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When the Growing Gets Tough: Ecological Restoration in Southern California Shrublands

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

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When the Growing Gets Tough: Ecological Restoration in Southern California Shrublands

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by

Shane Landau Dewees

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Research in the Media

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ABSTRACT

When the Growing Gets Tough: Ecological Restoration in Southern California Shrublands

by

Shane Landau Dewees

Habitat degradation and conversion have become a ubiquitous problem globally and are expected to increase with climate change. In areas where degradation and conversion have already occurred, ecological restoration – defined by the Society for Ecological Restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed – provides a promising avenue to conserve biodiversity and ecosystem function. However, while projects have achieved restoration success, that is not a consistent outcome, even in the most well-studied ecosystems. The burgeoning field of plant functional trait ecology posits, however, that there are fundamental relationships between plant functional traits and how species respond to their environment. Therefore, classifying species by their plant traits, instead of taxonomic identity, offers a promising way to expand the findings of restoration ecology research to new settings and species.

Here, I investigate how to conduct successful ecological restoration in the mediterranean shrublands of southern California, an ecosystem with very little ecological restoration research. Specifically, the research presented herein took place in the Los Padres National Forest, just outside Piru, California. This area has experienced extensive shrubland conversion to non-native grasses over the last few decades and has been identified as a

specific area of restoration interest by the United States Forest Service. I first conduct a regional spatial analysis to identify where and why shrublands are being lost to inform how I might conduct restoration. Second, I conducted a large-scale landscape restoration project with a physiologically diverse set of ten species, measured a variety of plant traits (i.e. wood density, integrated water use efficiency, and parts of the leaf economics spectrum) and measured daily microsite temperature (n = 115), humidity (n = 39) and soil moisture (n = 30). This then allowed us to map microsite environmental conditions across the whole landscape, assess how the microsite differences influenced survival, and test how plant traits related to these interspecific responses. Lastly, I conducted another restoration experiment with 13 shrubland species. This experiment evaluated how a spectrum of planting densities in a ‘restoration island’ approach influenced survival in the harshest parts of the landscape and how plant traits relate to those influences.

Our findings showed 1.) shrubland conversion is primarily happening in low elevation, southwest facing slopes (i.e. more arid slopes) and during periods of postfire drought. 2.) Low soil moisture and high vapor pressure deficit (VPD) are primary drivers of year one mortality. Additionally, species with higher water use efficiencies can survive high VPD if soil moisture remains moderate. Conversely, species on the more acquisitive side of the leaf economics spectrum can survive low soil moisture if VPD remains moderate. And 3.) in general plot level survival increases significantly with higher planting densities. Inclusion of plant traits revealed that more acquisitive species benefiting the most from this facilitation. Conversely, species with higher water use efficiencies were negatively impacted by higher planting densities. Overall, my dissertation details foundational knowledge for the restoration of southern California shrublands and more broadly shows the potential for plant

functional traits to inform restoration planning and increase the consistency of restoration success.

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I. Introduction

The restoration of degraded ecosystems has become a dominant focus of conservation efforts in the twenty-first century. As a result, the field of restoration ecology (the study of the relationships between organisms and their environment, specifically in a restoration context; Palmer et al., 2016) has blossomed, and a plethora of ecological theories have been studied and applied to restoration endeavors. The goal of ecological theories are to explain historical events, understand present observations, and predict future states (Scheiner & Willig, 2011). Therefore, the development of ecological theory specific to restoration ecology is especially imperative as ecological systems are increasingly altered and the successful outcome of restoration relies on the predictive accuracy of any guiding theory.

Restoration success is vexingly inconsistent, despite the growing use of ecological theory to inform restoration approaches (Christmann & Menor, 2021; Crouzeilles et al., 2016; Gómez-Aparicio et al., 2004; Nolan et al., 2021; Wortley et al., 2013). This holds true both across and within ecosystems, begging the question of how applicable any given study's findings are to new locations, and species.

The field of plant functional trait ecology posits that there are fundamental relationships and tradeoffs between plant traits (e.g. the leaf economics spectrum) and that these traits are functional in determining how species perform (i.e. survive, grow and reproduce) in their environment (Mcgill et al., 2006). Promising a way to transcend esoteric, species-by-species analyses, functional trait theory has been referred to as the 'holy grail' of community and functional ecology, because of its potential to make the findings of studies more easily applicable to new locations and species (Funk et al., 2017; Lavorel & Garnier, 2002). However, many plant functional trait studies focus predominantly on quantifying the relationship and trade-off

between traits and assume the “functional” aspect (i.e. that the traits in question mediate performance in a given environment). Additionally, in-depth studies that actually test the function of plant traits have mixed results and reveal an emerging theme of function being context dependent on intraspecific trait plasticity (Poorter et al., 2018), environmental variation (Rowland et al., 2021), and variation in plant size/age (Kitajima et al., 2002; Thorne, 1973). While several recent studies have suggested that plant trait theory can provide guidance to the field of ecological restoration (Balazs et al., 2022; Kimball et al., 2016; Merchant et al., 2023), empirical tests have been limited in their geographic and species palette scopes (Merchant et al., 2023, but see Gornish et al., 2023).

