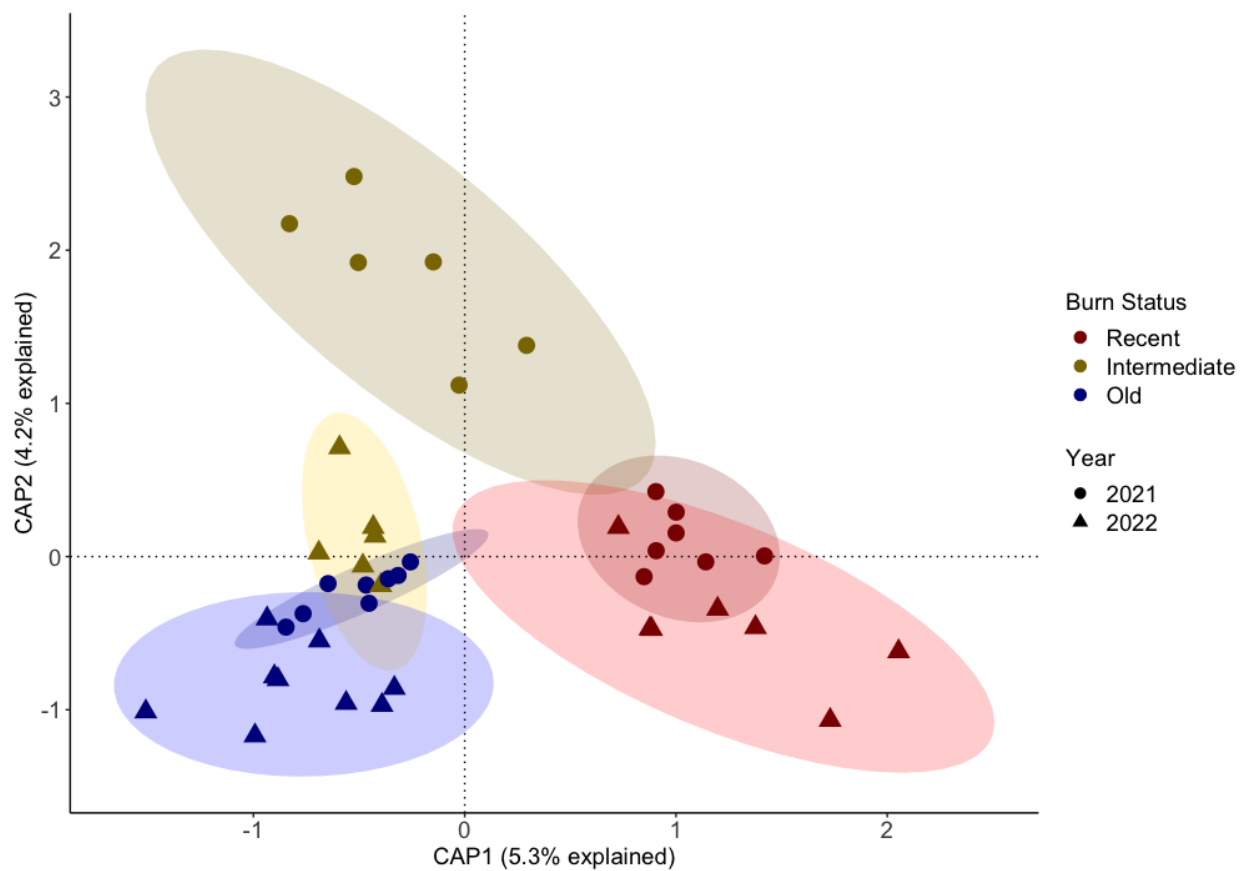
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CHAPTER 3

Flower visitation and pollination in post-fire coastal sage scrub

INTRODUCTION

Wildfire disturbances and recovery processes impact the presence of species and their interactions. Where wildfire is endemic, such as in Mediterranean ecosystems, plant and animal populations can persist after periodic burning via recruitment into the burned zone, or recovery in situ by individuals surviving the fire (Keeley et al., 2012, Bieber et al., 2022). For flowering plants, long-term persistence after fire then depends not only on this initial vegetation recruitment but also on its subsequent reproduction. Understanding how pollination is impacted by fire is important for long-term community recovery after burns as successful animal pollination is crucial to seed production for most flowering species (Ollerton et al., 2011).

Fire disturbance has both direct and indirect effects on insect pollinator activity. Direct effects of fire on pollinator presence include the removal of established nests of above-ground nesting species and the death of juveniles in less mobile life history stages (Cane & Neff, 2011). Fire changes the availability of above ground vegetation and litter and can impact the composition of bees via suitable nesting materials (Potts et al., 2005, Burkle et al., 2019). Landscape heterogeneity in the form of fire history patchiness can also help maintain pollinator diversity (Ponisio et al., 2016; Ulyshen et al., 2021), as fire refuges provided by recently unburned areas retain resources that are no longer present in recently burned patches (Adedoja et al., 2019). Some insect pollinators can recruit over

long distances in search of floral resources (Beekman & Ratnieks, 2001), making their removal by burns less likely to affect floral visitation. Even locally displaced pollinators which forage at shorter distances (Gathmann & Tscharntke, 2002) can still pollinate within burned areas if they are able to quickly reestablish nests or have fire refuges at close proximity. Distance of recruitment can vary by species and traits such as pollinator body size (Greenleaf et al., 2007), which could lead to different pollinator compositions depending on distance from the fire edge.

Fire can also indirectly affect local pollinator presence and activity through effects on local floral resources. Studies in Mediterranean ecosystems have found an increase in flowering forb diversity soon after fire (Potts et al., 2003, Keeley et al., 1981). Greater diversity does not always translate to higher flower counts after fire, however, due to the longer recovery time of mass-flowering shrub species (chapter 2). Fire-following species also emerge in recently burned sites, further increasing immediate post-fire diversity and differentiating burned communities from mature communities. Greater flowering diversity can attract a greater diversity of pollinators (Potts et al., 2003). Recent studies have shown that extended flowering time after fire can also extend the season of pollinator visitation, resulting in little difference in pollinator activity between burned and unburned sites in the early season, but higher pollinator activity in burned sites in late season (Mola & Williams, 2018). In grasslands, removal of dominant vegetation species by fire also results in greater forb flowering, promoting more insect pollinator visits compared to unburned areas (Goldas et al., 2022).

Where recent fire disturbance has altered pollinator availability and flowering community composition, we might also expect to see changes in pollinator visitation patterns which in turn influence pollen deposition. Changes in the openness of the habitat and nesting resources affect local pollinator abundances and diversity (Burkle et al., 2019), and may affect the identity of pollinators visiting the flowers. Such changes in pollinator identity could influence the amount of pollen transferred (Potts et al., 2001; Alarcon, 2009; Jakobsson et al. 2008; Page et al., 2021). Higher flowering density may increase the overall attractiveness of flower patches and increase the total number of visitors (Adedoja et al., 2022), however, pollinators may visit proportionally fewer flowers (Goulson, 2000). In that case, despite an increase in flowers produced by plants, the overall number of flowers receiving pollen on stigmas may be less impacted. A different flowering composition can also impact pollinator visitation due to competition for pollination with other plant species (Waser 1978), or the degree of heterospecific pollen transfer, especially in the absence of high pollinator constancy (Waser 1986). Pollinator constancy, where pollinators visit flowers from limited species during foraging bouts, helps with maintaining conspecific pollen transfer while avoiding heterospecific pollen transfer, the latter which can have a negative impact on seed set (Campbell & Motten, 1985; Morales & Traveset, 2008).

Coastal sage scrub (CSS) is a Mediterranean-type ecosystem found in the coastal California ecoregion, with mature stands characterized by a dominant cover of low-growing native shrubs interspersed with a substory of herbaceous forbs and grasses (Westman, 1981). Native communities persist under local fire regimes, with patterns of increased plant diversity shortly after fire slowly declining to the shrub-dominated steady state at

maturity. Post-fire recovery often takes the form of multiple transitional stages (Capitanio & Carcaillet, 2008), where the final outcome of the stand composition is determined by successful growth and reproduction of the vegetation during this process. While vegetation succession has been well studied in southern California CSS, we're not aware of any studies on post-fire plant-pollinator interactions. In this study, we examine pollinator visitation, pollinator diversity, and pollen transfer in southern California CSS sites with different post-fire ages to answer the following questions:

1.   How does post-fire status impact pollinator visitation and diversity, and are these effects associated with flower abundances?

2.   How does post-fire stage impact conspecific pollen transfer and heterospecific pollen transfer?

MATERIALS AND METHODS

Study sites

We collected data on flowering and pollinator visitation from 22 coastal sage scrub transects spread across an area of ~20 km2 in Orange County, California, USA from mid-March to mid-May in 2021 and 2022. Data collection took place during spring, corresponding with peak flowering in coastal sage scrub (Cleland et al., 2016).

The transects are a subset of previously established long-term vegetation monitoring sites by the Center for Environmental Biology at UC Irvine in partnership with The Nature Conservancy and the Natural Communities Coalition (Kimball et al. 2018). Three stages of recent fire history were included in the chosen transects: recently burned (7 sites, burned

in fall 2020, studied 0.5-1.5 y after burn), intermediate burned (4 sites, burned in fall 2017, 3.5-4.5 y after burn), and old burned (11 sites, over 10 y unburned). Each transect consisted of a 50 m transect line marked by two permanent stakes at the start and end points, and we collected flowering and pollinator data from ten non-fixed 1 x 1 m quadrats distributed in 5 m intervals alternating left and right of the transect line. To account for changes in flowering species and pollinator activity across the season, we surveyed transects in three consecutive rounds per year, except for two sites (one intermediate and one old burn) which were added to the dataset in the second round of 2021, and one recent burn site which was not visited in the second and third rounds of 2021.

Data collection

Flowering

To account for flowering species abundance and diversity across the transect, all species with open flowers were recorded for each 1 x 1 m quadrat, and flower abundances were obtained by totaling the number of open flowers for each species in bloom or estimating high-blooming species by counting the average number of open flowers on 10 randomly selected inflorescences and multiplying by the number of inflorescences (chapter 2).

We previously analyzed post-fire flowering in these coastal sage scrub sites (chapter 2). We found that while recent burn increased flowering diversity, there was limited effect on average flowering density. In our first year of study, recently burned sites had the highest flower density, but in the following year, old burned sites had the greatest number of flowers due primarily to profuse flowering by the shrub *Salvia mellifera*. We hypothesized

that such changes in flower density would impact overall pollinator visits. Recently burned sites also had higher diversity of flowering species compared to old burned sites (chapter 2), leading us to hypothesize that more recently burned coastal sage scrub would have a higher frequency of heterospecific pollen transfer. The higher diversity might also increase pollinator visits if additional plant species attract additional pollinator species to the area.

Pollinator visitation

To estimate pollinator activity and diversity, we observed visitation data in the field. We most often (52 out of 67 total days) surveyed two transects of different burn statuses (in random order) during each sampling day, to minimize effects of the weather on a particular day on pollinator visitation. During each transect survey, multiple quadrats were observed within each heterogeneous CSS transect. Quadrats where there were fewer than three individual plants flowering were not considered for observation due to the low chance of any pollinator activity. When there were fewer than 5 quadrats which had the minimum number of plants, we observed all quadrats. When there were more than 5 suitable flowering quadrats, we observed up to 5 quadrats, including the two quadrats with highest flower density and randomly selecting the rest from the suitable quadrats. More details on the specific number of quadrat observations for each transect visit are given in Appendix S3.1.

20-minute observation blocks were used for each selected quadrat to obtain good estimates of pollinator flower visitation rates (Fijen & Klejin, 2017). A sole observer performed each observation and noted the start and end time. During the observation

period, each pollinator entry into the quadrat, and each contact the individual pollinator made with the reproductive structures of open flowers in the quadrat was recorded. While insect to flower contact is an approximation for pollination, it is not a guarantee of pollen transfer. Major pollinator groups, such as bombyliid and syphrid flies, butterflies, and moths, were categorized on sight. Easily identified bee groups such as *Apis mellifera* and Bombus species were also noted as they entered the observation area. Other bee species were noted with identifying features such as estimated size, color, markings, and flying patterns. It was not feasible to catch individuals for identification when they entered quadrats due to potential interference with their subsequent movement. However, this meant that we were not always able to catch individuals when they were leaving the quadrat. In 2021, when possible, individuals were caught, photographed, and released after visitations. In 2022 we obtained permits from the Irvine Ranch Conservancy to catch individuals after visitations (when possible) to identify specimens in the lab. Ultimately, the pollinator groupings we used included *Apis mellifera*, *Bombus spp.*, and other bees divided by size class into < 5 mm, 5-10 mm, and 10-20 mm length categories. Other pollinator groups we observed included sawflies (Suborder: Symphyta), butterflies and moths (Order: Lepidoptera), syrphid flies (Family: Syrphidae), bombyliid flies (Family: Bombyliidae), other flies (Order Diptera), and hummingbirds. In total we had 11 pollinator categories.

Stigma collection and pollen transfer

To examine pollen transfer, we collected flower stigmas from quadrats after completing our observations in 2022. Stigmas were collected from up to 10 individuals of each species in bloom in each quadrat, for a total of 3084 stigmas across the season, and placed

individually in labeled microcentrifuge tubes. The stigmas were then stained with basic

fuchsin gel (Kearns & Inouye, 1993) and examined under a light microscope at x100 to

x200 magnification to identify conspecific and heterospecific pollen presence. Pollen on

stigmas was compared with pollen found in anthers of the same species to determine if it

was conspecific. To quantify the amount of pollen transfer, we also counted conspecific and

heterospecific pollen in the samples we collected in 2022.

ANALYSIS

All statistical analyses were performed using R version 4.2.3.

Pollinator visitation

To compare pollinator visitation among different burn statuses, we first calculated the

average flower visitation rate for all plant species for each transect by finding the mean of

the total number of flower visits across the 20-minute observations to our 1 m x 1 m

quadrats. We then used a generalized linear mixed model (R glmmTMB package ver. 1.1.8)

with a quasi-Poisson distribution to account for our overdispersed data. We included burn

status and year as interacting fixed effects, round of sampling as an additive fixed effect,

and transect as a random effect to account for repeated sampling over three rounds.

Next, we tested whether changes in flower visitation rate can be explained by flower

density. As there is heterogeneity in the number of flowers per observed quadrat even in

the same transect, we opted to look at the effect of flower number with each quadrat

observation as a separate data point. We used another generalized linear mixed model with

flower number, burn status, and year as interacting fixed effects and transect as random

effect, which also accounts for sampling of multiple quadrats per transect. Finally, we also tested the effect of flower number on visitation rates of pollinators divided into three large categories (*Apis* bees, non-*Apis* bees, and other pollinators) to determine whether different pollinators show different behaviors in each burn status. We ran generalized linear mixed models for the flower visitation rate for each pollinator category with flower number, burn status, and year as fixed factors, and then determined the slopes for each burn status and year (emmeans function, emtrends R package ver. 1.9.0).

Unique visitors

In addition to the number of flower visits, which is dependent on the number of flower contacts each pollinator makes rather than the overall abundance of pollinators, we also analyzed the effect of burn status on the number of pollinators that entered the quadrat during the observation period. Each entry of a pollinator into a quadrat was considered unique even though it is possible that the same insect entered more than once. We analyzed "unique visitors" using the same analyses as described above for "number of visits".

To determine whether pollinator communities differed across burn statuses and year, we ran a constrained ordination, canonical analysis of principal coordinates (CAP, capscale function, vegan package ver. 2.6.2), with Bray-Curtis dissimilarity (Anderson & Willis, 2003) on the unique pollinator entries for each quadrat observation in each pollinator category, including the *Apis*, non-*Apis* bees, and subdivisions of all other pollinator groups observed.

Diversity

To compare pollinator diversity across the different burn status and years we calculated a Shannon diversity index for each quadrat observation based on the counts of unique visitors to the site, with identities classified by our 11 pollinator types. We then ran linear mixed models (lme function, nlme package ver. 3.1.162) with burn status and year as interacting fixed effects and transect as a random effect.

To examine the effect of flower diversity on pollinator diversity, we calculated Shannon diversity indices for flower diversity for each quadrat observation and ran linear mixed models again with flower diversity included as an interacting factor with burn status and year, and transect as a random effect.

Pollen transfer

We selected five of the most common flowering species in our dataset to serve as focal species for our comparisons of pollen transfer, as many of the rarer flowering species were not found across many transects or across different burn statuses. These included three native species: the perennial shrub *Salvia mellifera*, the annual herb *Gilia angelensis*, the annual fire-following carpeting herb *Eucrypta chrysanthemifolia*, and two invasive species: the tall biennial mustard *Hirschfeldia incana* and the annual carpeting herb *Erodium cicutarium.* In total, these amounted to 2054 stigmas out of all 3084 stigmas collected. Using the 2022 data, we analyzed the effect of burn status on (1) conspecific pollen deposition, (2) heterospecific pollen deposition, and (3) the proportion of stigmas with any heterospecific pollen. For each of these three dependent variables we first calculated the

quadrat average for (1) and (2), and the proportion value for (3), and then averaged all quadrat values across the transect. We then analyzed the averages using one-way ANOVA with burn status as the fixed factor. Post-hoc tests (TukeyHSD function, R stats package 3.6.2) were also performed on significant ANOVAs to look for differences between pairs of burn status means. As a significant effect of burn status was detected for *Salvia mellifera* conspecific pollen count, we also analyzed how it depended upon both visitation rate to *Salvia mellifera* and burn status as separate factors in a linear model.

RESULTS

In total, we observed pollinators during 503 20-min observation blocks totaling 168 observation hours. The majority of pollinator visits came from Apis mellifera, comprising 58% and 70% of total observed flower visits in 2021 and 2022, respectively (Table 3.1). Based on our interaction matrix of flowering species and pollinator groups (Appendix S3.2), of the flowering species observed, *Salvia mellifera* received visits from the greatest number of pollinator groups, and *Apis mellifera* visited the broadest range of flowers, followed by non-*Apis* bees in the ~5mm category.

Pollinator visitation

Transect averages for the number of flower visits from all pollinators were significantly affected by the year of observation (p = 0.0002), with an overall average of 8.29 visits per 20-minute observation in 2021 vs 30.8 in 2022 (fig 3.1), and significant effects of sampling round (p=0.0186), with higher visits in the second round of sampling, closer to peak flowering in the middle of the season. We did not find significant effects of burn status (p =

0.475) or the interaction between burn status and year (p=0.0643) on mean total flower visits.

In a model that also included flower number, the number of visits from all pollinators combined per observation block increased significantly with flower number (p=2.69x10-8, Fig 3.2), and was again higher in 2022 but was not significantly affected by burn status (p=0.089). The slope of visits on flower number was higher in 2021 (slope = 0.161, SE = 0.0496, unit = visits/observation/flower) compared to 2022 (slope = 0.0938, SE = 0.013; interaction of flower number and year, p = 0.0132). There was also a three-way interaction effect between flower number, burn status, and year (p = 0.0489), suggesting the slope of visits against flower changed between different status and year combinations (fig. 3.2), with a significant pairwise contrast between recent and old burned sites between 2021 and 2022 (p=0.0008) where the trend of visits against flower abundance increased from 2021 to 2022 in recently burned sites while it decreased in old burned sites.

Dividing pollinator visits into three major categories (*Apis mellifera* bees, non-*Apis* bees, and other pollinators), number of visits per observation block by *Apis mellifera* increased significantly with flower count (fig. 3.3, p= 6.53x10-4), and sampling year (p=9.42 x 10-4) but was not significantly affected by the main effect of burn status (p=0.0954). The interaction between burn status and year influenced *Apis* visits (p=0.0452), likely due to the increase in visits between 2021 to 2022 for intermediate sites compared to the decreases between the same years for old burned sites, though pairwise contrasts did not

approach significance (p > 0.16). Thus, patterns for *Apis mellifera* were similar to those for all pollinators combined.

Non-*Apis* bee visitations were also significantly affected by flower number (p=0.0367), but with lower slopes of increase compared to *Apis mellifera* (fig. 3.3). The effect of burn status (p=0.274) and year of sampling (p=0.733) on non-*Apis* bee visits was not statistically significant, but the effect of flower number on visits depended on year (p=0.0418), with a greater slope of pollinator visits on flower count in 2021 (slope = 0.016, SE = 0.00477) compared to 2022 (slope=0.000528, SE = 0.0009). Visits from other (non-bee) visitors were not significantly affected by flower number (p=0.939), burn status (p=0.876), year (p=0.741), or any interactions between these factors.

The number of unique visitors (fig 3.4) was not significantly affected by burn status (p=0.217), year (p=0.146), or the interaction between burn status and year (p=0.65). However, when flower number was added to the model, unique visitors to quadrats (fig 3.5) rose significantly with increased flower number (p=0.00235). The number of unique *Apis mellifera* visitors for quadrat observations also increased significantly with flower count (p = 1.176x10-7). Significant interaction effects included a decrease in the change in visitors with flower count from 2021 (slope = 0.0131, SE = 0.0042) to 2022 (slope = 0.00588, SE = 0.00056) (p=0.0194). Year also had an interactive effect with burn status (p=0.00141), where the increase in mean visitors from 2021 to 2022 was significantly smaller in recently burned sites compared to old burned (0.13 vs 2.7, contrast p = 0.018). Three-way interactions between flower count, year, and burn status (p=2.096x10-4)

indicated the slope of visits on flowers changed more from 2021 to 2022 in old burned sites than intermediate (contrast p = 0.0443) or recent burned sites (contrast p < 0.0001).

Quadrat counts of unique non-*Apis* bee visitors also increased with flower count (p=0.00542) and were significantly affected by the interaction between flower count and year (p=0.00144), with greater increase in visitors with flower count in 2021 (slope = 0.00455, SE = 0.00149) compared to 2022 (-0.000205, SE = 0.0002).

Visits by other pollinators also responded to flower number (p = 0.0306) and the flower x year interaction (p=0.00140), with the slope of visitor number on flower number decreasing from 2021 (slope = 0.00205, SE = 0.000978) to 2022 (slope = -0.000147, SE = 0.000132). Overall, the increase in visits with density of flowers was greatest for Apis mellifera, followed by non-*Apis* bees, and finally other non-bee pollinators.

A CAP ordination on transect averages of unique pollinator visitors in each pollinator category showed substantial overlap of the three burn statuses (Fig 3.6), but there was a significant difference due to burn status (p = 0.001) likely because while all other pollinator categories did not differ much among burn statuses, *Apis mellifera* visitors were associated more with old burned sites. When both burn status and year were included as interacting constraints, burn status (p=0.001), year (p=0.023) and the interaction between status and year (p=0.032) were significant

Diversity

Pollinator diversity was not significantly affected by burn status (p=0.5), but was higher in 2021 compared to 2022 (p=0.016) by approximately 20%. When flower diversity was added to the model, year remained a significant effect on pollinator diversity (p=0.473), and pollinator diversity was positively associated with flower diversity (p=0.00418) (fig 3.7). However, there were no significant interactions of flower diversity with burn status or year.