My dissertation aims to further the field plant trait theory, specifically in a restoration context by focusing on southern Californian shrublands, which are comprised of two main vegetation communities: sage scrub and chaparral (Barbour et al, 2007). The sage scrub community is characterized by partially closed canopies of shrub and sub-shrub species 0.5-2m in height, most species of which are fully or partially drought deciduous and have whitish green leaves often with some degree of reflective trichomes or glaucous surface. Representative species include *Salvia leucophylla*, *S. apiana* and *Artemesia californica* (Rundel, 2007; Westman, 1981). Additionally, the sage scrub community is identified as threatened, with only an estimated 10% of its historic distribution remaining due largely to human development and altered disturbance regimes (Rundel, 2007). By contrast, the chaparral vegetation community is characterized by an extremely dense and closed canopy of evergreen shrubs 1.5-3m in stature. Chaparral typically occurs higher on the mountain slopes than sage scrub with a mix of sclerophyllous leaved dominants such as *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, *Malosma laurina*. *Ceanothus species* and *Arctostaphylos species*. (Gray, 1982; Keeley, 1998; Parker et al., 2016).

Both vegetation communities are adapted to the Mediterranean environment (i.e. hot-dry summers and cool-wet winters). Sage scrub and chaparral vegetation form discrete communities and naturally co-occur or intermingle on the same slopes, especially in years following fire (Westman, 1981). Sage scrub species are often viewed as early successional in disturbed chaparral (Hanes, 1971).

Chaparral conversion can consist of direct loss to urbanization and agriculture, and indirect loss as some combination of fire, drought or other stressors convert chaparral to other vegetation types. The extent and drivers of chaparral conversion to other vegetation types (type conversion) are not fully understood. Most recently, Syphard et al. (2018) found that, within seven central and southern California counties (comprising approximately 15,500,000 acres), approximately 75% of chaparral mapped in 1934 has converted to non-chaparral (including urbanized and agricultural landscapes), showing that chaparral loss is extensive and underscoring the need to understand the drivers of conversion.

The most commonly described form of chaparral conversion (to non-urban cover) is the conversion of native woody shrubs to non-native annual grasslands. Shrub cover is the most critical element contributing to chaparral persistence and resistance to non-native grass invasion (Keeley et al., 2005). The loss of shrubs typically occurs following disturbance and type conversion begins when there is a lack of shrub recovery following disturbance. Of the possible disturbances, short interval fire is considered to be one of the most influential drivers of vegetation change within chaparral (Haidinger & Keeley, 1993; Keeley & Brennan, 2012; Lippitt et al., 2013; Zedler et al., 1983). Although species within the chaparral community are adapted to regenerate following fire via resprouting or germination from fire-stimulated seeds, it is important to note that chaparral species are adapted to a specific fire regime, characterized by

high intensity crown fires punctuated by long fire free intervals (30 to 100 years) (Keeley & Fotheringham, 2001; Van de Water & Safford, 2011). Deviations from this fire regime, especially the shortening of the fire return interval, can reduce recruitment of some chaparral shrub species (e.g. immaturity risk to obligate seeders) and promote the invasion of non-native annual grasses (Jacobsen et al., 2004; Keeley & Brennan, 2012; Syphard et al., 2006; Zedler et al., 1983).

Climatic and topographic variables have also been shown to be important predictors of type conversion of chaparral to non-native annual grasses. Park et al. (2018) and Syphard et al. (2019) have found local moisture availability to be a primary contributor in the conversion of chaparral to herbaceous cover. Moisture availability (e.g. precipitation and moisture deficit) affects the postfire recovery of chaparral shrubs (Frazer & Davis, 1988; Pratt et al., 2014; Storey, Stow, Roberts, et al., 2021; Zedler et al., 1983), influences mortality and canopy thinning (Davis et al., 2002; Jacobsen et al., 2014; Jacobsen & Pratt, 2018), and leads to type conversion (Park et al., 2018). Landscape position (e.g. aspect and slope) also correlates with chaparral recovery and degradation following fire and serves as a proxy for climate exposure and moisture availability. The true relationship between these variables and conversion, however, likely varies through space and time. Discerning the relative importance of drivers of change (e.g. altered disturbance regime, climate, topography) is an important current challenge.