Pollen transfer

Conspecific and heterospecific pollen transfer for the five focal species (Fig 3.8, 3.9), showed no significant differences among burn statuses except possibly for conspecific pollen transfer in Salvia mellifera (p=0.0396, NS after correction for multiple comparisons of 5 species) which appeared highest in intermediate sites and lowest in old burned sites. Post-hoc comparisons showed that average counts in intermediate sites were significantly higher than old burned counts (Tukey test: diff = 9.86, p = 0.0466). Conspecific pollen count for *Salvia mellifera* did not increase significantly with visit number to that species (p=0.0859). Out of all the stigmas collected in 2022, 91.3% had some pollen deposition, and out of those stigmas 83.2% had only conspecific pollen. For the five focal species where there were more than 10 stigmas counted, the native perennial forb *Dichelostemma capitatum* had the highest percentage of stigmas that had some heterospecific pollen (63.7%). Out of the five focal species, *Gilia angelensis*, also a native forb, had the highest percentage of stigmas with heterospecific pollen (42.9%). The proportion of stigmas which had heterospecific pollen deposition for each species was not significantly different across different burn statuses (Fig 3.10).

DISCUSSION

In other areas around the world, fire has been shown to affect pollination either through direct effects on pollinators or indirectly by affecting floral and other (Carbone et al., 2024). While recovery patterns of vegetation have been well studied in southern California ecosystems, to our knowledge, this is one of the first studies which focuses on pollinator activity and pollen transfer after fire in coastal sage scrub. Comparing sites of three burn statuses, we found limited overall effects on pollinator visitation rates and pollen deposition on stigmas, but number of flower visits did rise with increased flower abundance. Most importantly, the rate at which pollinator visits increased with flower number was sometimes affected by year, burn status, or a combination of the two. When all pollinator types were combined, visits increased faster with flower number in 2021 compared to 2022. When burn status was also considered, the slope of visits on flowers decreased from 2021 to 2022 in old burned sites while increasing in recently burned sites. One possible explanation is that the exceptionally high abundances of *Salvia mellifera* flowers in old burned sites in 2022 swamped the pollinators such that their visitation tended to level off in the most flower dense plots.

How does post-fire stage impact pollinator visitation, and can this be explained by flowering abundances present at these sites?

Globally, pollinator abundances, especially for bee groups, are generally higher in recently burned areas compared to unburned areas (Mason et al., 2021; Banza et al., 2021), however there are conflicting reports about whether overall pollinator abundances are

higher in the first season after fire (Banza et al., 2021) or only after the first year (Mason et al., 2021). The same studies showed that in contrast to pollinator abundances, pollinator richness is not typically affected by recent fire. Previous studies also found an increase in pollinator floral visitation after recent burns, but this effect could be due to increased flowering densities (Goldas et al., 2022; Van Nuland et al., 2013). Furthermore, differences in flowering abundances between burned and unburned areas can be large or small depending on timing in the flowering season (Mola & Williams, 2018), and observed differences in pollinator abundances between burn statuses could be an effect of different flower availabilities at that time point. These examples suggest that the indirect effect of burning on pollinator visitation via changes in flowering number has a stronger effect than direct impacts of fire. Our results support this view, as visits increased with flower abundance, and we also observed a peak in total pollinator visits in the second round of sampling, at the height of flowering during the season. While studies looking at post-fire flowering across different Mediterranean systems have mostly found increases in flowering diversity in the immediate years after fire compared to longer unburned stands (Potts et al., 2003; Burkle et al., 2019), less is certain about floral abundance. While some species have been shown to increase flowering after a recent burn (Wrobleski & Kauffman, 2003), overall flowering abundance of all species present can vary due to yearly changes in environmental conditions such as water availability (Kuppler & Kotowska, 2021) presence of fire-following flowering species (Zirondi et al., 2021), and the flowering of high-flowering species (Chapter 2).

Different arthropod groups respond differentially to fire (Kral et al., 2017), and this holds true specifically for pollinators. Across both natural and cultivated habitats, bee abundance and species richness tend to increase after burns, while Lepidoptera tends to respond negatively (Nicholson & Egan, 2019), and little is known about bee subgroups. We also observed differences among pollinator groups in the increase in visits and number of visitors with flower number. When looking at pollinators divided into *Apis mellifera*, non-*Apis* bees, and non-bee pollinators, *Apis mellifera* had the strongest response to flower count in terms of visitation and unique visitors. Non-*Apis* bee visitors and visits also increased with flower numbers, but to a lesser degree compared to *Apis mellifera*. Our results are generally comparable to previous observations in undisturbed coastal sage scrub, where the observed number of honeybee visitors increased at a greater rate with increasing flower abundance compared with other insects (Hung et al., 2019). Interestingly, we found that these visitation responses to flower numbers were sometimes impacted by year, burn status, or a combination of both. For example, *Apis mellifera* visitors increased more with flower number in 2021 compared to 2022 and was also affected by a three-way interaction where the slope of visitors on flower number decreased from 2021 to 2022 in old burned sites but increased in intermediate and burned areas. These significant interaction effects seem to be driven in part by the large change in flowering in old burned sites between 2021 to 2022. With the high amounts of flowering of *Salvia mellifera* in 2022, it is possible that pollinators visited proportionally fewer flowers in these large patches (Goulson, 2003), resulting in a decrease in the rate at which pollinator visitations increase with flower count. We did not find an effect of burn, year, or flower on our non-bee pollinators' visitations or visitor numbers, but it is likely a result of their low presence in

our dataset. Furthermore, this is a heterogeneous group that includes groups ranging from flies to butterflies to hummingbirds, and the responses of each of these groups to fire are likely to be different (Nicholson & Egan, 2019).

Pollinator diversity was not significantly affected by burn status but did decrease between 2021 and 2022. The increase in mass flowering *Salvia mellifera* in 2022 might have contributed to this decrease, as these high-density patches attract more *Apis mellifera*, leading the *Apis* pollinator category to take up a greater proportion of overall visitors, lowering the evenness factor in our diversity calculations. Flowering diversity also had a positive effect on pollinator diversity, as in a study in the Mediterranean (Potts et al., 2003). However, this does not mean that the pollinator species composition remained the same across burn statuses, as we only accounted for broad pollinator categories. CAP analysis of pollinator compositions among different burn statuses showed that *Apis mellifera* was more strongly associated with old burned sites, while all other pollinator groups overlapped with all three burn statuses.

Overall, we did not find strong effects of burn status on average number of flowers visited. The high levels of vegetative heterogeneity among our sites could have played a role in increasing heterogeneity of pollinator visitation. It is possible that fire had limited effects on pollinator abundance at our sites even immediately after fire, as some other studies have found for *Apis mellifera* (Banza et al., 2021) and native bees (Love & Cane, 2016). In the latter, the identities of the species of solitary bee present in burned and old burned sites were different, however we did not have enough resolution in our pollinator species

identification to determine whether this was the case in our study system. Fire is known to have a more negative immediate impact on the presence of above ground nesting bees (Williams et al., 2010), as well as below ground nesting bees that nest at shallow depths (Banza et al., 2021) as their nests are more vulnerable to fire destruction. Freshly burned areas have more bare ground for ground-nesting bees and coarse woody debris for cavity-nesting bees (Burkle et al., 2019), but as new vegetation cover from short, high-density forbs increase in time after fire, older burns can hinder access to bare ground and negatively impact ground nesting bees (Williams et al., 2010) until shrub vegetation canopies with low undergrowth are re-established in mature stands. However, these patterns are highly dependent on the vegetation structure and fire patterns of the ecosystem being investigated. Coastal sage scrub burns with high severity crown fires (as noted in Keeley, 2006), which is mainly fed by the vegetation canopy rather than burning surface litter close to the ground. It is possible that this type of fire disturbance allows for better retainment of materials close to the ground, including ground-nesting species and nesting resources in the immediate years after fire.

How does post-fire stage impact pollen transfer, including conspecific pollen and heterospecific pollen transfer?

Amongst the common flowering species sampled in 2022, we observed a significant effect of burn status on conspecific pollen transfer only for *Salvia mellifera*, with greater conspecific pollen counts in intermediate sites compared to old burned sites. We did not observe any significant effects of burn status on other pollen metrics in *Salvia mellifera* or

for any of the other four abundant flowering species. We initially expected to observe more heterospecific pollen and movement of pollinators between heterospecific individuals in recently burned and intermediate sites, due to their higher flowering diversity compared to old burned sites (chapter 2). However, throughout all our observations for both years, we only witnessed two instances of pollinators moving between heterospecific species, possibly due to our small quadrat size not allowing us to track pollinators visiting more distant individuals.

Pollen deposition is affected by the identity of pollinator visitors. Amongst bees, pollinator effectiveness in a single visit tends to be less for *Apis mellifera* compared to other bees (Page et al., 2021). In California ecosystems, a high abundance of non-native *Apis mellifera* displaces native bees (Page & Williams, 2023, Hung et al., 2019). Differences in pollinator effectiveness between *Apis* and other bees may help explain our finding of greater conspecific pollen deposition on *Salvia mellifera* in intermediate sites. *Apis mellifera* accounted for ~89% and ~88% of total visitor counts to *Salvia mellifera* in old burn and recent burn sites, respectively, but only ~77% of visitors in intermediate sites. It is possible that this lowered proportion of less-effective honeybee visits and increased more-effective non-*Apis* visits in intermediate sites, explained the increased conspecific pollen deposition that we observed. We did not observe differences in conspecific pollen deposition with burn status for the other four species we analyzed. The two non-native forbs (*Erodium cicutarium* and *Hirschfeldia incana*) were visited by *Apis* mellifera and flies, while the two native forbs (*Eucrypta chrysanthemifolia* and *Gilia angelensis*) were visited by non-*Apis* bees and flies.

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Increases in conspecific pollen deposition also don't necessarily translate to increases in reproductive success. Outside of selfing, where pollen is transferred from the anther to the stigma of the same flower, conspecific pollen can also come from transfer between multiple flowers on the same plant (geitonogamous). For self-incompatible species, high amounts of pollen transfer from selfing or geitonogamy can be detrimental to seed set (de Jong et al., 1993). *Salvia mellifera*, the one species for which we demonstrated an effect on conspecific pollen deposition, is a self-incompatible species, meaning that increased geitonogamy would decrease fitness. Previous studies have shown that *Apis mellifera* does visit a higher number of flowers from the same plant in comparison to non-*Apis* pollinators (Travis & Kohn, 2023). For other native annual coastal sage scrub species, plants in areas with *Apis* present had reduced seed set compared to areas where *Apis* was experimentally removed (Nabors et al., 2018).

Heterospecific pollen deposition is dependent on pollinator identity (Jakobsson et al., 2008) on top of plant community composition. Our original hypothesis that more recently burned coastal sage scrub would have higher heterospecific pollen was suggested by greater diversity of non-native flowering species and flowering species in general compared to old burn sites (chapter 2). Non-native plant species can be sources of heterospecific pollen in co-flowering communities (Parra-Tabla et al., 2020), and plants in close proximity to non-native species at higher densities had more heterospecific pollen on stigmas in the native forb *Phacelia parryi* (Bruckman & Campbell, 2016). However, we did not find any significant differences between burn statuses for any of the five species we analyzed.

CONCLUSION

After fire, coastal sage scrub communities had a greater diversity of plant species, particularly forbs, compared to unburned communities (chapter 1) This diversity is maintained through intermediate sites approximately five years after fire as the dominant native shrub canopy recovers. The higher diversity of forbs translated to greater richness and diversity of the flowering community as well. However, greater flowering diversity did not necessarily correspond with greater flowering abundance (chapter 2), as the mass flowering shrub species in old burn sites produced a large number of flowers in favorable years, which overwhelmed the collective abundances of the forbs in more recently burned sites. In the end, these differences in flower count for the flowering communities across different burn ages and year had the greatest impact on number of pollinator visits (this chapter), but burn status had little effect on conspecific and heterospecific pollen transfer. While overall pollinator visitation did not differ markedly with burn status, the changes in relative abundance of honeybees compared to other pollinators resulted in subtle changes in how number of visits responded to flower number. To understand long-term persistence of coastal sage scrub flowering species further investigation is needed on how fire affects the next steps of plant reproduction, including seed production.

TABLES

Table 3.1 Total counts of flower visits in each of our 11 fine pollinator categories recorded per year of monitoring and burn status (**Apis** = *Apis mellifera,* **Bombus** = bumblebees, **20mm** = other bees size 10-20mm, **10mm** = other bees size 5-10mm, **5mm** = other bees size <5mm, **SAW** = sawflies, **LEP** = butterflies and moths, **SYP** = syphrid flies, **BOM** = bombyliid flies, **DIP** = other flies, **HUM** = hummingbirds).

Year	Status	BEE							FLIES			
		Apis	*Bombus*	20mm	10mm	5mm	SAW	LEP	SYP	BOM	DIP	HUM
2021	U	208	13	1	32	50	0	4	3	13	11	1
	M	85	12	1	21	28	0	1	4	26	4	5
	B	197	9	2	22	39	0	0	19	12	11	5
2022	U	567	13	5	44	69	1	8	13	15	10	6
	M	125	6	4	10	19	3	11	5	4	2	2
	B	243	5	2	25	30	3	26	29	25	9	2

Table 3.2 P values from ANOVA of average transect conspecific pollen deposition,

heterospecific pollen deposition, and % of stigmas with heterospecific pollen presence for

five common flowering species against burn status in 2022.

Flowering species	df	residuals	Conspecific pollen	Heterospecific pollen	% stigmas with het. pollen
Erodium cicutarium	2	41	0.945	0.302	0.062
Hirschfeldia incana	2	22	0.564	0.24	0.323
Eucrypta chrysanthemfolia	2	11	0.331	0.84	0.945
Gilia angelensis	2	18	0.355	0.368	0.262
Salvia mellifera	2	39	**0.0396***	0.09	0.903

* P < 0.05.

FIGURES

Figure 3.1. Violin plots of mean number of visits per 20-minute observations for all

pollinators, categorized by burn status and year. Each point represents the averaged values

of quadrat observations across one transect visit.
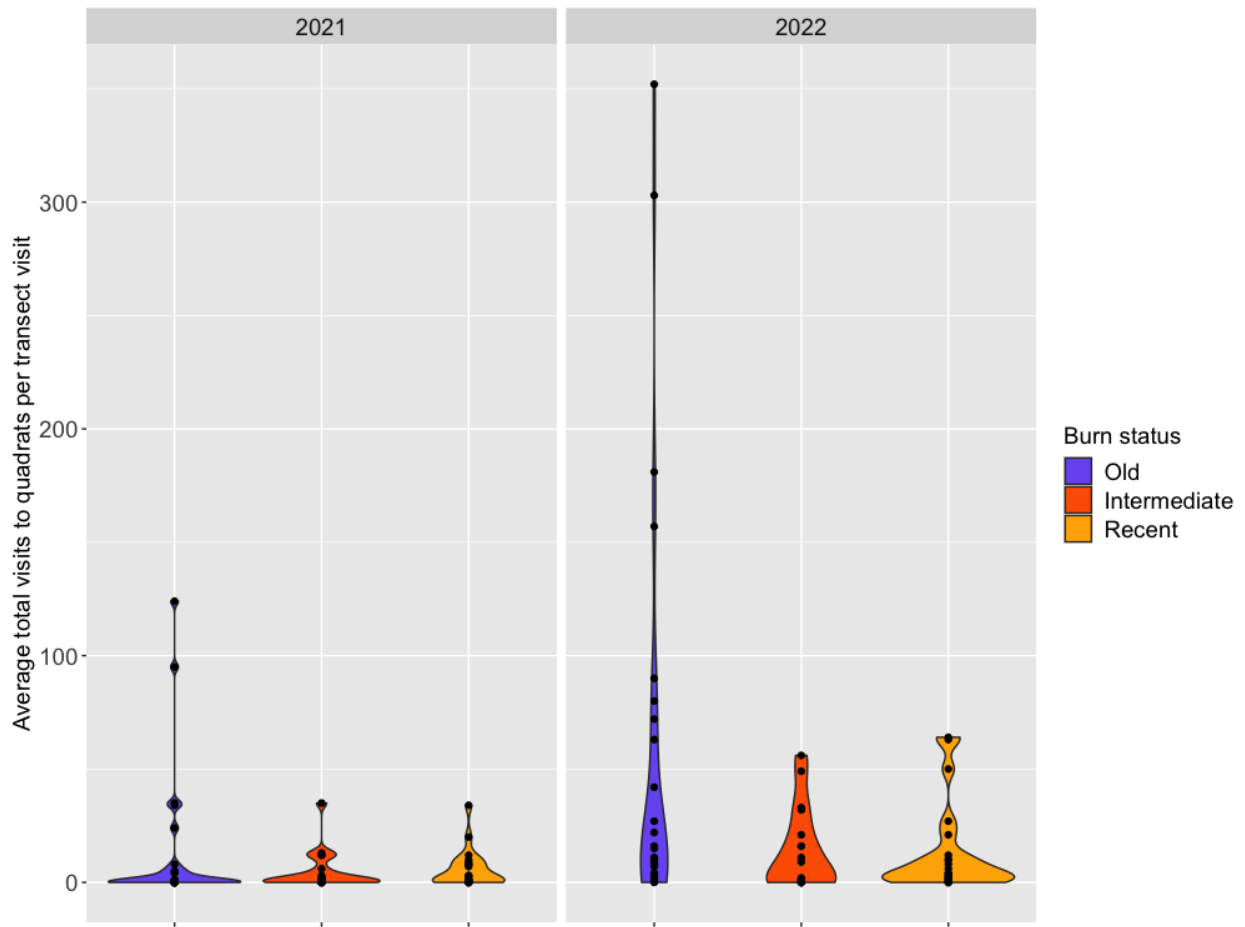
Figure 3.2. Flower visits for each 20-minute observation to a quadrat against flower count, separated by monitoring year and burn status. Shaded areas around linear regression lines represent 95% confidence intervals.
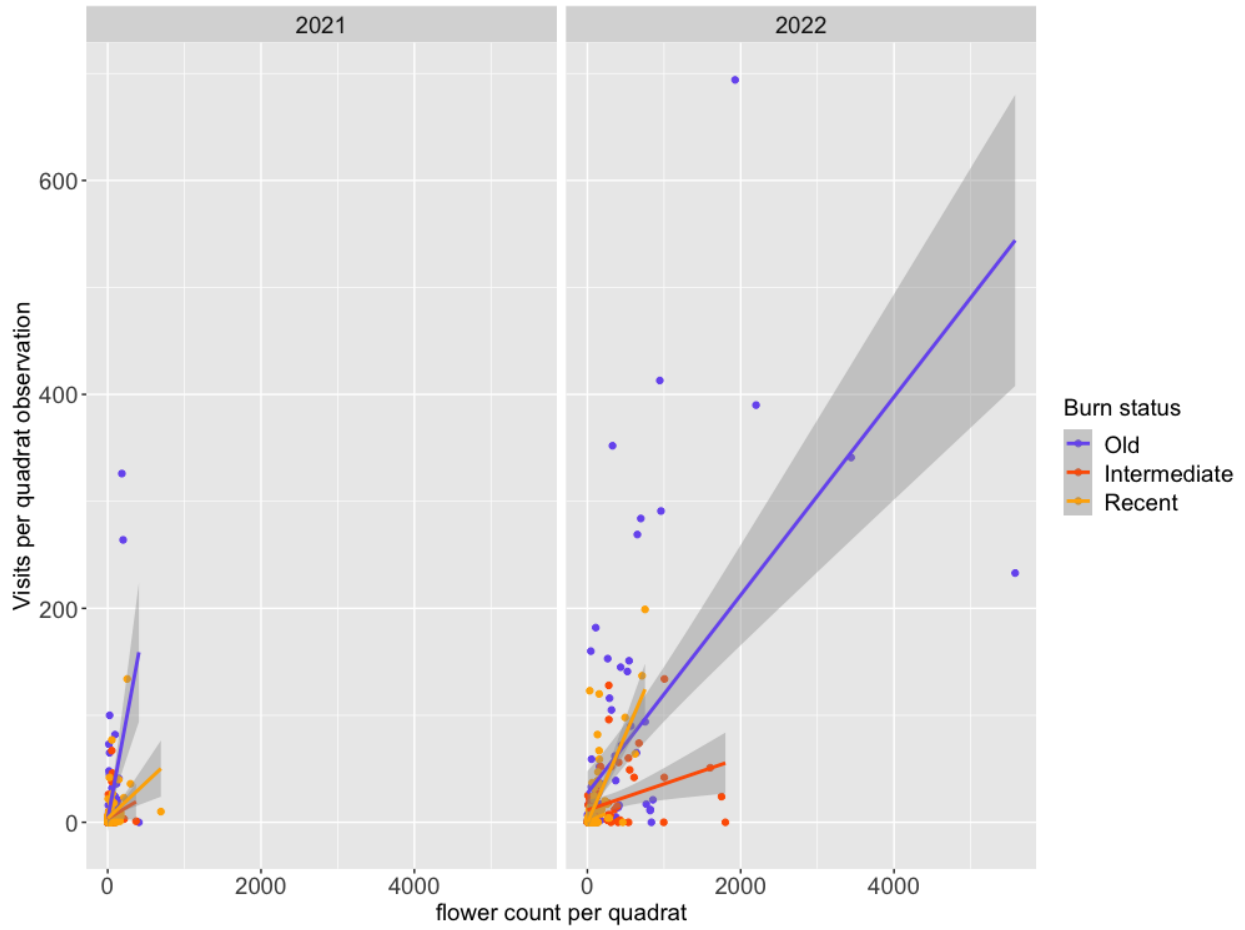
Figure 3.3. Visits for each 20 minute observation to a quadrat against flower count in the quadrat, separated by monitoring year, burn status, and pollinator type. Shaded areas around linear regression lines represent 95% confidence intervals.
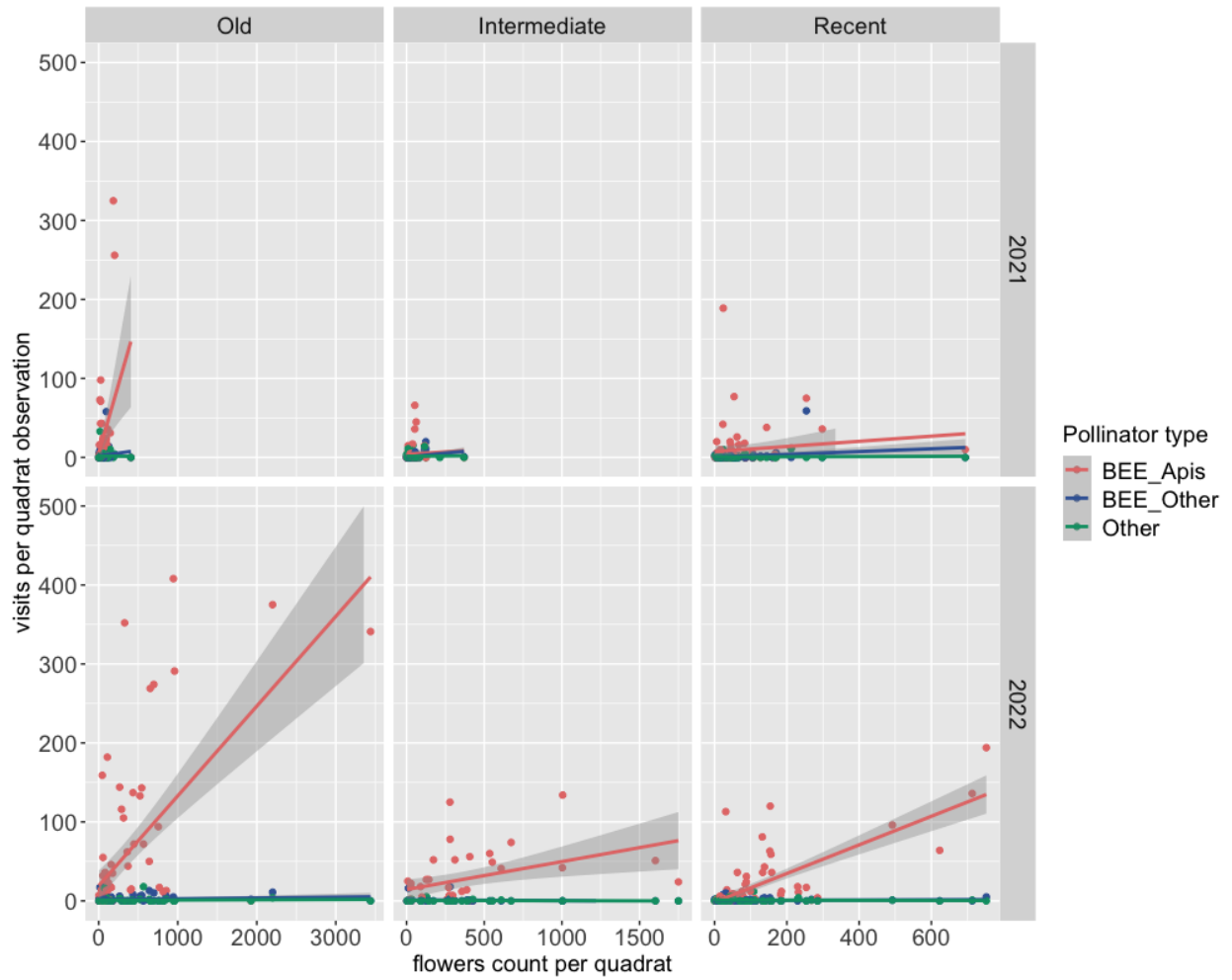
Figure 3.4. Violin plots of total unique visitors per 20-minute observations for all

pollinators, categorized by burn status and year. Each point represents the averaged values

of quadrat observations across one transect visit.
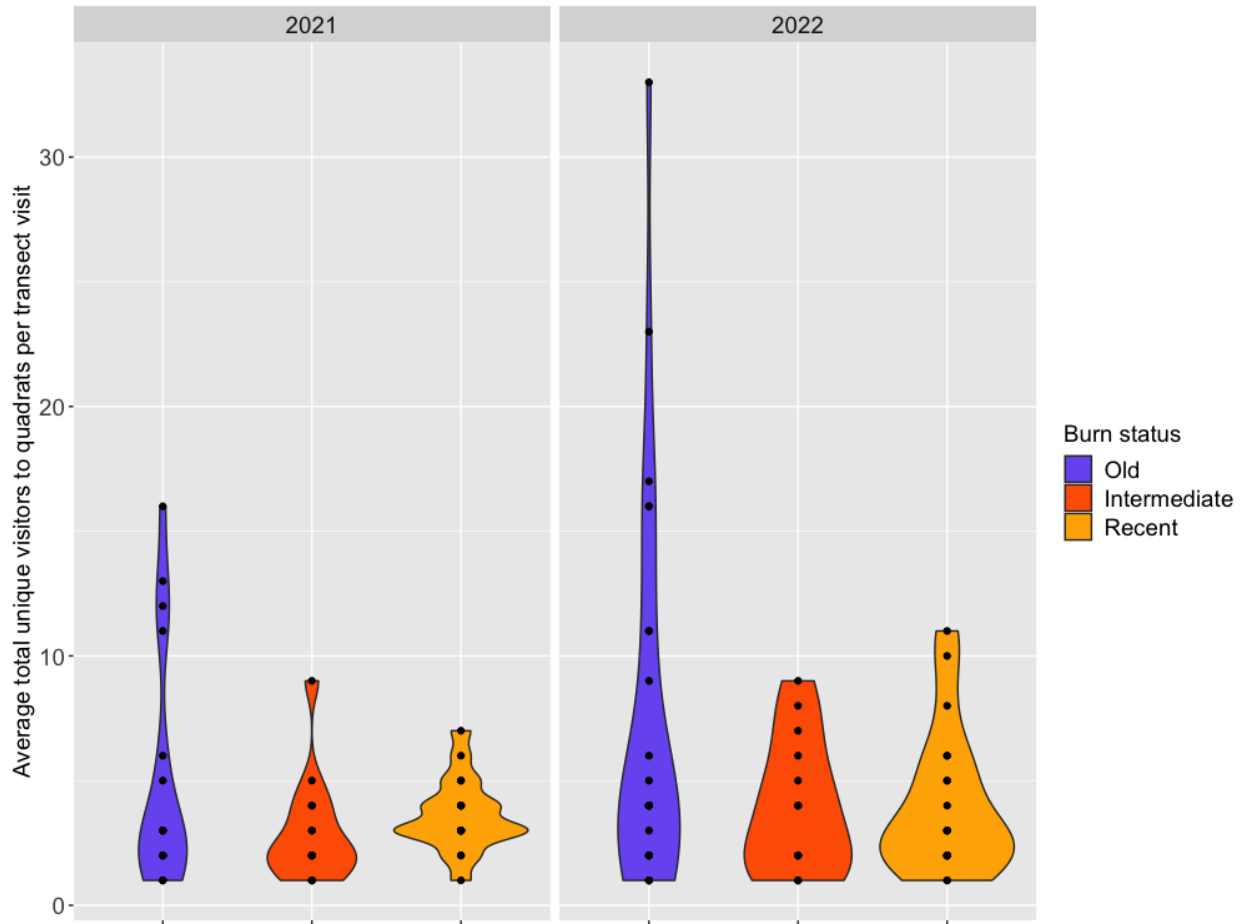
Figure 3.5. Unique visitors for each 20-minute observation (quadrat) against flower count (quadrat), separated by monitoring year, burn statuses, and pollinator type. Shaded areas around linear regression lines represent 95% confidence intervals.
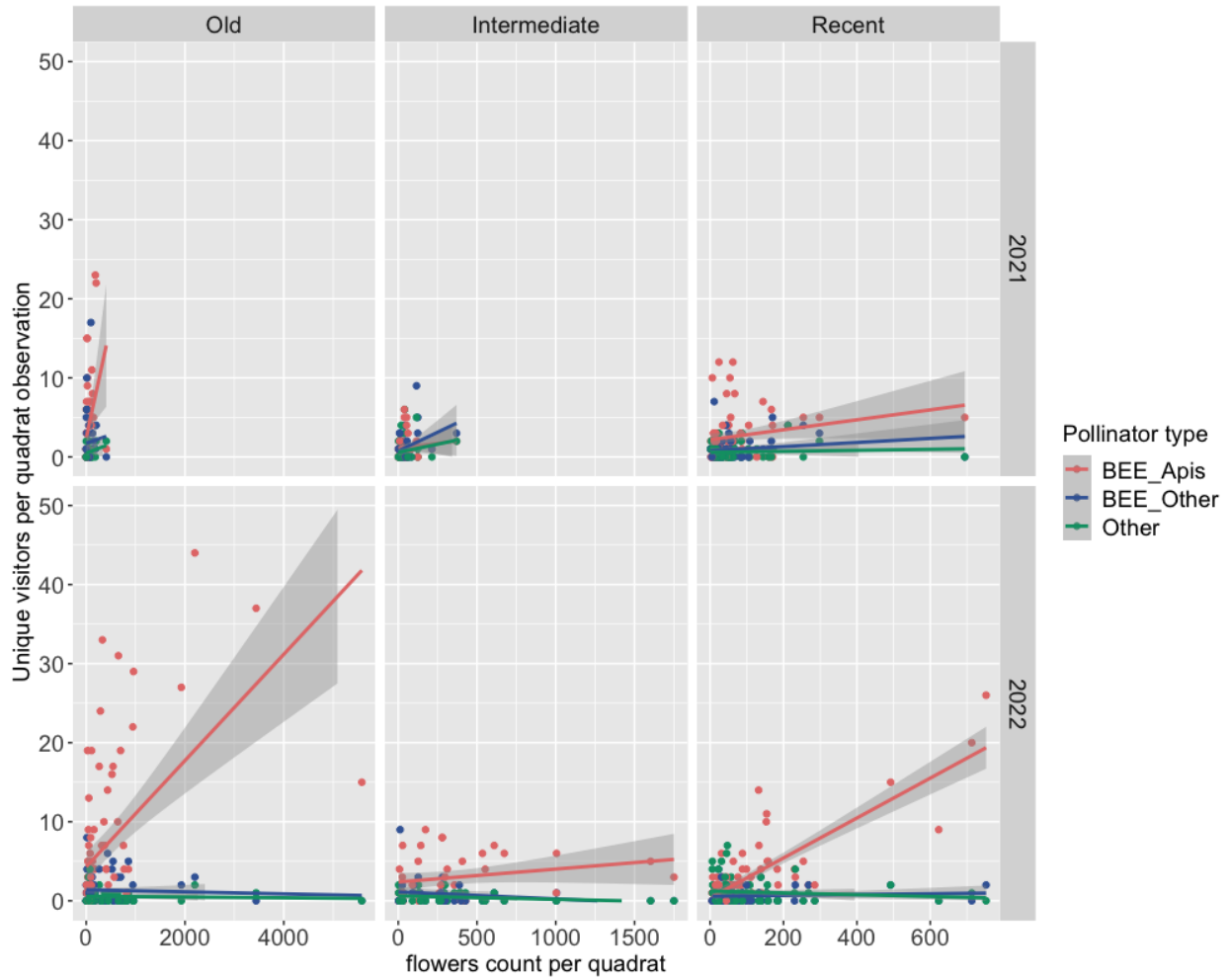
Figure 3.6. CAP analysis of unique pollinator visitors to quadrats across different burn statuses with both years of data included. Total observations included = 382. Ellipses show the burn status groupings with a 95% confidence level. Labelled species values from CAP analysis are overlaid on the same axes.
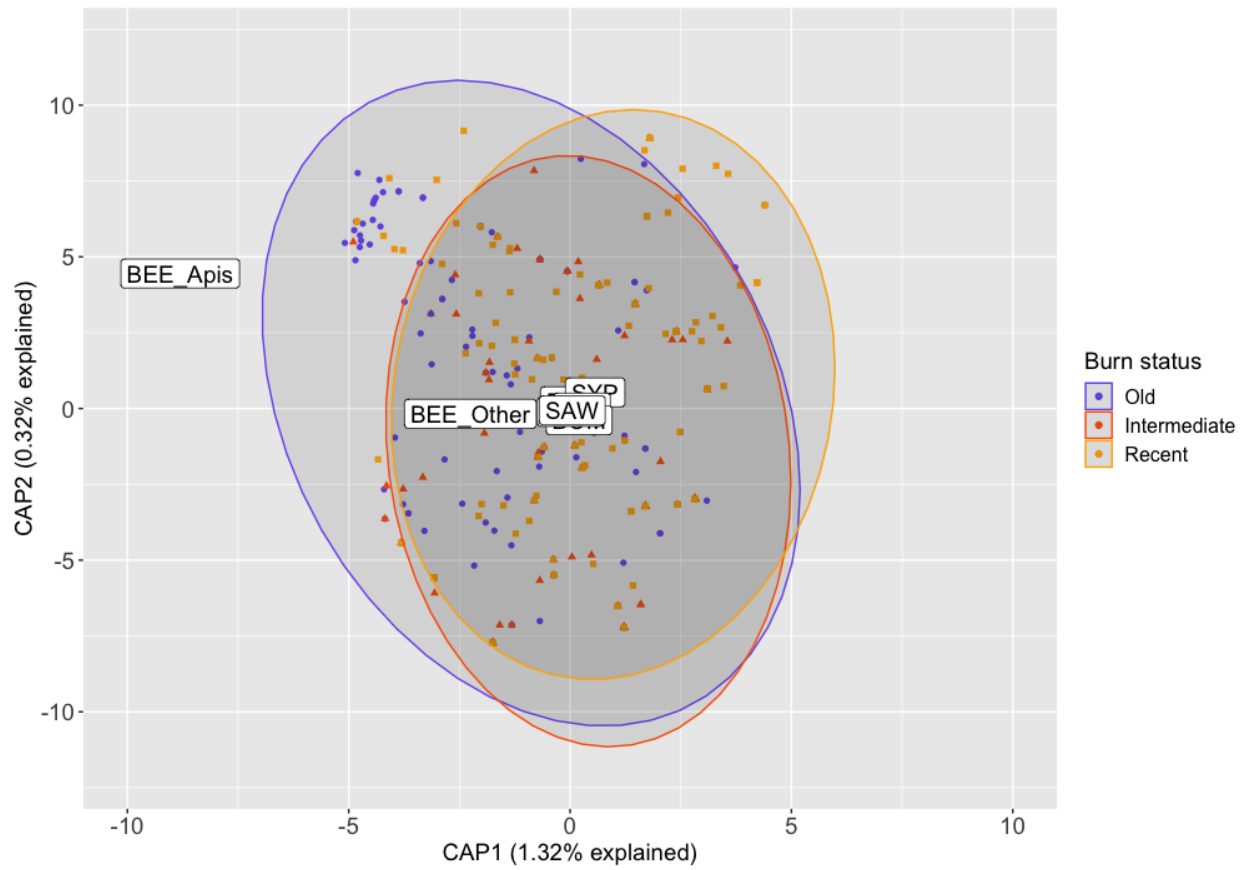
Figure 3.7. Diversity of pollinators (Shannon diversity) against diversity of flowers (Shannon diversity) for each burn status per monitoring year. Zeros indicate (pollinator or flower) species richness of 1. Shaded areas around regression lines represent 95% confidence intervals. Numbers on the top right of each grid denote slope and SE, respectively.
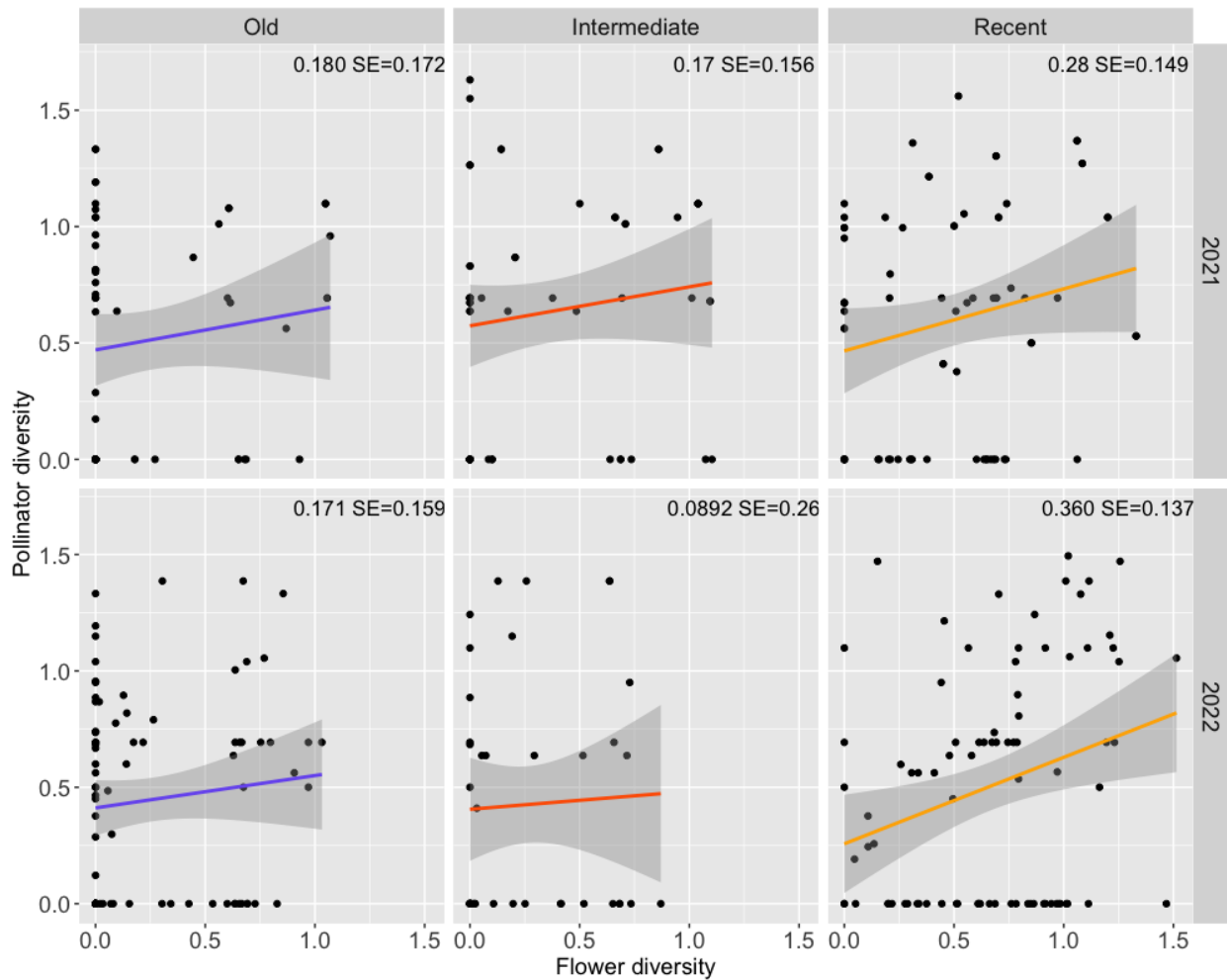
Figure 3.8. Average conspecific pollen count per transect visit. Boxplots show median,

quartiles, and whiskers represent 1.5x the interquartile range.
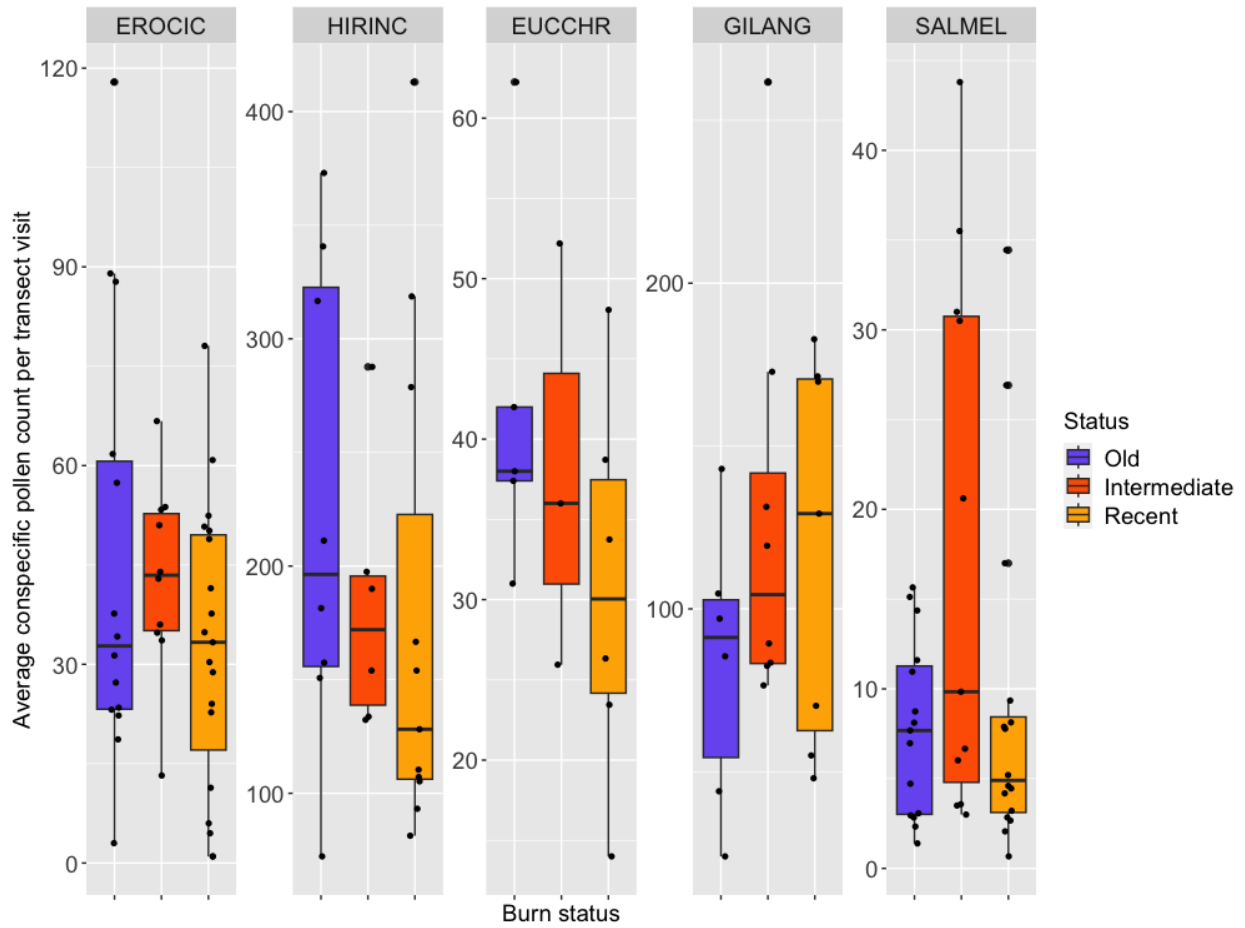
Figure 3.9. Average heterospecific pollen count per transect visit. Boxplots show median,

quartiles, and whiskers represent 1.5x the interquartile range.
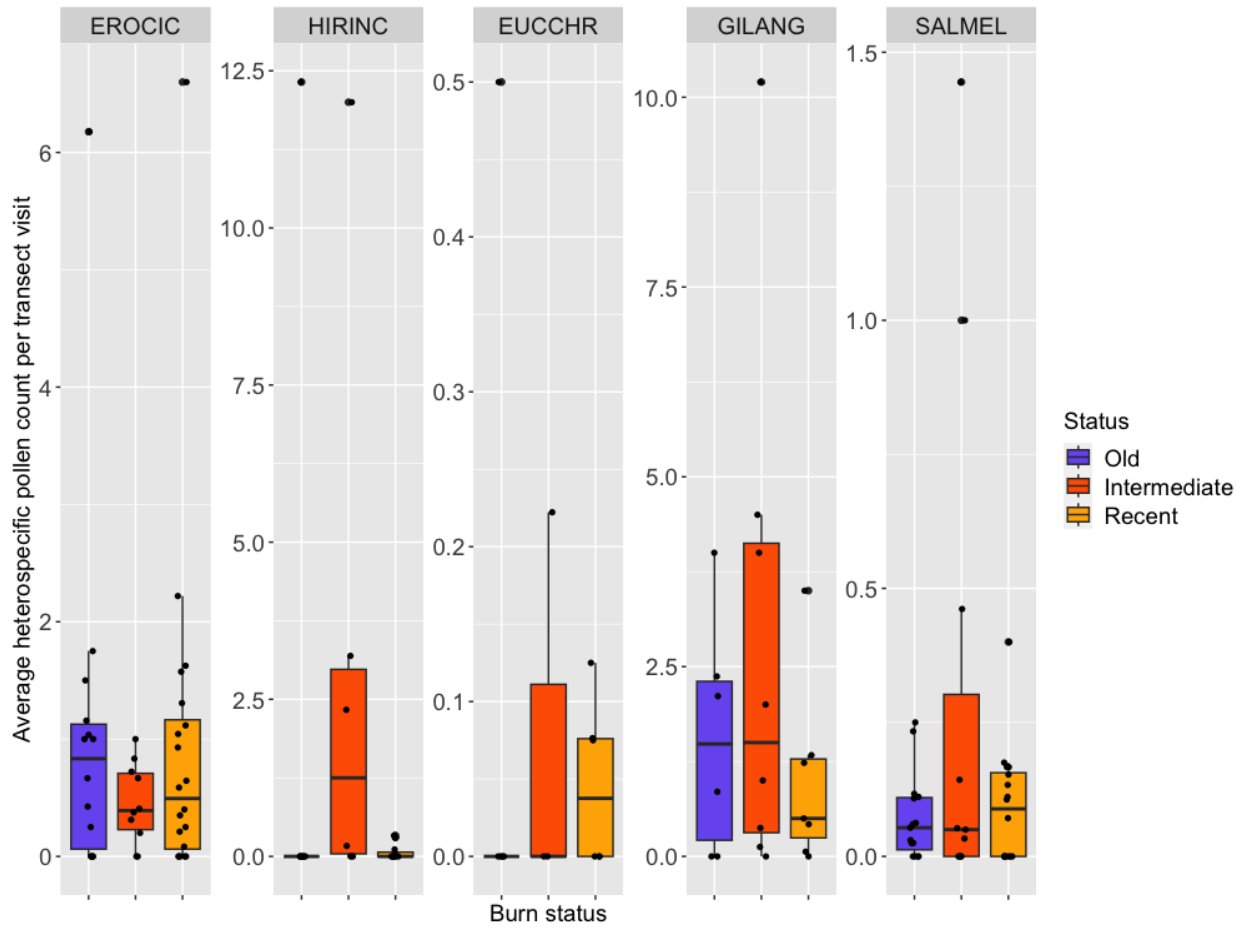
Figure 3.10. Average % of stigmas with heterospecific pollen presence per transect visit.