A better understanding of the complex interactions between drivers of type conversion and their relative importance in influencing the transitions between vegetation types in California, will prove beneficial for identifying shrubland areas most at risk of future conversion and where restoration efforts might be most successful across Mediterranean regions.

While there is a solid foundation of ecological research on the restoration of the sage scrub vegetation community (Bowler, 2000; Cox & Allen, 2008; DeSimone, 2011; Quon et al., 2019; Michael F. Allen, 1998), there is an absence of published research on chaparral restoration (Allen et al., 2018), with a dearth of reporting on chaparral restoration activities in general (but see VinZant, 2013). Under the right circumstances (i.e. close enough to intact stands for seed dispersal to occur), passive restoration of sage scrub has been shown to lead to establishment after removal of non-native cover (DeSimone, 2011). Additionally, where passive restoration does not lead to establishment, active restoration via both direct seeding and transplanting of seedlings has shown to be a feasible alternative (Cox & Allen, 2008; Quon et al., 2019). Conversely, the few reported chaparral restoration endeavors find no shrub establishment from the direct seeding for chaparral shrubs (Allen et al., 2018; Ma unpublished) and post-transplant survival only with intensive watering efforts that are likely unsustainable at large scales and in complex terrain (VinZant, 2013).

Therefore, my dissertation aims to inform the future practice of restoration in southern California shrublands through answering three guiding questions. First, I ask where and why vegetation conversion is occurring across a large ~53,000 acre fire scar? I accomplish this through manually classifying vegetation in aerial images from 1930 and 2009 and then training random forest models with climatic, topographic and fire data to determine the strongest predictors of conversion. Second, I ask how planting microsites and plant traits interact to determine restoration survival and growth? This question is investigated through a large-scale 8-acre restoration project, planting ~1600 individuals of 10 species. I then use environmental sensors, fine scale mapping and measured plant traits to analyse determinates of survival and growth. Third, I ask if ‘restoration islands’ can be used to increase survival in the most arid

microsites? I answered this question through another large-scale restoration experiment, planting 15 25 square foot plots with 80 plants each and a total of 13 species. After natural transplant shock induced mortality occurred, I was left with a range of plot densities to investigate how planting density in these ‘restoration’ islands influenced survival.

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II. Determining potential drivers of vegetation change in a Mediterranean environment

A. Abstract

The increased occurrences of drought and fire may be contributing to the loss of biodiverse ecosystems in Mediterranean regions. Specifically, the conversion of diverse native shrublands, such as chaparral, to non-native annual grassland by fire is of great conservation concern in California. To avoid or slow the loss of chaparral, it is important to understand the underlying

causes of landscape conversion. Studies investigating the interaction of multiple potential drivers are particularly crucial to identification of vulnerable areas of the landscape. Here I used aerial imagery to evaluate vegetation transitions between chaparral, sage scrub, grassland, and tree domination and their potential drivers within Ventura County, California, a strongly Mediterranean climate region. I used random forest algorithms and conditional inference trees to determine the climatic, topographic, and fire-related variables contributing most to vegetation change. Our results support that chaparral conversion to grass (27% of chaparral plots) is a result of landscape position, fire, and drought acting in tandem. In particular, lower elevation, southwest facing slopes that experience a post fire drought are at very high likelihood of conversion to non-native annual grass. Additionally, our results show that these grasslands, once formed, rarely convert to other community types. Therefore, protecting shrub dominated areas that are most likely to convert (low elevation, more southwest facing slopes, less annual precipitation) is crucial to preserving native vegetation diversity.

B. Introduction

Shrubland communities are the iconic vegetation types in Mediterranean regions and globally they are considered to be biodiversity hotspots (Rundel et al., 2016). In California, chaparral shrublands which are characterized by evergreen sclerophyllous shrubs, exhibit high floral diversity (Cowling et al., 1996; Parker et al., 2016) and endemism (Rundel et al., 2016). Despite being valued for multiple ecosystem services (Underwood et al. 2018), chaparral is increasingly under threat from human population growth (Syphard et al., 2018), climate change (Molinari et al., 2018), fire (Keeley & Brennan, 2012) and drought (Jacobsen & Pratt, 2018; Storey, Stow, Roberts, et al., 2021). Chaparral conversion can consist of direct loss to urbanization and agriculture, and indirect loss as some combination of fire, drought or other

stressors convert chaparral to other vegetation types. The extent and drivers of chaparral conversion to other vegetation types (type conversion) are not fully understood. Most recently, Syphard et al. (2018) found that, within seven central and southern California counties (comprising approximately 15,500,000 acres), approximately 75% of chaparral mapped in 1934 has converted to non-chaparral (including urbanized and agricultural landscapes), showing that chaparral loss is extensive and underscoring the need to understand the drivers of conversion.