Boxplots show median, quartiles, and whiskers represent 1.5x the interquartile range.
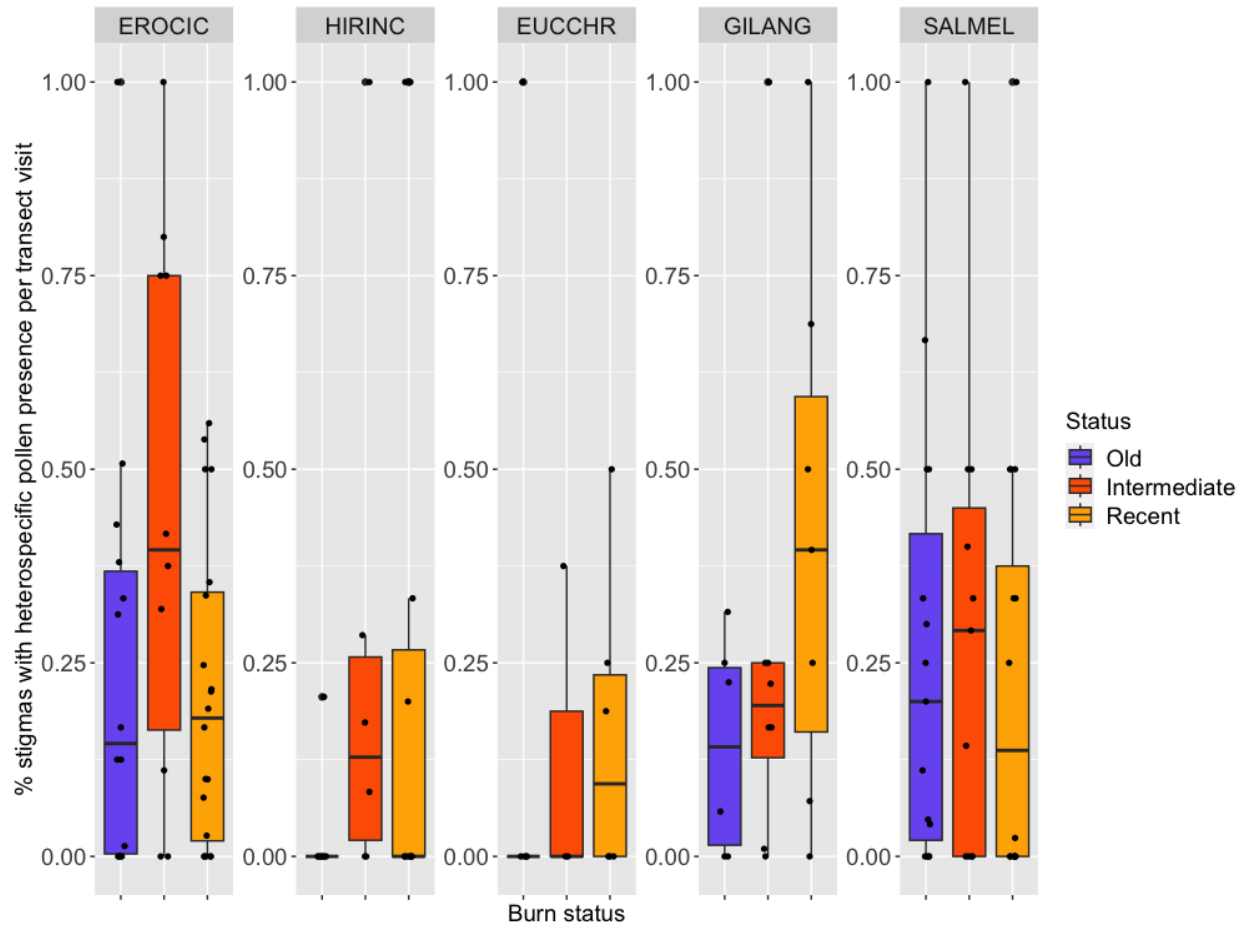
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APPENDIX

Appendix S1.1: Distribution of monitored CSS (green, N = 58) and GL (red, N = 39)

transects across inland Orange County, CA, USA. The shaded orange area indicates land that

was within the Canyon 2 Fire perimeter.
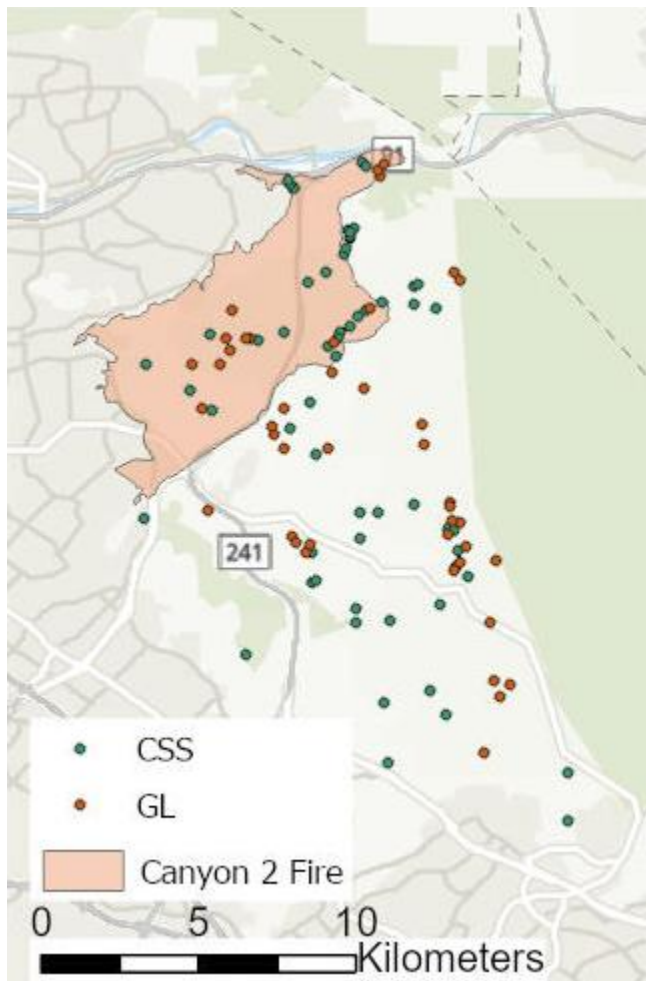
Appendix S1.2 Monitoring schedule of transects from 2007 to 2021. X indicates the transect was monitored in that year. Transect names are four part, with the first and second part indicating the zone of Orange County they are located, CSS = Coastal Sage Scrub, GL = Grassland, and the final number separating transects of the same type in the same zone.

Transect	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
OC_BD_CSS_2							x	x				x	x		
OC_BD_CSS_21							x	x				x	x		x
OC_BD_CSS_3							x	x			x	x	x		
OC_BKR_CSS_10			x	x	x	x	x	x	x	x				x	
OC_BKR_CSS_11			x	x	x	x	x	x	x	x	x				
OC_BKR_CSS_4															x
OC_BKR_CSS_7		x	x	x	x	x			x	x			x	x	
OC_BKR_CSS_8		x	x	x	x	x			x	x	x		x		
OC_BKR_GL_1						x	x	x		x	x		x		
OC_BKR_GL_10									x	x	x	x	x		x
OC_BKR_GL_2						x	x	x		x	x		x		
OC_BKR_GL_3									x		x			x	
OC_BKR_GL_4									x	x			x		
OC_BKR_GL_5									x	x					
OC_BKR_GL_6									x		x			x	
OC_BKR_GL_7									x		x			x	

OC_BKR_GL_8									x		x	x		x	
OC_COL_CSS_1									x		x	x	x		
OC_COL_CSS_2									x		x	x	x		
OC_COL_GL_1									x	x		x	x		
OC_COL_GL_2									x	x		x	x		
OC_COL_GL_3									x	x		x	x		
OC_GV_CSS_1											x				
OC_GV_CSS_2											x	x	x	x	
OC_GV_CSS_3											x	x	x	x	
OC_GYP_CSS_1									x			x	x	x	
OC_GYP_CSS_2									x			x	x	x	x
OC_GYP_CSS_4									x			x	x		
OC_GYP_CSS_5									x			x	x		
OC_GYP_CSS_6									x			x	x		
OC_GYP_CSS_7									x			x	x		
OC_GYP_CSS_8									x			x	x		
OC_GYP_CSS_9									x			x	x		
OC_I_CSS_1	x	x	x	x	x				x	x			x	x	
OC_I_CSS_12			x												
OC_I_CSS_13			x					x							
OC_I_CSS_14			x	x	x	x	x	x		x	x				
OC_I_CSS_15			x	x	x	x	x	x		x	x	x	x	x	x
OC_I_CSS_16			x	x	x	x	x	x		x	x	x	x	x	x

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OC_I_CSS_2	x	x	x	x	x				x	x		x	x	x	
OC_I_CSS_20						x	x	x		x	x				
OC_I_CSS_21						x	x	x		x	x				
OC_I_CSS_26						x	x	x		x	x				
OC_I_CSS_4															x
OC_I_CSS_40						x	x	x		x	x	x	x	x	x
OC_I_CSS_50						x	x	x		x	x	x	x	x	
OC_I_CSS_6		x	x	x	x	x			x	x			x		
OC_I_CSS_61						x	x	x		x	x	x	x		
OC_I_CSS_7															x
OC_I_CSS_71						x	x	x		x	x	x	x	x	
OC_I_CSS_8						x	x	x				x	x		
OC_I_CSS_82						x	x	x			x	x	x		
OC_I_CSS_90						x	x	x			x	x	x		
OC_I_CSS_91							x	x			x	x			
OC_I_CSS_92							x	x			x	x			
OC_I_GL_1	x	x	x	x	x				x	x		x	x		
OC_I_GL_10			x	x	x	x	x	x			x			x	
OC_I_GL_11			x	x	x	x	x	x			x			x	
OC_I_GL_12			x	x	x	x	x	x			x			x	
OC_I_GL_13				x	x										
OC_I_GL_14				x										x	
OC_I_GL_15						x	x	x			x	x	x	x	x

OC_I_GL_16						x	x	x		x	x	x	x	x	x
OC_I_GL_2	x	x												x	
OC_I_GL_21							x	x	x	x					
OC_I_GL_22							x	x	x	x		x	x		
OC_I_GL_23							x	x	x	x		x	x		
OC_I_GL_3		x	x											x	
OC_I_GL_31														x	
OC_I_GL_32														x	
OC_I_GL_33											x			x	
OC_I_GL_34											x			x	
OC_I_GL_35											x			x	
OC_I_GL_36											x			x	
OC_I_GL_4		x	x											x	
OC_I_GL_88							x	x		x	x		x	x	
OC_I_GL_9			x											x	
OC_I_GL_99						x	x	x		x	x		x	x	
OC_IRC_CSS_1													x		
OC_IRC_CSS_12													x		
OC_IRC_CSS_13													x		
OC_IRC_CSS_4													x		
OC_NBS_CSS_11										x	x				
OC_NGC_CSS_15										x	x	x	x	x	x
OC_NUW_CSS_14										x	x	x	x	x	x

OC_NWL_CSS_13										x	x	x	x	x	x
OC_PC_CSS_1															x
OC_SO_CSS_11															x
OC_SS_CSS_3	x	x			x	x			x	x				x	
OC_SS_CSS_4		x			x	x			x	x				x	
OC_SS_CSS_5		x			x	x			x	x				x	
OC_SS_GL_20						x			x	x		x			
OC_SS_GL_21						x		x	x	x		x	x		
OC_SS_GL_5		x	x											x	
OC_WH_CSS_2															x
OC_WH_CSS_9		x												x	

Appendix S1.3 All transects present in long term monitoring dataset with habitat type (Habitat), and their burn status from three recent fires (Santiago fire in 2007, Canyon 2 Fire in 2017, Silverado/Bond fire in 2020) N = unburned, Y = burned. Shaded transects were observed for flowering and pollinator activity in chapters 2 and 3. *transects were observed for chapter 2 and 3 but were not in the analysis for chapter 1.

Transect	Habitat	Santiago	Canyon2Fire	Silverado/Bond
OC_BD_CSS_2	CSS	N	N	N
OC_BD_CSS_21	CSS	N	N	N
OC_BD_CSS_3	CSS	N	N	N
OC_BKR_CSS_10	CSS	N	N	N
OC_BKR_CSS_11	CSS	N	N	N
OC_BKR_CSS_4	CSS	N	N	N
OC_BKR_CSS_7	CSS	N	N	N
OC_BKR_CSS_8	CSS	N	N	N
OC_COL_CSS_1	CSS	N	Y	N
OC_COL_CSS_2	CSS	N	Y	N
OC_GV_CSS_1	CSS	N	Y	N
OC_GV_CSS_2	CSS	N	Y	N
OC_GV_CSS_3	CSS	N	Y	N
OC_GYP_CSS_1	CSS	N	Y	N
OC_GYP_CSS_2	CSS	N	Y	N
OC_GYP_CSS_4	CSS	N	N	N
OC_GYP_CSS_5	CSS	N	N	N
OC_GYP_CSS_6	CSS	N	N	N
OC_GYP_CSS_7	CSS	N	N	N
OC_GYP_CSS_8	CSS	N	N	N
OC_GYP_CSS_9	CSS	N	N	N

OC_I_CSS_1	CSS	N	N	N
OC_I_CSS_12	CSS	N	N	N
OC_I_CSS_13	CSS	N	N	N
OC_I_CSS_14	CSS	N	N	N
OC_I_CSS_15	CSS	N	Y	N
OC_I_CSS_16	CSS	N	Y	N
OC_I_CSS_2	CSS	N	Y	N
OC_I_CSS_20	CSS	N	N	N
OC_I_CSS_21	CSS	N	N	N
OC_I_CSS_26	CSS	N	N	N
OC_I_CSS_4	CSS	N	Y	N
OC_I_CSS_40	CSS	N	Y	N
OC_I_CSS_50	CSS	N	Y	N
OC_I_CSS_6	CSS	N	N	N
OC_I_CSS_61	CSS	N	Y	N
OC_I_CSS_7	CSS	N	Y	N
OC_I_CSS_71	CSS	N	Y	N
OC_I_CSS_8	CSS	N	Y	N
OC_I_CSS_82	CSS	N	Y	N
OC_I_CSS_90	CSS	N	Y	N
OC_I_CSS_91	CSS	N	Y	N
OC_I_CSS_92	CSS	N	Y	N
OC_IRC_CSS_1	CSS	Y	N	Y
OC_IRC_CSS_12	CSS	Y	N	Y
OC_IRC_CSS_13	CSS	Y	N	Y
OC_IRC_CSS_4	CSS	Y	N	Y
OC_NBS_CSS_11	CSS	N	N	N
OC_NGC_CSS_15	CSS	N	N	N

OC_NUW_CSS_14	CSS	Y	Y	N
OC_NWL_CSS_13	CSS	Y	N	N
OC_PC_CSS_1	CSS	N	N	N
OC_SO_CSS_11	CSS	Y	Y	N
OC_SS_CSS_3	CSS	Y	N	Y
OC_SS_CSS_4	CSS	Y	N	Y
OC_SS_CSS_5	CSS	Y	N	Y
OC_WH_CSS_2	CSS	Y	N	N
OC_WH_CSS_9	CSS	Y	N	N
OC_BKR_GL_1	GL	N	N	N
OC_BKR_GL_10	GL	N	N	N
OC_BKR_GL_2	GL	N	N	N
OC_BKR_GL_3	GL	N	N	N
OC_BKR_GL_4	GL	N	N	N
OC_BKR_GL_5	GL	N	N	N
OC_BKR_GL_6	GL	N	N	N
OC_BKR_GL_7	GL	N	N	N
OC_BKR_GL_8	GL	N	N	N
OC_COL_GL_1	GL	N	Y	N
OC_COL_GL_2	GL	N	Y	N
OC_COL_GL_3	GL	N	Y	N
OC_I_GL_1	GL	N	Y	N
OC_I_GL_10	GL	N	N	N
OC_I_GL_11	GL	N	N	N
OC_I_GL_12	GL	N	N	N
OC_I_GL_13	GL	N	N	N
OC_I_GL_14	GL	N	Y	N
OC_I_GL_15	GL	N	Y	N

OC_I_GL_16	GL	N	Y	N
OC_I_GL_2	GL	Y	N	Y
OC_I_GL_21	GL	N	N	N
OC_I_GL_22	GL	N	N	N
OC_I_GL_23	GL	N	N	N
OC_I_GL_3	GL	N	Y	Y
OC_I_GL_31	GL	N	Y	N
OC_I_GL_32	GL	N	Y	N
OC_I_GL_33	GL	N	Y	N
OC_I_GL_34	GL	N	N	N
OC_I_GL_35	GL	N	N	N
OC_I_GL_36	GL	N	Y	N
OC_I_GL_4	GL	Y	N	Y
OC_I_GL_88	GL	N	N	N
OC_I_GL_9	GL	N	Y	N
OC_I_GL_99	GL	N	N	N
OC_L_GL_4	GL	Y	N	N
OC_SS_GL_20	GL	Y	N	Y
OC_SS_GL_21	GL	Y	N	Y
OC_SS_GL_5	GL	Y	N	Y
OC_IRC_CSS_8*	CSS	Y	N	Y
OC_IRC_CSS_23*	CSS	Y	N	Y

Appendix S1.4 List of all species codes (spCode) and corresponding species names (spName), growth habits (gHabit), and native/non-native status (Nat_Non). Nomenclature follows Jepson Flora Project names. (Jepson Flora Project. (2023). *Jepson eFlora (eds.)*. Retrieved 27 February 2023, from https://ucjeps.berkeley.edu/eflora/)

spCode	spName	gHabit	Nat_Non
ACMAME	Acmispon_americanus	Forb	NATIVE
ACMARG	Acmispon argophyllus	Forb	NATIVE
ACMGLA	Acmispon_glaber	Forb	NATIVE
ACMHER	Acmispon heermannii	Forb	NATIVE
ACMMAR	Acmispon_maritimus	Forb	NATIVE
ACMMIC	Acmispon_micranthus	Forb	NATIVE
ACMSPP	Acmispon_species	Forb	NATIVE
ACMSTR	Acmispon_strigosus	Forb	NATIVE
ACMWRA	Acmispon_wrangelianus	Forb	NATIVE
ACOMIC	Acourtia_microcephala	Forb	NATIVE
ADEFAS	Adenostoma_fasciculatum	Shrub	NATIVE
AGOGRA	Agoseris_grandiflora	Forb	NATIVE
AGOSPP	Agoseris species	Forb	NATIVE
AGRPAL	Agrostis_pallens	Grass	NATIVE
AMBACA	Ambrosia_acanthicarpa	Forb	NATIVE
AMBCON	Ambrosia_confertiflora	Forb	NATIVE
AMBPSI	Ambrosia_psilostachya	Forb	NATIVE
AMSINT	Amsinckia_intermedia	Forb	NATIVE

AMSMEN	Amsinckia_menziesii	Forb	NATIVE
AMSRET	Amsinckia retrorsa	Forb	NATIVE
ANAARV	Anagallis_arvensis	Forb	NONNATIVE
ANTCAU	Anthriscus caucalis	Forb	NONNATIVE
ANTCOU	Antirrhinum_coulterianum	Forb	NATIVE
ANTKEL	Antirrhinum_kelloggii	Forb	NATIVE
ANTNUT	Antirrhinum_nuttallianum	Forb	NATIVE
APIANG	Apiastrum_angustifolium	Forb	NATIVE
ARIPUR	Aristida purpurea	Grass	NATIVE
ARTCAL	Artemisia_californica	Shrub	NATIVE
ARTPAL	Artemisia_palmeri	Forb	NATIVE
ASCFAS	Asclepias fascicularis	Forb	NATIVE
ASTGAM	Astragalus gambelianus	Forb	NATIVE
ATHPUS	Athysanus pusillus	Forb	NATIVE
ATRSEM	Atriplex semibaccata	Forb	NONNATIVE
AVEBAR	Avena_barbata	Grass	NONNATIVE
AVEFAT	Avena_fatua	Grass	NONNATIVE
AVESPP	Avena_species	Grass	NONNATIVE
BACPIL	Baccharis_pilularis	Shrub	NATIVE
BACSAL	Baccharis_salicifolia	Shrub	NATIVE
BLOCRO	Bloomeria_crocea	Forb	NATIVE
BOTBAR	Bothriochloa barbinodis	Grass	NATIVE
BOWINC	Bowlesia_incana	Forb	NATIVE
BRADIS	Brachypodium_distachyon	Grass	NONNATIVE

BRANIG	Brassica_nigra	Forb	NONNATIVE
BROCAR	Bromus_carinatus	Grass	NATIVE
BROCAT	Bromus_catharticus	Grass	NONNATIVE
BRODIA	Bromus_diandrus	Grass	NONNATIVE
BROHOR	Bromus_hordeaceus	Grass	NONNATIVE
BROMAD	Bromus_madritensis	Grass	NONNATIVE
BROSPP	Bromus_species	Grass	NONNATIVE
BROTEC	Bromus tectorum	Grass	NONNATIVE
CALBRE	Calandrinia breweri	Forb	NATIVE
CALCAT	Calochortus_catalinae	Forb	NATIVE
CALMAC	Calystegia_macrostegia	Forb	NATIVE
CALMEN	Calandrinia_menziesii	Forb	NATIVE
CALSPL	Calochortus_splendens	Forb	NATIVE
CALSPP	Calochortus_species	Forb	NATIVE
CALWEE	Calochortus weedii var. weedii	Forb	NATIVE
CAMBIS	Camissoniopsis_bistorta	Forb	NATIVE
CAMHIR	Camissonia_hirtella	Forb	NATIVE
CAMMIC	Camissoniopsis_micrantha	Forb	NATIVE
CAMSPP	Camissoniopsis_species	Forb	NATIVE
CAPBUR	Capsella bursa-pastoris	Forb	NONNATIVE
CARPYC	Carduus_pycnocephalus	Forb	NONNATIVE
CARSPP	Carex_species	Grass	NATIVE
CARTRI	Carex triquetra	Grass	NATIVE
CASEXS	Castilleja_exserta	Forb	NATIVE

CAUHET	Caulanthus_heterophyllus	Forb	NATIVE
CAUSPP	Caulanthus species	Forb	NATIVE
CEACRA	Ceanothus_crassifolius	Shrub	NATIVE
CEAGRE	Ceanothus_greggii	Shrub	NATIVE
CEAMEG	Ceanothus_megacarpus	Shrub	NATIVE
CEAOLI	Ceanothus_oliganthus	Shrub	NATIVE
CEASPP	Ceanothus_species	Shrub	NATIVE
CEATOM	Ceanothus_tomentosus	Shrub	NATIVE
CENMEL	Centaurea_melitensis	Forb	NONNATIVE
CERBET	Cercocarpus_betuloides	Shrub	NATIVE
CERGLO	Cerastium_glomeratum	Forb	NONNATIVE
CHAALB	Chamaesyce_albomarginata	Forb	NATIVE
CHAART	Chaenactis_artemisiifolia	Forb	NATIVE
CHAGLA	Chaenactis_glabriuscula	Forb	NATIVE
CHASPP	Chaenactis_species	Forb	NATIVE
CHEALB	Chenopodium album	Forb	NONNATIVE
CHECAL	Chenopodium_californicum	Forb	NATIVE
CHEMUR	Chenopodium murale	Forb	NONNATIVE
CHLPAR	Chlorogalum_parviflorum	Forb	NATIVE
CHLPOM	Chlorogalum_pomeridianum	Forb	NATIVE
CHLSPP	Chlorogalum_species	Forb	NATIVE
CHOPAR	Chorizanthe parryi	Forb	NATIVE
CIROCC	Cirsium_occidentale	Forb	NATIVE
CIRSPP	Cirsium_species	Forb	NATIVE

CLAPAR	Claytonia_parviflora	Forb	NATIVE
CLAPER	Claytonia_perfoliata	Forb	NATIVE
CLAPUR	Clarkia_purpurea	Forb	NATIVE
COLHET	Collinsia_heterophylla	Forb	NATIVE
CONARV	Convolvulus_arvensis	Forb	NONNATIVE
CONCAN	Conyza_canadensis	Forb	NATIVE
CONMAC	Conium_maculatum	Forb	NONNATIVE
CORFIL	Corethrogyne_filaginifolia	Forb	NATIVE
CORRIG	Cordylanthus_rigidus	Forb	NATIVE
CRACON	Crassula_connata	Forb	NATIVE
CROSET	Croton_setigerus	Forb	NATIVE
CRYINT	Cryptantha_intermedia	Forb	NATIVE
CRYMIC	Cryptantha_micromeres	Forb	NATIVE
CRYMUR	Cryptantha_muricata	Forb	NATIVE
CRYSPP	Cryptantha_species	Forb	NATIVE
CUPFOR	Hesperocyparis_forbesii	Shrub	NATIVE
CUSCAL	Cuscuta_californica	Forb	NATIVE
CUSSPP	Cuscuta_species	Forb	NATIVE
CYLPRO	Cylindropuntia prolifera	Shrub	NATIVE
CYNCAR	Cynara_cardunculus	Forb	NONNATIVE
CYPERA	Cyperus eragrostis	Grass	NATIVE
DATWRI	Datura wrightii	Forb	NATIVE
DAUPUS	Daucus_pusillus	Forb	NATIVE
DEIFAS	Deinandra_fasciculata	Forb	NATIVE

DEISPP	Deinandra_species	Forb	NATIVE
DENRIG	Dendromecon_rigida	Forb	NATIVE
DICCAP	Dichelostemma_capitatum	Forb	NATIVE
DISSPI	Distichlis_spicata_	Forb	NATIVE
DISSPP	Distichlis_spicata	Grass	NATIVE
DUDLAN	Dudleya_lanceolata	Forb	NATIVE
DUDVIS	Dudleya viscida	Forb	NATIVE
ELEMON	Eleocharis_montevidensis	Grass	NATIVE
ELEPAL	Eleocharis_palustris	Forb	NATIVE
ELYCON	Elymus_condensatus	Grass	NATIVE
ELYSPP	Elymus_species	Grass	NATIVE
EMMPEN	Emmenanthe_penduliflora	Forb	NATIVE
ENCCAL	Encelia_californica	Shrub	NATIVE
ENCFAR	Encelia_farinosa	Shrub	NATIVE
EPICAN	Epilobium_canum	Forb	NATIVE
ERIBON	Erigeron bonariensis	Forb	NONNATIVE
ERICON	Eriophyllum_confertiflorum	Forb	NATIVE
ERICRA	Eriodictyon_crassifolium	Shrub	NATIVE
ERIELO	Eriogonum_elongatum	Forb	NATIVE
ERIFAS	Eriogonum_fasciculatum	Shrub	NATIVE
ERIFOL	Erigeron_foliosus	Forb	NATIVE
ERIPAL	Ericameria_palmeri	Shrub	NATIVE
ERIPIN	Ericameria_pinifolia	Shrub	NATIVE
ERISAP	Eriastrum sapphirinum	Forb	NATIVE

ERISPP1	Ericameria_species	Shrub	NATIVE
ERISPP2	Erigeron_species	Forb	NATIVE
ERISPP3	Eriophyllum species	Forb	NATIVE
EROBOT	Erodium_botrys	Forb	NONNATIVE
EROBRA	Erodium_brachycarpum	Forb	NONNATIVE
EROCIC	Erodium_cicutarium	Forb	NONNATIVE
EROMOS	Erodium_moschatum	Forb	NONNATIVE
EROSPP	Erodium_species	Forb	NONNATIVE
ESCCAL	Escholzia_californica	Forb	NATIVE
EUCCHR	Eucrypta_chrysanthemifolia	Forb	NATIVE
EULCAL	Eulobus_californicus	Forb	NATIVE
EUPALB	Euphorbia_albomarginata	Forb	NATIVE
EUPPEP	Euphorbia peplus	Forb	NONNATIVE
FESARU	Festuca_arundinacea	Grass	NONNATIVE
FESMIC	Festuca microstachys	Grass	NATIVE
FESMYU	Festuca_myuros	Grass	NONNATIVE
FESOCT	Festuca_octoflora	Grass	NONNATIVE
FESPER	Festuca_perennis	Grass	NONNATIVE
FESSPP	Festuca_species	Grass	NONNATIVE
FOEVUL	Foeniculum_vulgare	Forb	NONNATIVE
FRIBIF	Fritillaria_biflora	Forb	NATIVE
FUNCYN	Funastrum_cynanchoides	Forb	NATIVE
GALAND	Galium_andrewsii	Forb	NATIVE
GALANG	Galium_angustifolium	Forb	NATIVE

GALAPA	Galium_aparine	Forb	NATIVE
GALNUT	Galium_nuttallii	Forb	NATIVE
GALPAR	Galium_parisiense	Forb	NONNATIVE
GALSPP	Galium_species	Forb	NATIVE
GASPHL	Gastridium_phleoides	Grass	NONNATIVE
GAZLIN	Gazania linearis	Forb	NONNATIVE
GILANG	Gilia_angelensis	Forb	NATIVE
GILCAP	Gilia_capitata	Forb	NATIVE
GILDIE	Gilia diegensis	Forb	NATIVE
GNASPP	Gnaphalium spp	Forb	NATIVE
GRICAM	Grindelia_camporum	Forb	NATIVE
GUTCAL	Gutierrezia_californica	Forb	NATIVE
GUTSAR	Gutierrezia_sarothrae	Forb	NATIVE
GUTSPP	Gutierrezia_species	Forb	NATIVE
HARPAL	Harpagonella_palmeri	Forb	NATIVE
HAZSQU	Hazardia_squarrosa	Shrub	NATIVE
HEDCRE	Hedypnois_cretica	Forb	NONNATIVE
HELANN	Helianthus_annuus	Forb	NATIVE
HELECH	Helminthotheca_echioides	Forb	NONNATIVE
HELGRA	Helianthus_gracilentus	Forb	NATIVE
HELSCO	Helianthemum_scoparium	Forb	NATIVE
HESFOR	Hesperocyparis forbesii	Shrub	NATIVE
HESWHI	Hesperoyucca_whipplei	Shrub	NATIVE
HETARB	Heteromeles_arbutifolia	Shrub	NATIVE

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HETGRA	Heterotheca grandiflora	Forb	NATIVE
HIRINC	Hirschfeldia_incana	Forb	NONNATIVE
HORMUR	Hordeum_murinum	Grass	NONNATIVE
HORVUL	Hordeum vulgare	Grass	NONNATIVE
HYPGLA	Hypochaeris_glabra	Forb	NONNATIVE
HYPSPP	Hypochaeris_species	Forb	NONNATIVE
ISOMEN	Isocoma_menziesii	Shrub	NATIVE
JEPPAR	Jepsonia parryi	Forb	NATIVE
JUNBAL	Juncus balticus	Grass	NATIVE
JUNSPP	Juncus_species	Forb	NATIVE
JUNXIP	Juncus_xiphioides	Forb	NATIVE
KECANT	Keckiella_antirrhinoides	Shrub	NATIVE
KECCOR	Keckiella_cordifolia	Shrub	NATIVE
LACSER	Lactuca_serriola	Forb	NONNATIVE
LAECOU	Laennecia_coulteri	Forb	NATIVE
LAMAUR	Lamarckia_aurea	Grass	NONNATIVE
LASCAL	Lasthenia_californica	Forb	NATIVE
LASCOR	Lasthenia coronaria	Forb	NATIVE
LASGRA	Lasthenia_gracilis	Forb	NATIVE
LATVES	Lathyrus vestitus	Forb	NATIVE
LAYPLA	Layia_platyglossa	Forb	NATIVE
LEPNIT	Lepidium_nitidum	Forb	NATIVE
LINCAN	Nuttallanthus_texanus	Forb	NATIVE
LINDIA	Linanthus dianthiflorus	Forb	NATIVE

LINSPP	Linanthus_species	Forb	NATIVE
LOGARI	Logfia arizonica	Forb	NATIVE
LOGFIL	Logfia_filanginoides	Forb	NATIVE
LOGGAL	Logfia_gallica	Forb	NONNATIVE
LOMLUC	Lomatium lucidum	Forb	NATIVE
LONSUB	Lonicera_subspicata	Shrub	NATIVE
LOTCOR	Lotus corniculatus	Forb	NONNATIVE
LUPAGA	Lupinus concinnus	Forb	NATIVE
LUPBIC	Lupinus_bicolor	Forb	NATIVE
LUPHIR	Lupinus_hirsutissimus	Forb	NATIVE
LUPMIC	Lupinus microcarpus	Forb	NATIVE
LUPSPA	Lupinus_sparsiflorus	Forb	NATIVE
LUPSPP	Lupinus_species	Forb	NATIVE
LUPSUC	Lupinus_succulentus	Forb	NATIVE
LUPTRU	Lupinus_truncatus	Forb	NATIVE
LYSARV	Lysimachia_arvensis	Forb	NONNATIVE
MALFAS	Malacothamnus_fasciculatus	Shrub	NATIVE
MALLAU	Malosma_laurina	Shrub	NATIVE
MALPAR	Malva_parviflora	Forb	NONNATIVE
MALSAX	Malacothrix_saxatilis	Forb	NATIVE
MARMAC	Marah_macrocarpa	Forb	NATIVE
MARVUL	Marrubium_vulgare	Forb	NONNATIVE
MEDPOL	Medicago_polymorpha	Forb	NONNATIVE
MEDSPP	Medicago_species	Forb	NONNATIVE

MEDTRU	Medicago truncatula	Forb	NONNATIVE
MELIMP	Melica_imperfecta	Grass	NATIVE
MELIND	Melilotus_indicus	Forb	NONNATIVE
MELSPP	Melilotus species	Forb	NONNATIVE
MICCAL	Micropus_californicus	Forb	NATIVE
MICLIN	Microseris_lindleyi	Forb	NATIVE
MIMAUR	Mimulus_aurantiacus	Shrub	NATIVE
MIRLAE	Mirabilis_laevis	Forb	NATIVE
MUHMIC	Muhlenburgia_microsperma	Forb	NATIVE
MUHRIG	Muhlenbergia_rigens	Grass	NATIVE
MUIMAR	Muilla maritima	Forb	NATIVE
NASLEP	Stipa_lepida	Grass	NATIVE
NASPUL	Stipa_pulchra	Grass	NATIVE
NOLCIS	Nolina_cismontana	Shrub	NATIVE
NOLSPP	Nolina_species	Shrub	NATIVE
OENSAR	Oenanthe_sarmentosa	Forb	NATIVE
OPULIT	Opuntia_littoralis	Shrub	NATIVE
OPUORI	Opuntia_oricola	Shrub	NATIVE
OSMTEN	Osmadenia_tenella	Forb	NATIVE
OXAALB	Oxalis_albicans	Forb	NATIVE
OXAPES	Oxalis_pes-caprae	Forb	NONNATIVE
PECLIN	Pectocarya_linearis	Forb	NATIVE
PELMUR	Pellaea_mucronata	Forb	NATIVE
PENCLA	Pennisetum_clandestinum	Grass	NONNATIVE

PENSPE	Penstemon spectabilis	Forb	NATIVE
PENTRI	Pentagramma_triangularis	Forb	NATIVE
PHACAM	Phacelia campanularia	Forb	NATIVE
PHACIC	Phacelia_cicutaria	Forb	NATIVE
PHADIS	Phacelia distans	Forb	NATIVE
PHAPAR	Phacelia_parryi	Forb	NATIVE
PHARAM	Phacelia ramosissima	Forb	NATIVE
PHASPP	Phacelia_species	Forb	NATIVE
PHOAUR	Pholistoma_auritum	Forb	NATIVE
PLACAL	Platystemon_californicus	Forb	NATIVE
PLACAN	Plagiobothrys canescens	Forb	NATIVE
PLACOL	Plagiobothrys_collinus	Forb	NATIVE
PLAERE	Plantago_erecta	Forb	NATIVE
PLANOT	Plagiobothrys_nothofulvus	Forb	NATIVE
PLAOVA	Plantago_ovata	Forb	NATIVE
PLAPAT	Plantago patagonica	Forb	NATIVE
PLASPP	Plagiobothrys_species	Forb	NATIVE
POAANN	Poa_annua	Grass	NONNATIVE
POASEC	Poa secunda	Grass	NATIVE
POLVIR	Polypogon_viridis	Grass	NONNATIVE
PORGRA	Porophyllum_gracile	Forb	NATIVE
PRUILI	Prunus_ilicifolia	Shrub	NATIVE
PSEBEN	Pseudognaphalium beneolens	Forb	NATIVE
PSEBIO	Pseudognaphalium_bioletti	Forb	NATIVE

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PSECAL	Pseudognaphalium_californicum	Forb	NATIVE
PSELUT	Pseudognaphalium luteoalbum	Forb	NONNATIVE
PSEMIC	Pseudognaphalium microcephalum	Forb	NATIVE
PSESPP	Pseudognaphalium_species	Forb	NATIVE
PSESTR	Pseudognaphalium stramineum	Forb	NATIVE
PSIBRE	Psilocarphus_brevissimus	Forb	NATIVE
PTEDRY	Pterostegia_drymarioides	Forb	NATIVE
QUEAGR	Quercus_agrifolia	Shrub	NATIVE
QUEBER	Quercus_berberidifolia	Shrub	NATIVE
QUEDUM	Quercus_dumosa	Shrub	NATIVE
QUESPP	Quercus_species	Shrub	NATIVE
RAFCAL	Rafinesquia_californica	Forb	NATIVE
RAPSAT	Raphanus_sativus	Forb	NONNATIVE
RHACRO	Rhamnus_crocea	Shrub	NATIVE
RHAILI	Rhamnus_ilicifolia	Shrub	NATIVE
RHASPP	Rhamnus_species	Shrub	NATIVE
RHUINT	Rhus_integrifolia	Shrub	NATIVE
RHUOVA	Rhus_ovata	Shrub	NATIVE
RIBIND	Ribes_indecorum	Shrub	NATIVE
RIBSPP	Ribes_species	Shrub	NATIVE
ROMCOU	Romneya_coulteri	Shrub	NATIVE
RUMCAL	Rumex californicus	Forb	NATIVE
RUMCRI	Rumex crispus	Forb	NONNATIVE
SALAPI	Salvia_apiana	Shrub	NATIVE

SALAUS	Saltugilia_australis	Forb	NATIVE
SALCOL	Salvia_columbariae	Forb	NATIVE
SALLAS	Salix_lasiolepis	Shrub	NATIVE
SALLEU	Salvia_leucophylla	Shrub	NATIVE
SALMEL	Salvia_mellifera	Shrub	NATIVE
SALSPP	Salvia species	Shrub	NATIVE
SALTRA	Salsola_tragus	Forb	NONNATIVE
SAMNIG	Sambucus_nigra	Shrub	NATIVE
SANARG	Sanicula_arguta	Forb	NATIVE
SANBIP	Sanicula bipinnatifida	Forb	NATIVE
SANSPP	Sanicula_species	Forb	NATIVE
SCHBAR	Schismus_barbatus	Grass	NONNATIVE
SCRCAL	Scrophularia_californica	Forb	NATIVE
SENCAL	Senecio californicus	Forb	NATIVE
SENVUL	Senecio_vulgaris	Forb	NONNATIVE
SIDMAL	Sidalcea malviflora	Forb	NATIVE
SILCON	Silene coniflora	Forb	NONNATIVE
SILGAL	Silene_gallica	Forb	NONNATIVE
SILMAR	Silybum_marianum	Forb	NONNATIVE
SISBEL	Sisyrinchium_bellum	Forb	NATIVE
SISIRI	Sisymbrium_irio	Forb	NONNATIVE
SISOFF	Sisymbrium_officinale	Forb	NONNATIVE
SISORI	Sisymbrium_orientale	Forb	NONNATIVE
SISSPP	Sisymbrium species	Forb	NONNATIVE

SOLAME	Solanum_americanum	Forb	NATIVE
SOLNIG	Solanum_nigra	Forb	NONNATIVE
SOLPAR	Solanum_parishii	Shrub	NATIVE
SOLUMB	Solanum_umbelliferum	Shrub	NATIVE
SOLXAN	Solanum_xanti	Shrub	NATIVE
SONASP	Sonchus_asper	Forb	NONNATIVE
SONOLE	Sonchus_oleraceus	Forb	NONNATIVE
SONSPP	Sonchus_species	Forb	NONNATIVE
STEDIE	Stephanomeria_diegensis	Forb	NATIVE
STEEXI	Stephanomeria exigua	Forb	NATIVE
STEMED	Stellaria_media	Forb	NONNATIVE
STENIT	Stellaria_nitens	Forb	NATIVE
STICOR	Stipa coronata	Grass	NATIVE
STIMIL	Stipa_miliacea	Grass	NONNATIVE
STISPE	Stipa_speciosa	Grass	NATIVE
STISPP	Stipa_species	Grass	NATIVE
TAROFF	Taraxacum_officinale	Forb	NONNATIVE
TAUARG	Tauschia arguta	Forb	NATIVE
TAUSPP	Tauschia species	Forb	NATIVE
THYLAC	Thysanocarpus laciniatus	Forb	NATIVE
TOXDIV	Toxicodendron_diversilobum	Shrub	NATIVE
TOXFRE	Toxicoscordion_fremontii	Forb	NATIVE
TRIALB	Trifolium_albopurpureum	Forb	NATIVE
TRICIL	Trifolium_ciliolatum	Forb	NATIVE

TRIHIR	Trifolium_hirtum	Forb	NONNATIVE
TRILANA	Trichostema_lanatum	Shrub	NATIVE
TRILANC	Trichostema lanceolatum	Forb	NATIVE
TRIMIC	Trifolium_microcephalum	Forb	NATIVE
TRIREP	Trifolium_repens	Forb	NONNATIVE
TRITRI	Trifolium_trichocalyx	Forb	NATIVE
TRIWIL	Trifolium_willdenovii	Forb	NATIVE
TRIWOR	Trifolium wormskioldii	Forb	NATIVE
URTDIO	Urtica dioica	Forb	NATIVE
VERLAS	Verbena_lasiostachys	Forb	NATIVE
VICAME	Vicia americana var. americana	Forb	NATIVE
VIOPED	Viola_pedunculata	Forb	NATIVE

Appendix S1.5: Methods and outputs for spatial autocorrelation analysis

In response to results that suggest burned and unburned GL transects had pre-fire differences in species composition driven by annual grass species in the *Avena* and *Bromus* genera, we calculated spatial autocorrelation on the covers of the species of interest. Taking the final year of pre-fire data (2017), latitude and longitude coordinates for the beginning point of each measured transect were used to generate a matrix of inverse distance weights, and the Moran.I function from the R "ape" package was used to calculate Moran's I.