The most commonly described form of chaparral conversion (to non-urban cover) is the conversion of native woody shrubs to non-native annual grasslands. Shrub cover is the most critical element contributing to chaparral persistence and resistance to non-native grass invasion (Keeley et al., 2005). The loss of shrubs typically occurs following disturbance and type conversion begins when there is a lack of shrub recovery following disturbance. Of the possible disturbances, short interval fire is considered to be one of the most influential drivers of vegetation change within chaparral (Haidinger & Keeley, 1993; Keeley & Brennan, 2012; Lippitt et al., 2013; Zedler et al., 1983). Although species within the chaparral community are adapted to regenerate following fire via resprouting or germination from fire-stimulated seeds, it is important to note that chaparral species are adapted to a specific fire regime, characterized by high intensity crown fires punctuated by long fire free intervals (30 to 100 years) (Keeley & Fotheringham, 2001; Van de Water & Safford, 2011). Deviations from this fire regime, especially the shortening of the fire return interval, can reduce recruitment of some chaparral shrub species (e.g. immaturity risk to obligate seeders) and promote the invasion of non-native annual grasses (Jacobsen et al., 2004; Keeley & Brennan, 2012; Syphard et al., 2006; Zedler et al., 1983).

Climatic and topographic variables have also been shown to be important predictors of type conversion of chaparral to non-native annual grasses. Park et al. (2018) and Syphard et al. (2019) have found local moisture availability to be a primary contributor in the conversion of chaparral to herbaceous cover. Moisture availability (e.g. precipitation and moisture deficit) affects the postfire recovery of chaparral shrubs (Frazer & Davis, 1988; Pratt et al., 2014; Storey, Stow, Roberts, et al., 2021; Zedler et al., 1983), influences mortality and canopy thinning (Davis et al., 2002; Jacobsen et al., 2014; Jacobsen & Pratt, 2018), and leads to type conversion (Park et al., 2018). Landscape position (e.g. aspect and slope) also correlates with chaparral recovery and degradation following fire and serves as a proxy for climate exposure and moisture availability. The true relationship between these variables and conversion, however, likely varies through space and time. Discerning the relative importance of drivers of change (e.g. altered disturbance regime, climate, topography) is an important current challenge.

A better understanding of the complex interactions between drivers of type conversion and their relative importance in influencing the transitions between vegetation types in California, will prove beneficial for identifying shrubland areas most at risk of future conversion and where restoration efforts might be most successful across Mediterranean regions. California chaparral has been shown to be physiologically similar to other Mediterranean climate shrublands in Chile (Cody & Mooney, 1978; Parsons & Moldenke, 1975; Rundel et al., 2016), the Mediterranean basin (Naveh & Whittaker, 1980; Rundel et al., 2016; Specht, 1969a, 1969b), Australia (Rundel et al., 2016; Specht, 1969a, 1969b), and southern Africa (Rundel et al., 2016). Additionally, all five Mediterranean regions are experiencing shortened fire return intervals due to anthropogenic pressure (Syphard et al., 2009) and shortened fire return intervals have also been shown to negatively affect Mediterranean shrublands in South Africa (Kraaij, 2010; Kraaij

et al., 2013; Van Wilgen et al., 2010), Australia (Enright et al., 2011, 2014), Chile (Smith-Ramírez et al., 2021), and the Mediterranean Basin (Abdel Malak & Pausas, 2006; Santana et al., 2014). Therefore, a deeper understanding for how climate, topography, and fire, interact to drive type conversion in California chaparral, should provide insight to how these potential stressors are affecting the physiologically similar shrublands of the other four Mediterranean climate regions.

In this study, I explore potential drivers of vegetation change in an area (Piru Fire, Los Padres National Forest in Ventura County, California) known to be experiencing frequent fire and in close proximity to areas of high conservation (California Condor sanctuary), recreation (Lake Piru), and infrastructural (Pyramid Dam) value. Through the use of fire history maps, historical aerial imagery across 79 years, and detailed biophysical data, I address the following questions: (1) What is the extent of vegetation conversion to and from chaparral? (2) What local climatic, topographic, and fire-related variables are most influential in the observed conversion to and from chaparral?