Moran's I outputs for *Avena* and *Bromus* spp. in Grassland (GL) transects pre-fire. *$P < 0.05$. **$P < 0.01$. ***$P < 0.001$ Bolded values indicate $P < 0.05$.

Species	Observed	Expected	s.d.	P
Avena fatua	0.0514	-0.0556	0.106	0.315
Avena barbata	0.074	-0.0556	0.066	0.0493
All Avena	-0.0612	-0.0556	0.105	0.957
Bromus diandrus	-0.0509	-0.0556	0.102	0.964
All Bromus	0.0995	-0.0556	0.105	0.138

Appendix S1.6: Methods and results for precipitation analysis

S1.6.1 Methods:

Precipitation data were obtained from the Tustin Irvine Ranch weather station (location: 33°43'54.3"N, 117°47'04.9"W) through OC public works' hydrology portal (http://hydstra.ocpublicworks.com/web.htm). Annual changes in precipitation levels affect the amount of vegetation cover, especially for the annual grasses and forbs. To test whether cumulative yearly precipitation between June and March could explain any interannual changes in absolute cover, we analyzed the data from burned and unburned sites after 2017, with burn status and precipitation as factors (Method 1). As there are only four years of data, and we are only considering one wildfire event and its post-fire precipitation patterns, any conclusions related to how post-fire precipitation patterns affect recovery will be limited.

S1.6.2 Results:

The Canyon 2 fire was immediately followed by a dry 2018 season with only approximately 105mm of rainfall between June 2017 and March 2018, compared to a long term average of 323mm for the June to March period (Tustin, U.S. Climate Data). This was then followed by a wet year in 2019 (484mm), 298mm in 2020, and 135mm in 2021 (see S1.6.3). These precipitation levels significantly affected the absolute cover of native plants, native grasses, native forbs, and non-native forbs in CSS (S1.6.4), with higher cover corresponding with higher precipitation levels in both burned and unburned sites. Only non-native grasses showed an interaction between precipitation and burn status, which may come from the

unusual increase in cover in burned sites in 2019 corresponding with higher precipitation levels, while cover in unburned sites decreased (S1.6.4).

In GL, absolute cover of total native plants and absolute cover of native forbs both increased with precipitation across the four years (Appendix S1.6.5). The vegetation categories (total native plant cover, native forb cover) for which precipitation was significant correspond with those in which year was a significant factor in the year x burn analysis above, except for non-native grasses, where cover depended on year but not precipitation. Plots of absolute cover against precipitation) showed a general positive correlation between cumulative rainfall and native plant cover in both burned and unburned sites, except for non-native forb cover and native grass cover. In unburned sites, both non-native forb cover and native grass cover were highest in a low rainfall year (2021), whereas in burned sites they increased with precipitation (S1.6.3).

S1.6.3 Figure showing absolute cover of growth forms after fire against cumulative June-March precipitation from the preceding year. Panels on the left are for coastal sage scrub (CSS), and panels on the right are for grasslands (GL). Error bars represent standard error. Data from sites that were burned in 2017 are shown in red (label Y) while those that were unburnt are shown in blue (N). A: native plants. B: native shrubs. C: Native forbs. D: Non-native forbs. E: Native grasses. F: Non-native grasses.

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S1.6.4. Results of linear mixed-effect models of CSS native/non-native growth form covers for Method 1. Burn status (burn) was included as a factor and cumulative June-March precipitation (ppt) from the preceding year, with only data post 2017 included in the model. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

Community	Cover type	Factors	Absolute cover		Relative cover	
			Chisq	P	Chisq	P
Method 1	Native plants	Ppt Burn Ppt x Burn	**13.5** **21.0** 3.08	**2.37e-04** **4.49e-06** 0.0790	1.0e-04 **35.3** 0.497	0.991 **2.84e-09** 0.481
	Native shrubs	Ppt Burn Ppt x Burn	0.329 **73.2** 0.441	0.566 **<2e-16** 0.507	**24.6** **87.6** **11.8**	**7.09e-07** **< 2.2e-16** **5.93e-04**
	Native grasses	Ppt Burn Ppt x Burn	7.96 2.68 0.0069	**0.00477** 0.102 0.934	4.06 2.87 0.18	0.0439 0.0902 . 0.671
	Non-native grasses	Ppt Burn Ppt x Burn	0.132 0.0015 **14.6**	0.716 0.969 **1.3e-04**	4.67 4.42 1.76	0.0308 0.0355 0.185
	Native forbs	Ppt Burn Ppt x Burn	**8.73** 0.633 5.08	**0.00312** 0.426 0.0242	**9.52** **11.7** 2.50	**0.00204** **6.40e-04** 0.114
	Non-native forbs	Ppt Burn Ppt x Burn	**9.60** 1.42 3.68	**0.00195** 0.234 0.0550	5.02 **17.8** 3.46	0.0251 **2.5e-05** 0.063

S1.6.5. Results of linear mixed-effect models of GL native/non-native growth form covers for Method 1. Burn status (burn) was included as a factor and cumulative June-March precipitation (ppt) from the preceding year, with only data post 2017 included in the model. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

Community	Cover type	Factors	Absolute cover		Relative cover	
			Chisq	P	Chisq	P
Method 1	Native plants	Ppt Burned Ppt x Burn	**14.4** 1.38 0.0084	**1.47e-04** 0.239 0.927	1.60 1.69 0.0543	0.205 0.194 0.816
	Native shrubs	Ppt Burned Ppt x Burn	0.0685 2.07 0.0034	0.794 0.150 0.953	2.52 2.54 1.13	0.112 0.111 0.289
	Native grasses	Ppt Burned Ppt x Burn	1.22 6.09 3.60	0.269 0.0136 0.0577 .	0.257 5.08 1.33	0.612 0.0243 0.249
	Non-native grasses	Ppt Burned Ppt x Burn	2.17 1.70 1.65	0.141 0.193 0.199	2.63 0.0156 0.0015	0.105 0.901 0.969
	Native forbs	Ppt Burned Ppt x Burn	**18.7** 0.0143 0.480	**1.49e-05** 0.905 0.489	**16.8** 4.0e-04 1.09	**4.17e-05** 0.984 0.296
	Non-native forbs	Ppt Burned Ppt x Burn	1.89 0.0039 2.14	0.169 0.950 0.143	0.733 3.65 0.136	0.392 0.0559 . 0.713

Appendix S1.7 Relative cover of growth forms over time. Panels on the left are for coastal sage scrub (CSS), and panels on the right are for grasslands (GL). Error bars represent standard error. The shaded box shows years after the 2017 Canyon 2 Fire. Data from sites that were burned in 2017 are shown in red (label Y) while those that were unburnt are shown in blue (N). A: native plants. B: native shrubs. C: Native forbs. D: Non-native forbs. E: Native grasses. F: Non-native grasses.
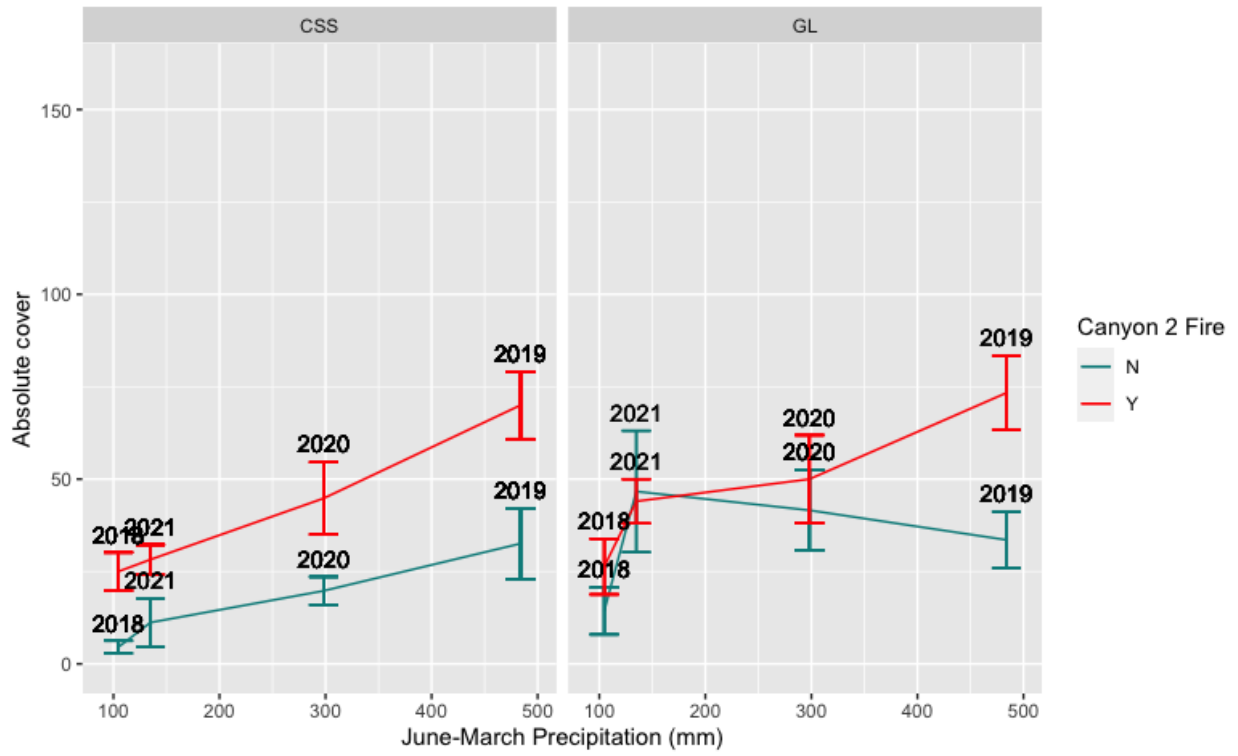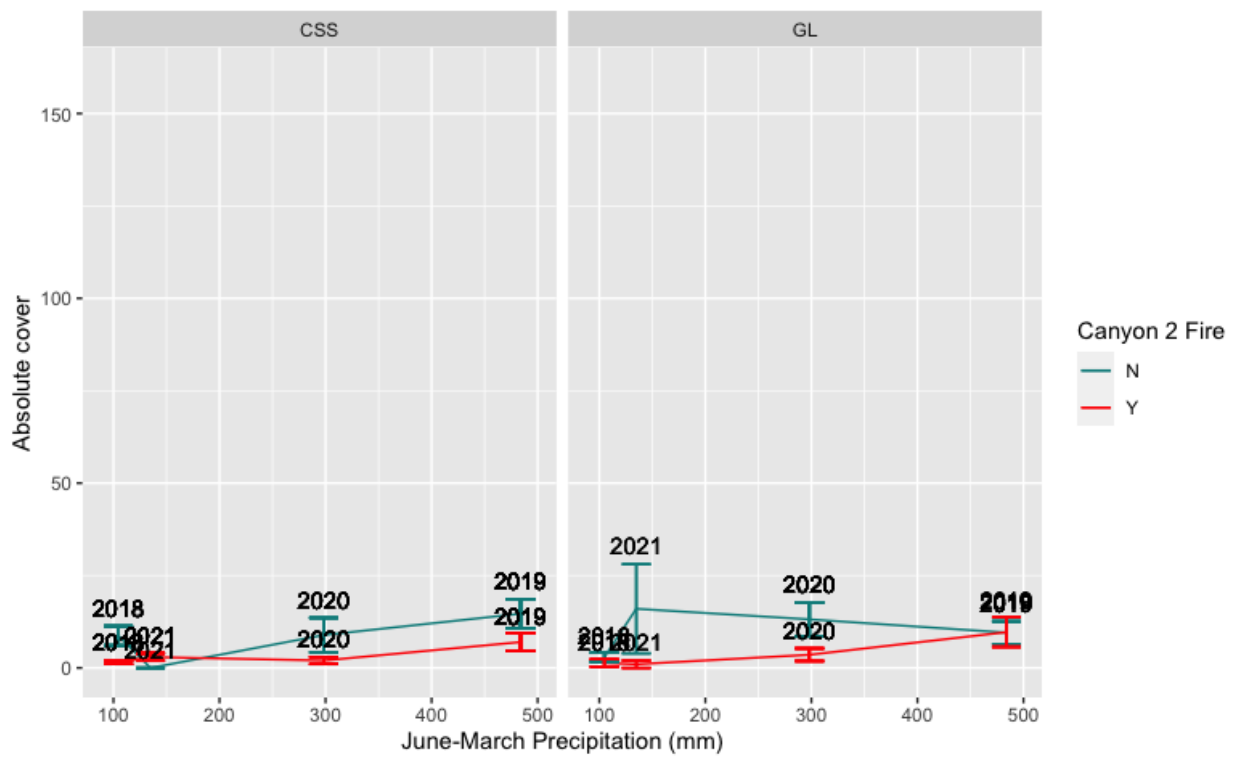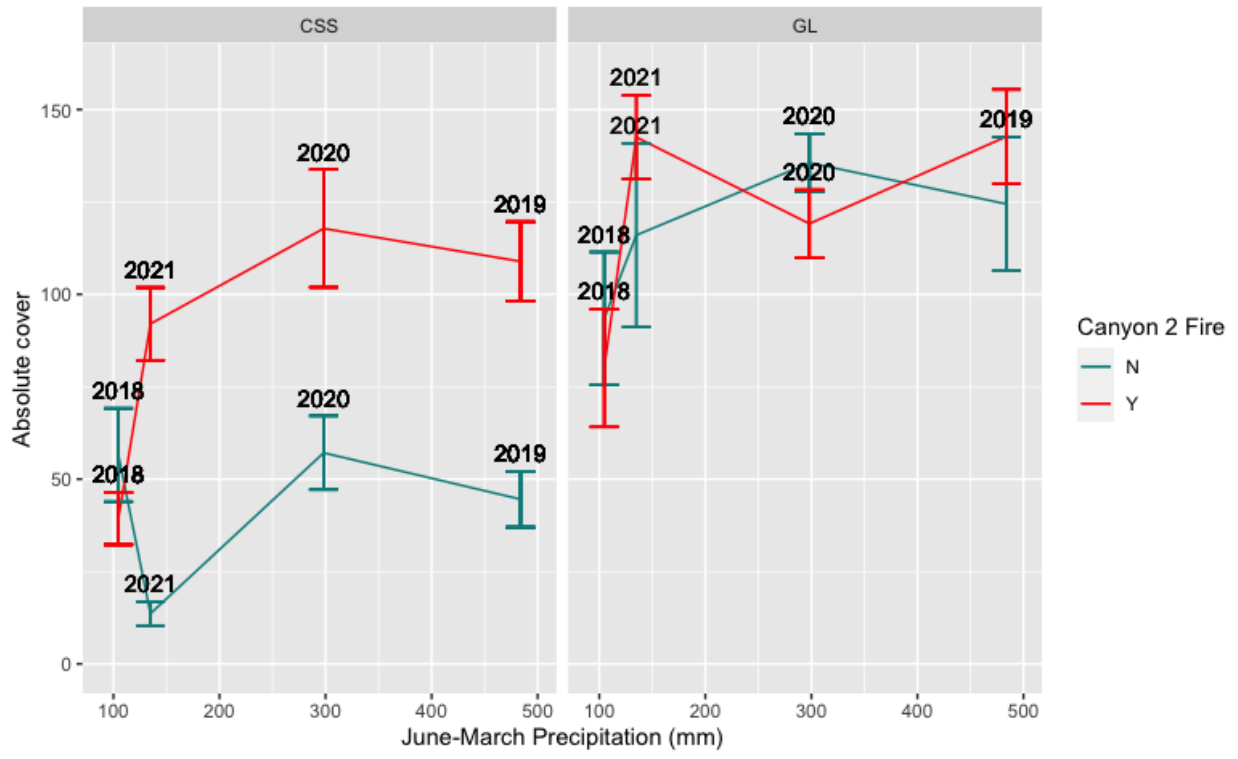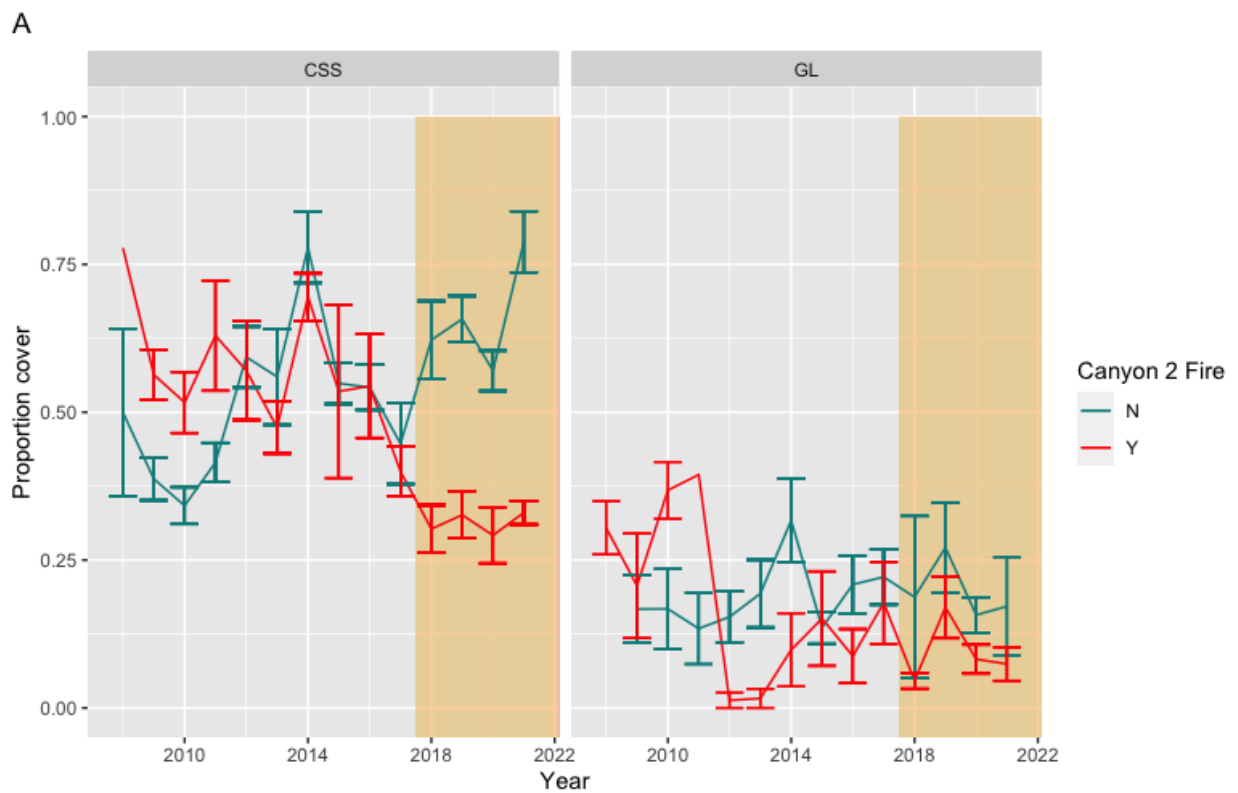
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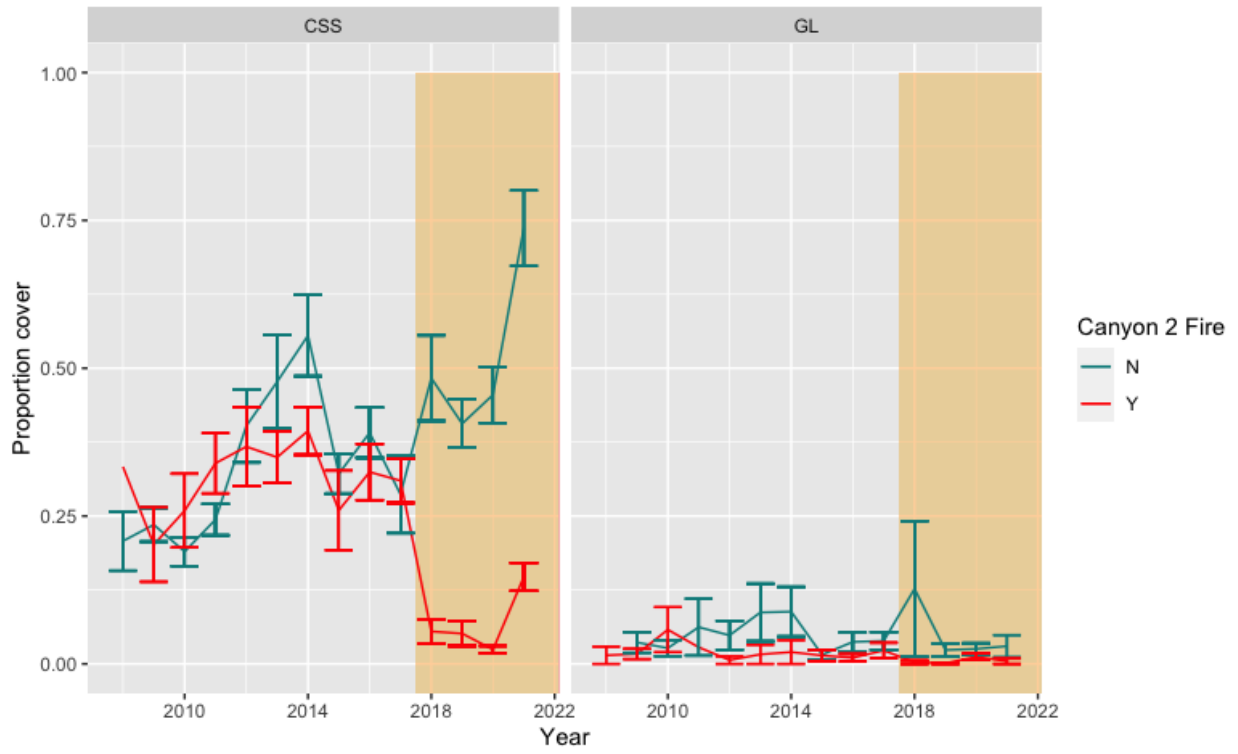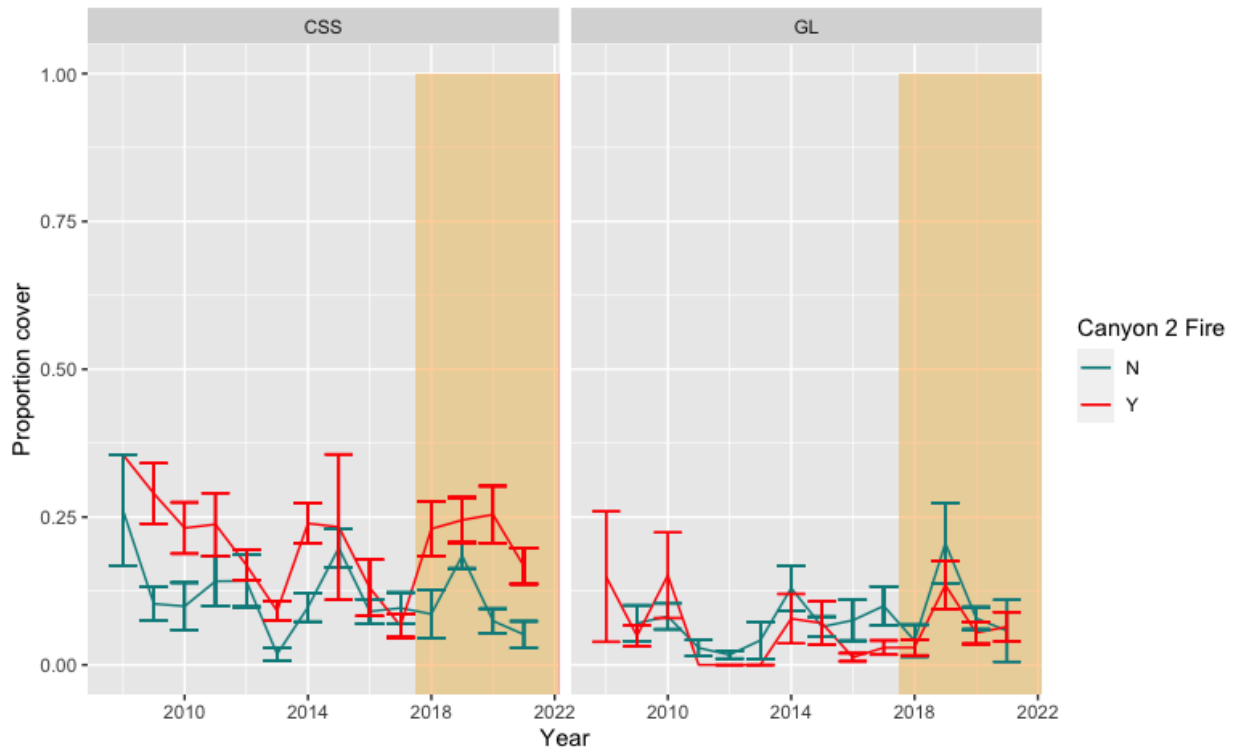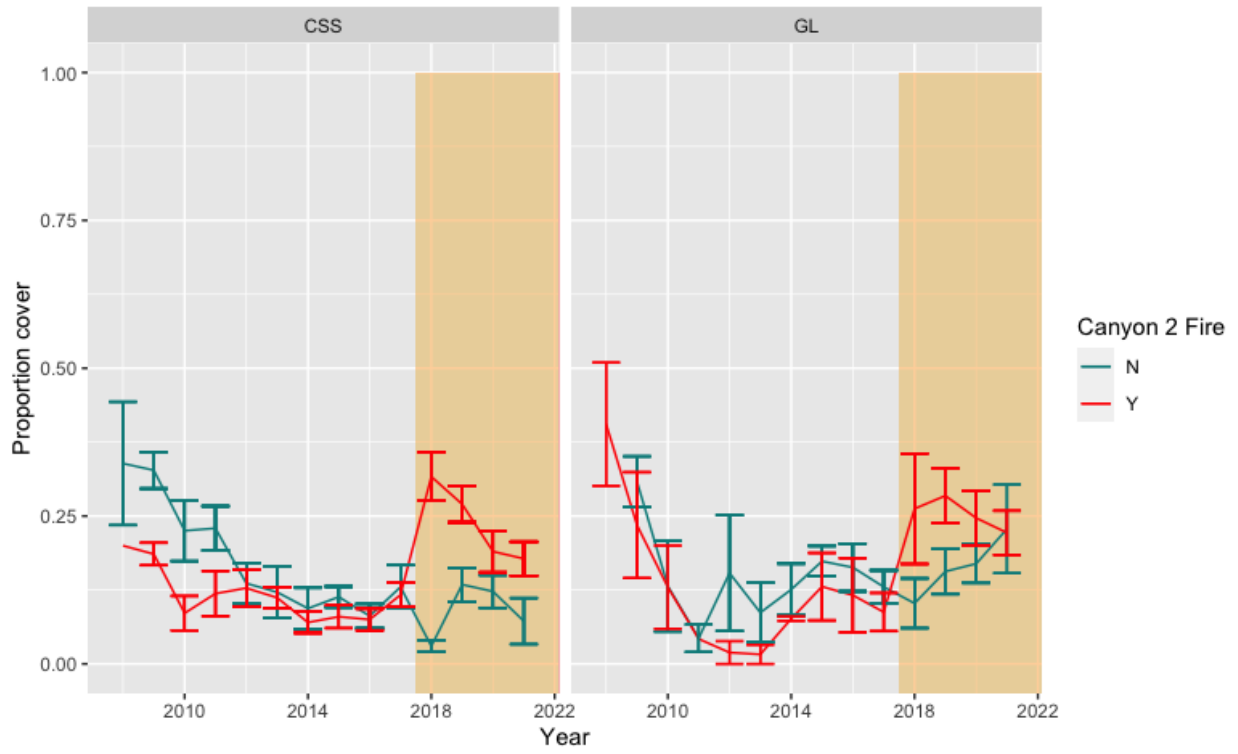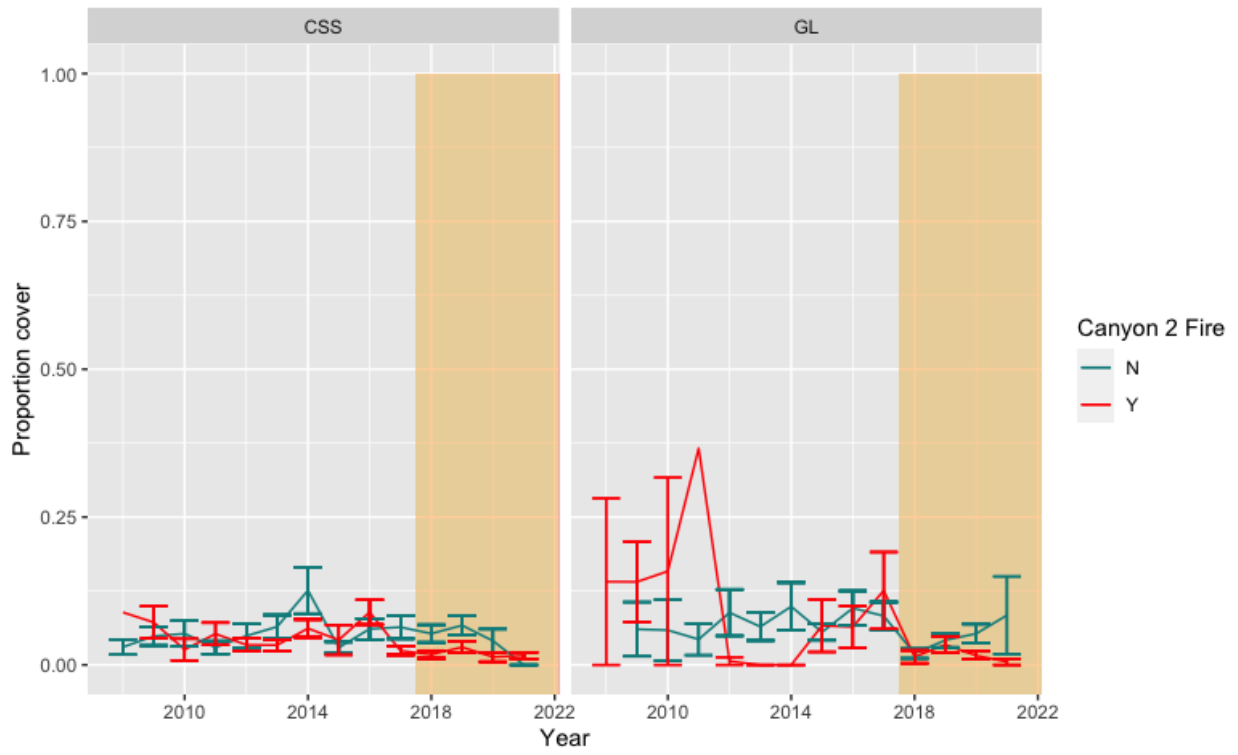
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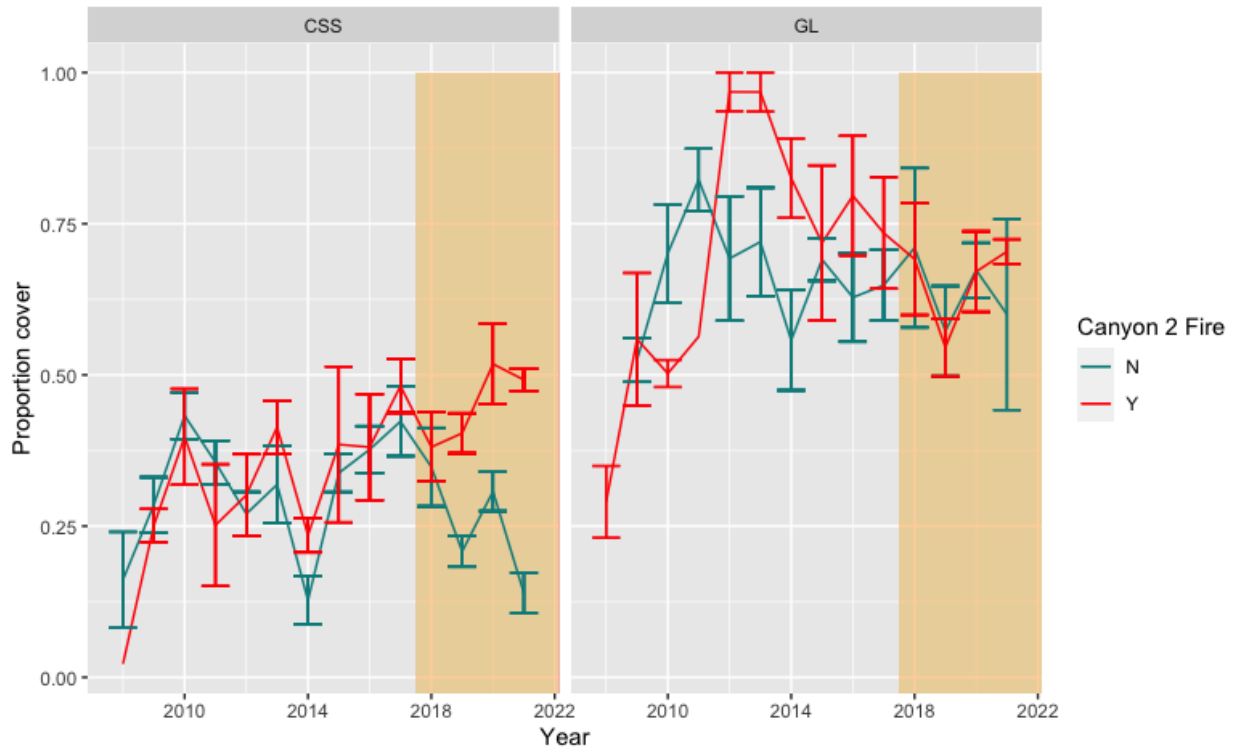
Appendix S1.8. Results of linear mixed-effect models of CSS native/non-native growth form covers for Method 1. Factors are whether or not the site burned and year as a categorical variable, with only data post 2017 included in the model. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

Method of analyses	Cover type	Factor	Df	Absolute cover		Relative cover	
				Chisq	P	Chisq	P
Method 1: Post 2017 data	Native plants	Year	3	**18.88**	**2.89e-04**	4.95	0.176
		Burned	1	**30.72**	**2.98e-08**	**31.94**	**1.595-08**
		Year x Burn	3	5.12	0.162	5.74	0.125
	Native Shrubs	Year	3	**15.44**	**1.48e-03**	**73.41**	**7.93e-16**
		Burned	1	**73.23**	**< 2.2e-16**	**95.91**	**<2.2e-16**
		Year x Burn	3	8.28	0.0406	**44.03**	**1.48e-09**
	Native Grasses	Year	3	8.71	0.0335	6.85	0.0767
		Burned	1	3.27	0.0705	3.55	0.0594
		Year x Burn	3	0.277	0.964	0.324	0.956
	Non-native Grasses	Year	3	4.16	0.245	**14.51**	**2.28e-03**
		Burned	1	1.06	0.304	0.475	0.491
		Year x Burn	3	**52.85**	**1.97e-11**	**26.13**	**8.96e-06**
	Native Forbs	Year	3	**14.01**	**2.89e-03**	**14.19**	**2.66e-03**
		Burned	1	0.0275	0.868	**10.3**	**1.33e-03**
		Year x Burn	3	**14.39**	**2.42e-03**	5.18	0.159
	Non-native Forbs	Year	3	10.0	0.0186	6.84	0.0773
		Burned	1	3.89	0.0485	**37.77**	**7.94e-10**
		Year x Burn	3	4.76	0.190	**13.08**	**4.47e-03**

Appendix S1.9. Results of linear mixed-effect models of CSS native/non-native growth form covers for Method 2. Only sites burned in the Canyon 2 Fire were included, with each year after fire compared to pre-fire values. Mean difference is the % difference in absolute or relative cover from listed year to pre-fire. Bolded values indicate significant values. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

| Method of analyses	Cover type	Year compared with pre-fire	df	Absolute cover		Relative cover	
				Mean difference	P	Mean difference	P
Method 2	Native plants	2018	4	**-48.84**	**0**	**-21.4**	**0**
		2019		12.95	0.0266	**-19.1**	**0**
		2020		-1.17	0.886	**-22.2**	**0**
		2021		**-22.02**	**0.003**	**-28.2**	**0**
	Native Shrubs	2018	4	**-39.06**	**0**	**-27.5**	**0**
		2019		**-33.49**	**0**	**-28.8**	**0**
		2020		**-39.02**	**0**	**-28.5**	**0**
		2021		**-31.38**	**0**	**-24.1**	**0**
	Native Grasses	2018	4	**-4.66**	**8.0e-04**	**-25.7**	**0.0014**
		2019		1.13	0.407	-1.34	0.0901
		2020		-3.92	0.0426	**-3.22**	**0.0045**
		2021		**-4.53**	**8.9e-03**	-3.62	**0.0005**
	Non-native Grasses	2018	4	**-22.51**	**5.5e-03**	-0.0471	0.987
		2019		**49.80**	**0**	2.24	0.437
		2020		**61.74**	**0**	**13.2**	**0.0016**
		2021		**48.83**	**0**	**20.9**	**0.0000**
	Native Forbs	2018	4	-8.19	0.35	8.63	4.1e-03
		2019		**45.23**	**0**	**10.1**	**8.0e-04**
		2020		**42.33**	**0**	9.52	0.0238
		2021		16.18	0.0201	1.07	0.775
	Non-native Forbs	2018	4	9.99	0.053	**21.2**	**0.0000**
		2019		**56.63**	**0**	**16.5**	**0.0000**
		2020		**30.86**	**0**	8.56	0.0194
		2021		15.01	0.0166	7.84	0.0132

Appendix S1.10.Results of linear mixed-effect models of GL native/non-native growth form covers for Method 1. Factors are whether or not the site burned and year as a categorical variable, with only data post 2017 included in the model. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

Community	Cover type	Factors	Df	Absolute cover		Relative cover	
				Chisq	P	Chisq	P
Method 1	Native plants	Year Burned Year x Burn	3 1 3	**16.73** 0.529 0.769	**8.04e-04** 0.467 0.857	4.47 2.88 0.73	0.22 0.090 0.87
	Native shrubs	Year Burned Year x Burn	3 1 3	0.601 2.07 0.226	0.896 0.150 0.973	5.65 4.34 2.85	0.13 0.037 0.42
	Native grasses	Year Burned Year x Burn	3 1 3	1.68 2.60 3.58	0.64 0.107 0.31	0.82 1.82 2.18	0.85 0.18 0.54
	Non-native grasses	Year Burned Year x Burn	3 1 3	**14.1** 0.462 6.93	**2.76e-03** 0.497 0.0742	4.01 0.10 0.24	0.26 0.75 0.97
	Native forbs	Year Burned Year x Burn	3 1 3	**20.62** 0.009 0.56	**1.26e-04** 0.924 0.906	**18.82** 0.14 0.89	**0.00030** 0.71 0.83
	Non-native forbs	Year Burned Year x Burn	3 1 3	9.60 2.56 8.89	0.0222 0.109 0.0309	3.13 **7.51** 2.62	0.37 **0.0062** 0.45

Appendix S1.11. Results of linear mixed-effect models of GL native/non-native growth form covers for Method 2. Only sites burned in the Canyon 2 Fire were included, with each year after fire compared to pre-fire values. Mean difference is the % difference in absolute or relative cover from listed year to pre-fire. Bolded values indicate significant values. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05 after Bonferroni correction for 5 related tests (uncorrected P < 0.01)

Community	Cover type	Year compared with pre-fire	df	Absolute cover		Relative cover	
				Mean difference	P	Mean difference	P
Method 2	Native plants	2018 2019 2020 2021	4	-20.96 23.38 -14.65 -5.77	0.027 0.014 0.097 0.60	-8.42 4.04 -7.01 -3.52	0.014 0.22 0.031 0.38
	Native shrubs	2018 2019 2020 2021	4	-2.74 -2.74 -1.98 -1.62	0.086 0.086 0.18 0.40	-1.45 -1.63 -1.07 -1.09	0.037 0.020 0.11 0.20
	Native grasses	2018 2019 2020 2021	4	-14.52 -6.18 -13.25 -10.72	0.020 0.30 0.025 0.15	-6.52 -4.53 -5.84 -5.65	0.025 0.12 0.033 0.11
	Non-native grasses	2018 2019 2020 2021	4	**-34.55** 28.12 2.61 22.94	**0.0088** 0.030 0.82 0.14	-9.24 **-24.0** -2.53 -11.4	0.089 **0.0001** 0.63 0.094
	Native forbs	2018 2019 2020 2021	4	-4.73 **31.27** 1.13 5.69	0.47 **0.00** 0.85 0.47	-1.06 **9.57** 0.444 2.52	0.69 **0.0007** 0.99 0.42
	Non-native forbs	2018 2019 2020 2021	4	10.18 **54.18** 21.66 **29.33**	0.25 **0.00** 0.013 **0.009**	**17.3** **19.4** 10.2 14.3	**0.0023** **0.0007** 0.040 0.033

Appendix S1.12. Results of linear mixed model of species richness and diversity in burned vs unburned sites after 2017. A total of 106 transect observations were included for CSS and 55 for GL. Sample size (number of transect-year combinations) is given in parentheses. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05.

Community	Variable	Factors	Chisq	Df	P
CSS (N=106)	Species Richness	Year Burned Year x Burn	87.51 3.78 24.02	3 1 3	**2.2e-16** 0.0519 **2.47e-05**
	H. Diversity	Year Burned Year x Burn	6.26 8.38 6.88	3 1 3	0.109 **0.00379** 0.0759
GL (N = 55)	Species Richness	Year Burned Year x Burn	22.43 1.85 3.39	3 1 3	**5.32e-05** 0.17 0.36
	H. Diversity	Year Burned Year x Burn	12.47 0.87 2.21	3 1 3	**0.0059** 0.35 0.53

Appendix S1.13. Results of t-tests on species richness and diversity in burned and unburned sites, comparing each year after burn with pooled pre-burn data. N = number of samples, Mean = average species richness or H diversity. *P < 0.05. **P < 0.01. ***P < 0.001 Bolded values indicate P < 0.05.

| Category	Year	N	Species richness		H diversity	
			Mean	P	Mean	P
Burned CSS	Pre	40	27		1.88	
	2018	19	22.5	**0.0059**	1.94	0.47
	2019	19	29.3	0.23	1.93	0.63
	2020	9	25.4	0.47	1.45	**0.0012**
	2021	12	29.7	0.15	1.71	0.11
Unburned CSS	Pre	55	26.1		1.84	
	2018	12	20.2	**0.013**	1.60	**0.044**
	2019	19	31.8	**0.0083**	1.73	0.30
	2020	10	23.8	0.34	1.51	**0.012**
	2021	6	16	**0.0013**	1.43	**0.014**
Burned GL	Pre	15	18.1		1.21	
	2018	6	17.3	0.86	0.969	0.40
	2019	6	22.2	0.40	1.43	0.43
	2020	9	21.7	0.38	1.17	0.87
	2021	4	16.5	0.78	0.917	0.37
Unburned GL	Pre	49	19.9		1.38	
	2018	6	14	0.078	0.769	**0.014**
	2019	8	23.4	0.22	1.58	0.37
	2020	14	20.2	0.90	1.12	0.14
	2021	2	16.5	0.55	1.34	0.92