C. Methods

Study area: The study area is located within the 2003 Piru Fire (21,346.51 hectares) (Figure 1) in the Los Padres National Forest, Ventura County, California. Limitations in historical imagery constrained the study area to 83% of the fire scar (Figure 1). This region is characterized by having hot-dry summers and cool-wet winters. The 2003 Piru Fire scar was chosen because the fire took place over a range of vegetation communities including fully degraded non-native grasslands, sage scrub, various chaparral alliances, and tree communities and I have excellent quality historic (1930) and recent (2009) imagery for the region. The Piru Fire also burned across a wide spectrum of elevations, distance from roads, special use designations (e.g. wilderness),

fire histories, and climate variation. Therefore, the fire scar presents an ideal area for investigating factors correlated with vegetation fluxes while holding the regional species pool and general distance from coast constant, as within species differences in cavitation resistance (and thus drought resistance) have been observed at larger geographic distances (Jacobsen et al., 2014).

Data sets: The historic images used for the vegetation classification were obtained from the Map and Image Laboratory at the University of California, Santa Barbara. All historic images (17 total) are from the 1930 flight C-870 and were mapped on a scale of 1:18,000. Our contemporary 2009 image was obtained from the United States Geological Survey (USGS) Digital Orthophoto Quarter Quads (DOQQ) (Table 1). The DOQQ is a true color aerial photograph at one-meter spatial resolution. Using ENVI 4.8 +IDL (Exelis Visual Information Solutions, Boulder, Colorado), our 1930 images were then georectified to the DOQQ image using between 300-400 ground control points (GCP). GCPs were selected from temporally stable objects such as trees, rock outcrops, roads, and permanent structures. Each image was then warped using triangulation and pixels were resampled to the nearest neighbor, creating a georectified image with one-meter spatial resolution. Mosaicked images were then validated for spatial accuracy by identifying 40-100 GCPs and ensuring a root mean square error of 10 pixels or less.

Elevation data (Table 1) were used to generate slope and aspect using ArcGIS's Surface toolset (ESRI, Redlands, California) in the Spatial Analyst toolbox. Aspect degrees were converted to "southwestness" using $\cos(\text{aspect} - 225^\circ)$, to transform it from a circular to linear scale with more ecological meaning (Beers et al., 1966) where values range from negative one (northeast) to one (southwest). Solar radiation was generated from the elevation data using

ArcGIS's Area Solar Radiation tool in the Solar Radiation toolset (ESRI, Redlands, California) in the Spatial Analyst toolbox. Default settings were used except for the time configuration option, which was set to 'special days' for computing the solar radiation for the summer solstice, equinox, and winter solstice.

Seven climatic variables were used in the analysis: mean annual precipitation, minimum January temperature, maximum August temperature, mean annual temperature, maximum January vapor pressure deficit (VPD), maximum August VPD, and minimum precipitation anomaly postfire (PRISM Climate Group). Minimum postfire precipitation anomaly was calculated for each plot and consisted of the lowest postfire precipitation anomaly (year's precipitation – precipitation normal) from a given plot's fire history. Precipitation anomalies were calculated for the year of fire, and individual years up to five years after the fire. Then, the precipitation anomaly, including summed anomalies over multiple years, that led to the most accurate random forest model (discussed below) for each analysis was selected. For both analyses, this ended up being the summed anomaly from the year of fire through four years after fire (Appendix S1: Table S1).

The above climate variables were selected out of the numerous variables available because they provide general insight into how site aridity varies seasonally and spatially. Additionally mean annual precipitation (Park et al., 2018; Storey, Stow, O'Leary, et al., 2021), mean annual temperature (Storey, Stow, O'Leary, et al., 2021), and postfire precipitation anomaly (Jacobsen & Pratt, 2018; Paddock et al., 2013; Pratt et al., 2014) have been shown to influence chaparral conversion to non-native grass. The remaining climate variables directly contribute to winter and summer drought conditions experienced by plants and negatively affect chaparral shrubs (Davis et al., 2002; Jacobsen & Pratt, 2018; Paddock et al., 2013; Storey, Stow,

Roberts, et al., 2021). Thirty-year normals ranging from 1981-2010 were used for all seven variables, along with yearly precipitation data (only available at a coarser resolution) for precipitation anomaly (Table 1). Although the climate normal data do not represent the full temporal span of our study, I use it generally to infer potential climate effects on vegetation change through time.

Edaphic variables used in the analysis were Soil Survey Geographic database (SSURGO) variables obtained from the United States Department of Agriculture's (USDA) Web Soil Survey application. The variables used were percent silt, clay, and sand content, percent organic matter, soil bulk density, and available water supply (Table 1). All variables were calculated from 0-150cm soil depths. These six variables were selected to broadly represent the myriad of soil characteristics that could be influencing vegetation.