Appendix S1.14. CAP analysis of vegetation community composition in burned and
unburned GL sites after the canyon II fires. Total observations = 30, unique transects = 58.
The points visualizes individual observations of transects, with paths connecting different
years' observations from a unique transect: transects that were burned in 2017 are
represented by a red arrow (Y) and unburned transects with blue (N). Species values are
overlaid on the same CAP axes, with labels categorized based on growth form and native
status (native grass = red, native forb = black, non-native forb = green, non-native grass =
blue). Only species with CAP absolute values greater than 0.3 are shown. Ellipses show the
burn/year combination groups with 95% confidence level.
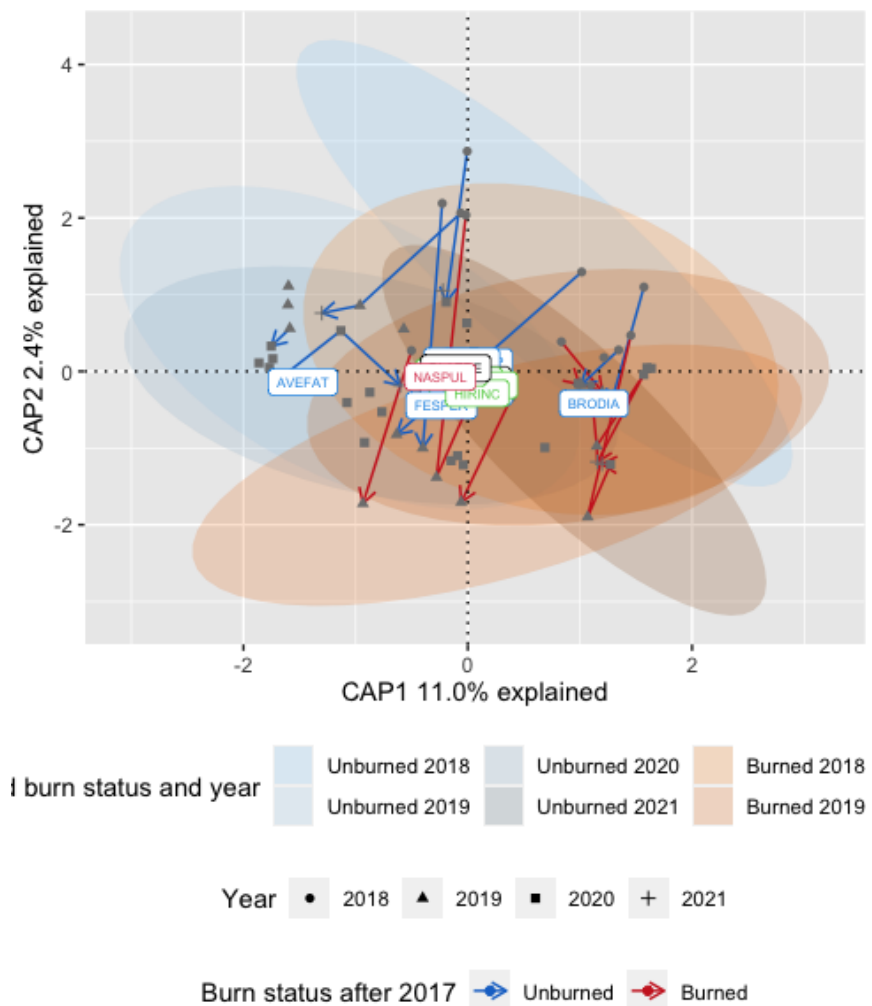
Appendix S1.15. CAP analysis of vegetation community composition in GLsites that burned in 2017 only, comparing pre fire and each subsequent year after fire. Points are connected for each unique transect =13, showing its trajectory through time. N = 52. Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native grass = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Ellipses show the burn/year combination groups with 95% confidence level.
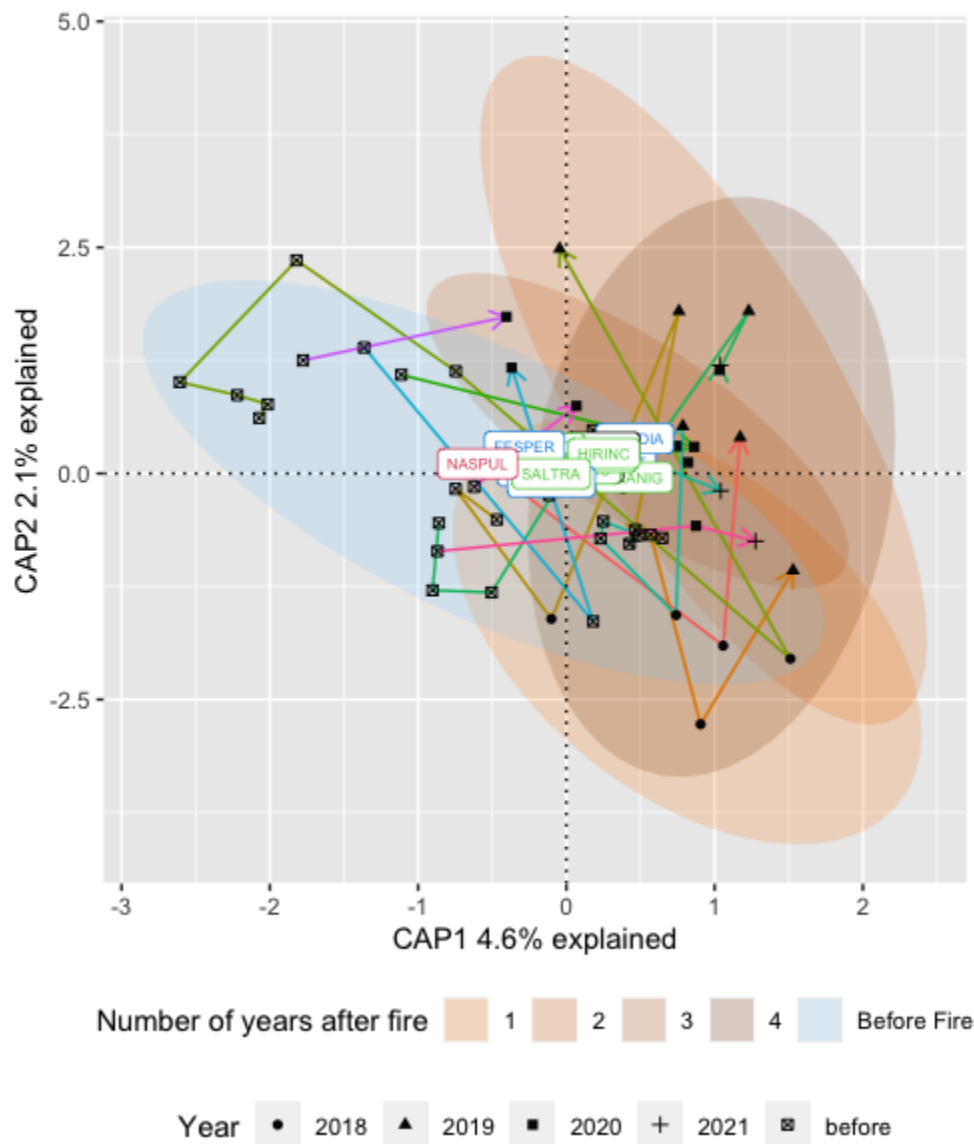
Appendix S1.16. CAP analysis of vegetation community composition in burned and unburned CSS sites, including all data before and after the canyon II fires. Unique transects = 58. N= 270. Points visualize individual observations of transects and paths connect different years' observations from a unique transect: transects that were burned in 2017 are represented by a red arrow (Y) and unburned blue (N). Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Ellipses show the burn/year combination groups with 95% confidence level.
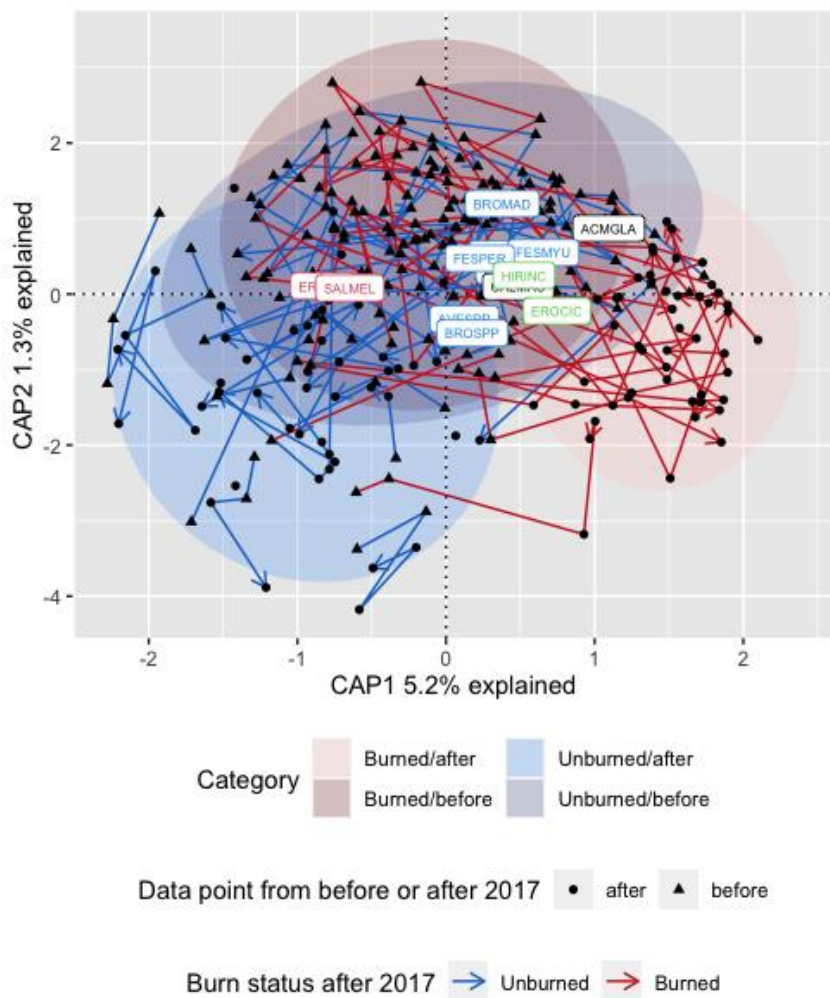
Appendix S1.17. CAP analysis of vegetation community composition in burned and unburned GL sites, including all data before and after the Canyon 2 fire. Unique transects = 39. N= 165. Points visualize individual observations of transects and paths connect different years' observations from a unique transect: transects that were burned in 2017 are represented by a red arrow (Y) and unburned blue (N). Species values are overlaid on the same CAP axes, with labels categorized based on growth form and native status (native shrub = red, native forb = black, non-native forb = green, non-native grass = blue). Only species with CAP absolute values greater than 0.3 are shown. Ellipses show the burn/year combination groups with 95% confidence level.
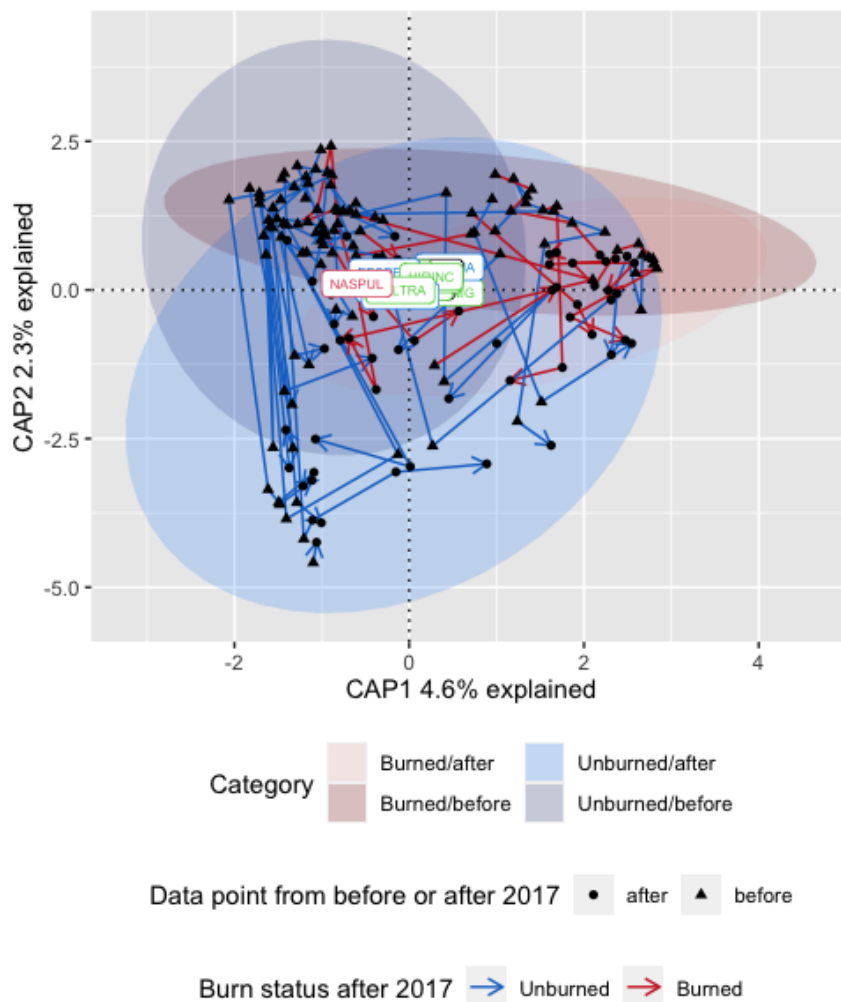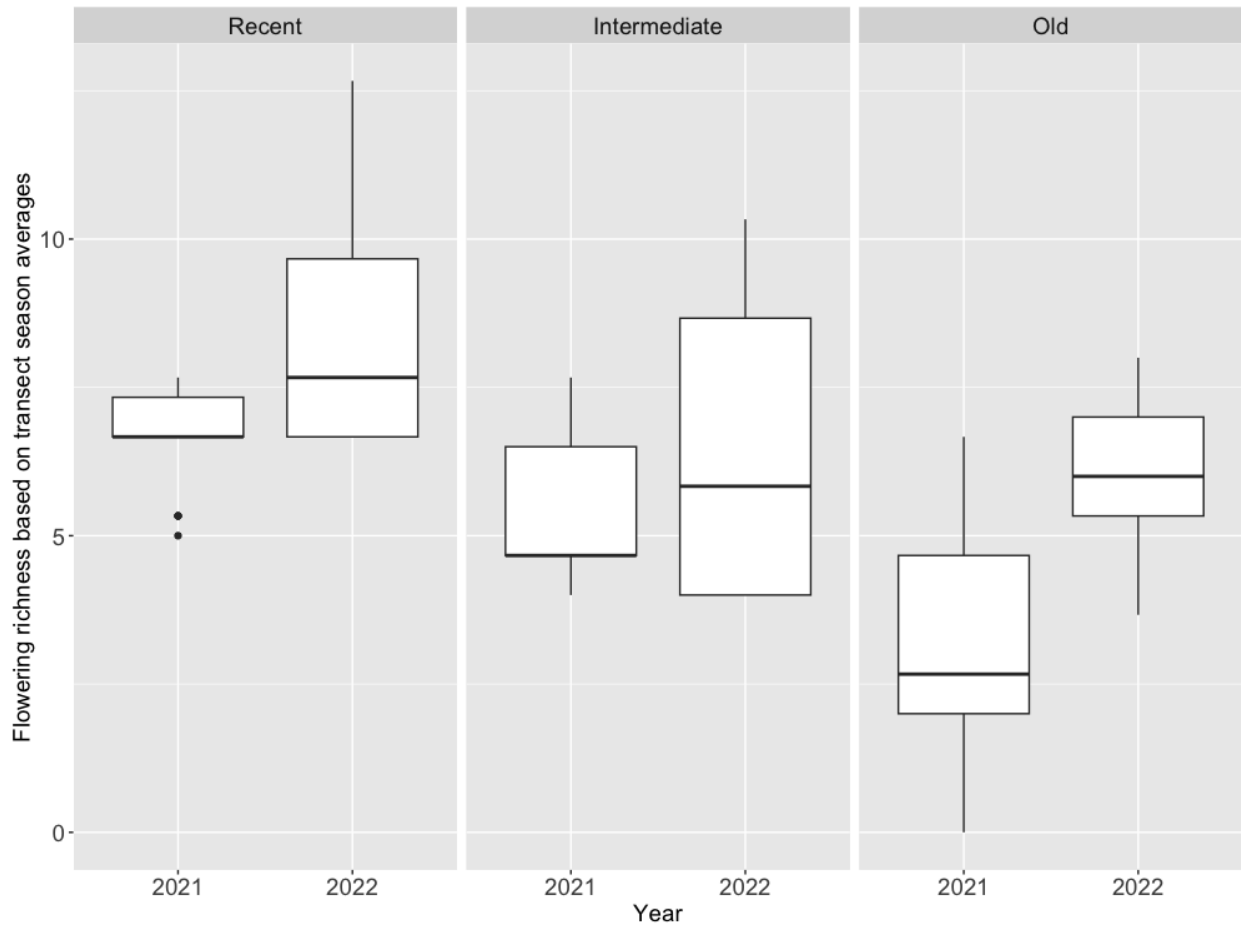
Appendix S2.1 Boxplots of season average flowering richness calculated from averaging flowering richness across sampling rounds for each transect each year. Observations are separated by burn status across the different panels.

Appendix S2.2 Boxplots of season average flowering diversity calculated from averaging flowering diversities across sampling rounds for each transect each year. Observations are separated by burn status across the different panels.
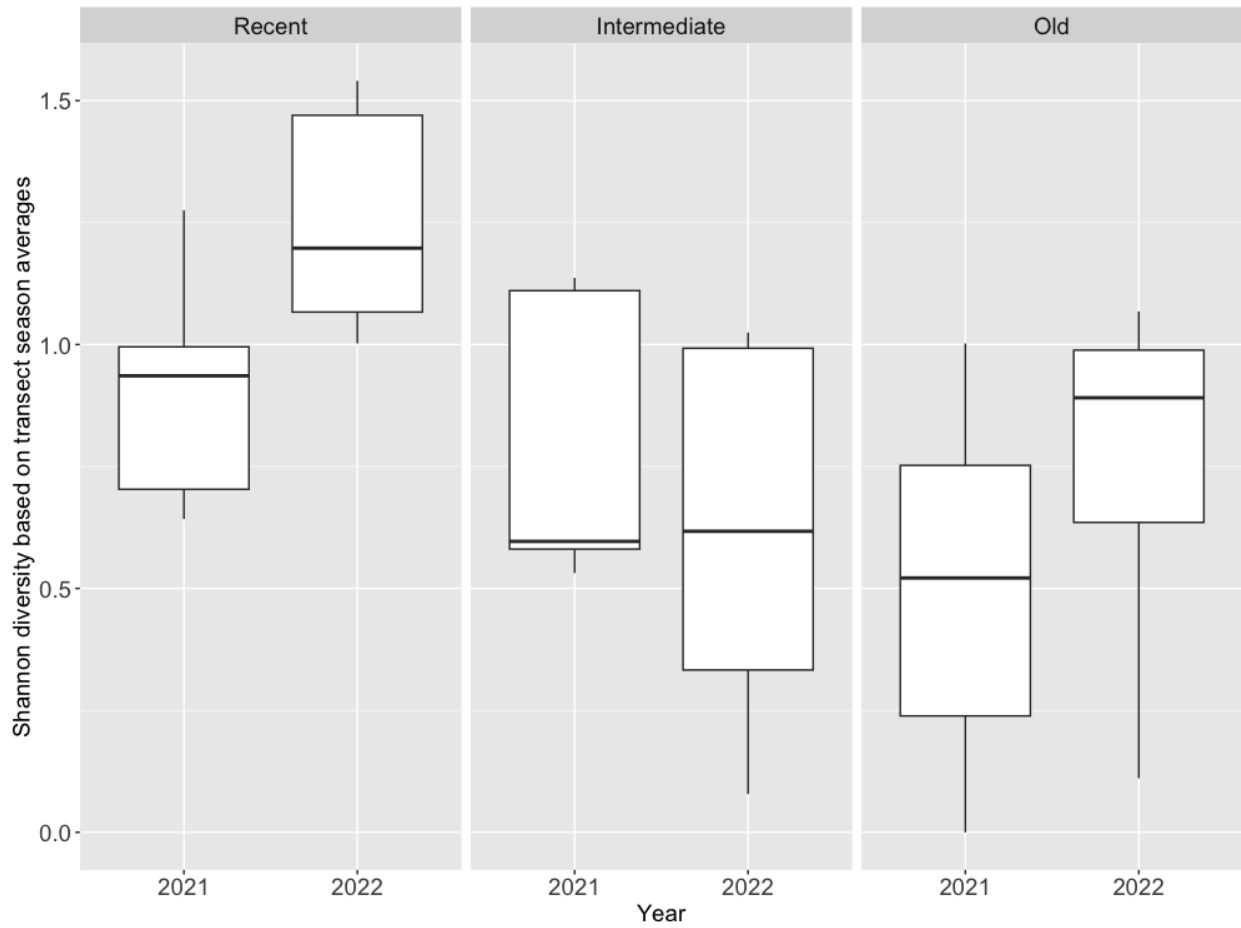
Appendix S3.1 Record of full 20-minute pollinator observations performed for each coastal sage scrub transect visit across observation years and monitoring rounds. Transect names are abbreviated from Appendix S1.3 to only include the location code and number.

Transect	Year	Round	Observations
BD21	2021	1	4
BD21	2021	2	2
BD21	2021	3	4
BD21	2022	1	5
BD21	2022	2	5
BD21	2022	3	5
BKR07	2021	1	0
BKR07	2021	2	0
BKR07	2021	3	0
BKR07	2022	1	1
BKR07	2022	2	0
BKR07	2022	3	3
BKR10	2021	1	1
BKR10	2021	2	4
BKR10	2021	3	3
BKR10	2022	1	3
BKR10	2022	2	4
BKR10	2022	3	4
GYP01	2021	1	1
GYP01	2021	2	5
GYP01	2021	3	5
GYP01	2022	1	2
GYP01	2022	2	3
GYP01	2022	3	5
GYP02	2021	1	2
GYP02	2021	2	3
GYP02	2021	3	4
GYP02	2022	1	1
GYP02	2022	2	4
GYP02	2022	3	3
GYP04	2021	1	0
GYP04	2021	2	5
GYP04	2021	3	6
GYP04	2022	1	2

GYP04	2022	2	5
GYP04	2022	3	5
GYP08	2021	1	2
GYP08	2021	2	5
GYP08	2021	3	4
GYP08	2022	1	5
GYP08	2022	2	4
GYP08	2022	3	2
GYP09	2021	1	5
GYP09	2021	2	4
GYP09	2021	3	4
GYP09	2022	1	5
GYP09	2022	2	3
GYP09	2022	3	3
I02	2021	1	6
I02	2021	2	5
I02	2021	3	6
I02	2022	1	0
I02	2022	2	3
I02	2022	3	3
I08	2021	1	4
I08	2021	2	4
I08	2021	3	1
I08	2022	1	1
I08	2022	2	4
I08	2022	3	5
I14	2021	1	5
I14	2021	2	5
I14	2021	3	4
I14	2022	1	5
I14	2022	2	4
I14	2022	3	4
I15	2021	1	3
I15	2021	2	3
I15	2021	3	4
I15	2022	1	2
I15	2022	2	3
I15	2022	3	6
I20	2021	2	2
I20	2021	3	2

I20	2022	1	1
I20	2022	2	4
I20	2022	3	5
I40	2021	1	6
I40	2021	2	6
I40	2021	3	7
I40	2022	1	2
I40	2022	2	4
I40	2022	3	7
I50	2021	2	5
I50	2021	3	5
I50	2022	1	1
I50	2022	2	6
I50	2022	3	5
IRC01	2021	1	1
IRC01	2021	2	4
IRC01	2021	3	6
IRC01	2022	1	6
IRC01	2022	2	5
IRC01	2022	3	5
IRC08	2021	1	6
IRC08	2021	2	6
IRC08	2021	3	5
IRC08	2022	1	5
IRC08	2022	2	5
IRC08	2022	3	5
IRC13	2021	1	5
IRC13	2022	1	0
IRC13	2022	2	5
IRC13	2022	3	4
IRC23	2021	1	4
IRC23	2021	2	5
IRC23	2021	3	4
IRC23	2022	1	4
IRC23	2022	2	6
IRC23	2022	3	5
SS03	2021	1	6
SS03	2021	2	5
SS03	2021	3	5
SS03	2022	1	3

SS03	2022	2	5
SS03	2022	3	5
SS04	2021	1	0
SS04	2021	2	6
SS04	2021	3	6
SS04	2022	1	5
SS04	2022	2	5
SS04	2022	3	5
SS05	2021	1	4
SS05	2021	2	6
SS05	2021	3	5
SS05	2022	1	5
SS05	2022	2	5
SS05	2022	3	5

Appendix S3.2 All interactions observed between flowering species and pollinator groups

for each burn category per year. Each colored box represents at least one flower visit.

Pollinator abbreviations are as follows: BEE_Apis = *Apis mellifera*, BEE_Bombus = *Bomsbus*

spp., BEE_Other _5,10,20 = Non-*Apis* bees in <5mm, 5-10mm, and 10-20mm sizes, SAW =

sawflies, LEP = Lepidoptera, DIP = true flies which do not include syphrids or bombylids,

LID = Bombyliid flies, SYP = Syrphid flies, HUM = hummingbirds) Full names of the

flowering species can be found in chapter 1 Appendix S1.4.