The Euclidean distance from roads was calculated using the Distance toolset in the ArcGIS Spatial Analyst toolbox and was manually assigned a resolution of 10m (Table 1). Primary and secondary roads (interstate and state highways and freeways, state routes, and prominent roads) were used in the analysis, as finer scale road layers represent paths less traveled and do not have the same potential for disturbance and movement of weeds.

Fire variables were generated from the California Department of Forestry and Fire Protection's (CAL FIRE) Fire and Resource Assessment Program's (FRAP) fire perimeter dataset, which includes wildfires and prescribed burns. This dataset is a joint effort by the US Forest Service (USFS), CAL FIRE/FRAP, Bureau of Land Management (BLM), and National Park Service (NPS) and ranges from 1878-present. The minimum fire size required for inclusion in the FRAP data set varies depending on which organization is reporting, but most fires reported were at least 10 acres in size. The minimum fire return interval (defined as the smallest number

of fire free years a given plot experienced), and number of fires from 1912 to 2009 were calculated from the FRAP database. Despite the FRAP data encompassing a wider range of fire years, I selected to use fires between 1912-2009 to include fire years prior to the onset of the earliest imagery acquisition and fires during the images' timespan. Additionally, for plots that did not burn before 2003, I assigned a minimum fire return interval of 86 years (equal to 1912-2009 fire history time period).

Vegetation classification: Vegetation was classified by eye for both the 1930 and 2009 images using ArcMap 10.2 (ESRI, 2014). First, 2000 points were randomly generated across the Piru Fire scar with a minimum distance of 90m between each point. Then a 30m radius circle was generated around each random point, with the point as the center. These served as our study plots to track vegetation change through time and represent three percent of the fire scar. Each plot was then verified to fall in natural vegetation; the presence of urban, agriculture, roads, water features, or rock and/or barren soil (although vegetated plots with only partial rock and/or barren soil were included) in either the 1930 or 2009 images resulted in the exclusion of the point/plot. Additionally, any plots that burned after 2003 were removed, to ensure adequate time for recovery between the most recent fire and the 2009 image date. In each of the remaining 565 plots, vegetation type was classified using 50 randomly generated points (Appendix S2).

The vegetation type (i.e. tree, chaparral, sage scrub, or grass) was determined visually using texture, canopy structure, and coloration associated with the pixel (one meter) associated with each of the 50 points. While the resolution of the aerial imagery was not appropriate for determining the type of herbaceous cover, I assume that herbaceous cover represents non-native annual grassland based on extensive invasion of non-native grasses (*Bromus* and *Avena* sp.) in this area (USDA-Forest Service 2018; Kelly et al., 2005; Wieslander, 1935; personal field

observations) with annual mustard (*Brassica nigra*) as a common component. Percent vegetation cover in a plot was calculated as the number of points classified as a given vegetation type divided by 50 (total number of points) and then multiplied by 100. Each plot was assigned a primary, secondary, and, when applicable, tertiary vegetation type based off the percent present in a given plot. For example, a plot with chaparral having a percent cover of 60%, sage scrub having a percent cover of 30% and grass having a percent cover of 10% would be assigned a primary cover of chaparral, secondary cover of sage scrub, and tertiary cover of grass. The associated primary vegetation type (vegetation type with the highest percent cover) in 1930 and 2009 were used to determine type conversion (defined here as a switch in a plot's primary vegetation class) with each of the 565 plots being assigned to one of sixteen conversion categories (e.g. chaparral → sage scrub, sage scrub → chaparral, chaparral → chaparral, etc.). In addition to the conversion category, each plot had topographic, climate, anthropogenic and fire-related variables appended as the mean value of all sampled pixels (50 points). The plot data were used as the level of replication (n=565) to evaluate the drivers of vegetation type conversion.

Analysis of vegetation cover change & conversion: Analyses on the predictor variables contributing to the observed vegetation dynamics were performed independently for changes in plot-level chaparral cover (continuous percent cover response variable, hereafter 'chaparral cover change') and chaparral conversion to grass (binary response variable [converted to grass or remained chaparral], hereafter 'chaparral conversion'). None of the other conversion classes had sufficient plots for sophisticated statistical analyses (Appendix S3: Table 1). Contributions of our predictor variables to the observed vegetation dynamics were first analyzed using machine learning (i.e. random forest and conditional inference trees) to predict chaparral cover change

and conversion. This allowed the predictor variables to be ranked by their relative importance (random forest) and identify interactions between the variables (conditional inference trees). I then used more traditional regression approaches (i.e. linear regression) for formal hypothesis testing.

Two decision tree analyses were used to test how the predictor variables compared to each other and interacted to drive chaparral cover change and conversion. First, a random forest analysis was performed using all of the predictor variables (Appendix S4) and the number of variables tested at each split (*mtry*) and number of trees created (*ntree*) optimized for the lowest mean of squared residuals (cover change analysis; *mtry* = 10 *ntree* = 500) and lowest out of bag error rate (type conversion analysis; *mtry* = 6 *ntree* = 900) using the *randomForest* package (Liaw & Wiener, 2002) in R (R Core Team, 2021) . The algorithm was trained on 80% of the randomly selected data and then tested for accuracy on the remaining 20% of the data.

Because some of the predictor variables were highly correlated, a second random forest analysis was performed after excluding highly correlated (Pearson's $r > 0.7$) variables in most cases. The climatic variables minimum postfire precipitation anomaly, mean annual precipitation, maximum January VPD, and maximum August VPD were selected for use over the temperature variables because of their expected direct contribution to a plant's water status. Additionally, in the cases of VPD and solar radiation, winter and summer values were included despite high correlation because I specifically wanted to investigate the seasonal role those variables had. Lastly, elevation, bulk density, and percent sand content were dropped due to their high correlation with variables expected to have a more direct contribution to a plant's water status. These second iterations of the random forest analysis optimized *mtry* and *ntree* to obtain

the lowest mean of squared residuals (cover change analysis; $mtry = 6$ $ntree = 700$) and lowest out of bag error rate (type conversion analysis; $mtry = 2$ $ntree = 900$).

The random forest analysis calculates the increase in mean square error associated with randomly changing values for each variable (percent increase in mean square error) for continuous response variables and the decrease in model accuracy associated with removing a variable (mean decrease in accuracy) for discrete variables. These values were used to evaluate the relative importance of climate, topographic and fire variables to chaparral cover change and conversion, with a higher value meaning higher relative importance. Accuracy of the random forest models were evaluated through root mean square error (chaparral cover change) and the Cohen's kappa (chaparral conversion), which has been shown to be a more robust measure of accuracy for a confusion matrix compared with producers, user's, and overall accuracy measures (Cohen, 1960).

To identify the interactions between predictor variables, I developed conditional inference trees for both the cover change and type conversion analyses using the partykit package (Hothorn et al., 2006) in R (R Core Team, 2021). Decision trees allowed for the identification of interacting variables that drive chaparral cover change and type conversion to grass. They were also used to determine if threshold values exist for predictor variables and can inform whether cover change and conversion is more or less likely. The decision tree was trained on 80% of the data after correlated variables were removed (same data used for the second random forest models) and its accuracy was tested on the remaining 20%. Accuracy was evaluated by root mean square error for the cover change analysis and calculating Cohen's kappa coefficient (Cohen, 1960) for the type conversion analysis.

Due to the large grouping of plots with fire return intervals greater than or equal to 81-years (Table 2), I repeated the above analyses on the data subset to only include minimum fire return intervals less than or equal to 34-years and then again on data subset to only include minimum fire return intervals greater than or equal to 81-years (Appendix S5)

I then used more traditional regression-based analyses to perform formal hypothesis testing. For the chaparral cover change analysis, I performed single variable linear regression to test the relationship between cover change and each independent variable separately. The r^2 value from the linear regression was used to determine the variability in cover change explained by a given independent variable and the p-value (at $p = 0.05$) was used to test the null hypothesis that the independent variable had no effect on cover change.

For the conversion analysis, I compared the differences in central tendencies for each independent variable. These were evaluated in one of two ways depending on if the variable was normally distributed. For predictor variables with normal distribution (i.e. elevation, slope, summer solar radiation, and maximum August temperature), difference in means between converted and non-converted plots was tested for significance using a two-sided Welch's t-test and the effect size of that difference was evaluated by calculating Cohen's d. For non-normally distributed variables (secondary cover in 1930, southwestness, equinox solar radiation, winter solar radiation, distance from roads, mean annual precipitation, mean annual temperature, minimum January temperature, maximum January and August VPD, percent clay, percent sand, percent silt, organic matter, bulk density, available water supply, and minimum postfire precipitation anomaly), difference in medians was tested for significance using a Wilcoxon rank sum test and the effect size of that difference was evaluated by calculating the rank biserial effect size. All statistical testing for central tendencies was performed in R version 4.0.2 (R Core Team,

2021) using the statsExpressions package (Patil, 2021). For the categorical fire variables, the differences in distributions were analyzed with contingency tables and then evaluated for significant differences by performing Chi-square tests for independence. The p-value (at $p = 0.05$) was used to test the null hypothesis that there is no difference in distribution of minimum fire return intervals between plots that remained chaparral or converted to grass. Chi-squared tests were also performed in R using the stats package (R Core Team, 2021).

D. Results

Vegetation fluxes: Chaparral was the dominant (primary) vegetation type in 67% of the plots in 1930 and declined to 49% in 2009 (Figure 2). While the majority of the plots with chaparral as the primary vegetation type in 1930 remained stable (69%), meaning the primary vegetation type remained the same in 1930 and 2009, 27% of chaparral plots switched to grass as the primary vegetation type in 2009 (i.e. experienced conversion). In addition to chaparral conversion at the plot scale, there were also declines in chaparral cover within plots. The median percent cover of chaparral in all plots dropped from 68% in 1930 to 44% by 2009 ($p < 0.01$; Figure 3A). The median percent cover of chaparral in plots where it was the primary vegetation type also dropped from 82% in 1930 to 74% by 2009 ($p < 0.01$; Figure 4A).

Grasslands were the only vegetation type to increase in dominance from 1930 (14%) to 2009 (41%; Figure 2). Plots with grass as the primary vegetation type in 1930 showed a high level of stability, with only fourteen percent converting to another vegetation community by 2009 (Figure 2). The median percent cover of grass in all plots also increased from 18% in 1930 to 38% by 2009 ($p < 0.01$; Figure 3B). Additionally, the median percent cover of grass in plots where it was the primary vegetation type also increased from 64% in 1930 to 68% by 2009 ($p < 0.01$; Figure 4B).

Plots with sage scrub as the primary vegetation type in 1930 were the only plots that had higher levels of conversion (86%) than stability (14%; Figure 2). Of the 1930 sage scrub plots that converted, 87% of those converted to plots with grass as the primary vegetation type in 2009 (Figure 2); resulting in a decrease in sage scrub dominance from 13% of plots in 1930 to only 4% of plots in 2009 (Figure 2). While there was not a significant change in median percent cover of sage scrub measured across all plots ($p = 0.950$; Figure 3C), the percent cover of sage scrub in plots where it was the primary vegetation type did significantly drop from 66% in 1930 to 64% by 2009 ($p < 0.01$; Figure 4C).

Plots with trees as the primary vegetation type in 1930 remained relatively stable, with 79% of those plots maintaining trees as the primary vegetation type by 2009 (Figure 2). Tree dominance was nonetheless rare comprising 6% of plots in both 1930 and 2009 (Figure 2). These plots also did not experience a significant change in median percent cover either for all plots ($p = 0.56$; Figure 3D) or only plots where trees were the primary vegetation type ($p = 0.390$; Figure 4D).

Drivers of chaparral cover change: The random forest analysis for drivers of chaparral cover change showed southwestness and maximum January VPD to have the largest percent increase in mean square error, (Figure 5A; variance explained = 35.91% and RMSE = 21.20): when southwestness or maximum January VPD were randomly changed by the model, there was the largest increase in predictive error compared with any other single variable. Reductions in chaparral cover were observed in plots with more southwest facing and had higher maximum January VPDs (Table 3). Minimum postfire precipitation anomaly, minimum fire return interval, percent silt and clay in soil, distance from roads, and mean annual precipitation normals all had relatively high percent increases in mean square error (Figure 5A). Reductions in chaparral cover

were observed in plots with more negative postfire precipitation anomalies, shorter fire return intervals, higher percent silt and clay contents, closer to roads, and lower mean annual precipitation normals (Table 3).

The decision tree created from the conditional inference tree analysis had its root node split on maximum January VPD, meaning it was the most influential variable for initially partitioning the cover change data (Figure 5B, RSME = 24.10). Maximum January VPD split at a threshold with values higher than 12.48 hectopascals exhibiting the greatest loss in chaparral cover. At lower VPDs, the next/final split was on southwestness: more southwest facing slopes showed more negative cover change. At higher VPDs, the next split was on mean annual precipitation (624mm/year). At lower mean annual precipitations, the next and final split was on southwestness, with more southwest facing slopes exhibiting more negative changes in percent chaparral cover. At higher mean annual precipitation values, the next and final split was on distance from roads (711m) with more negative cover change closer to roads.

Drivers of chaparral conversion to grass: The random forest analysis for chaparral conversion showed that southwestness, minimum postfire precipitation anomaly, and percent cover of the secondary vegetation type in 1930 had the three largest mean decreases in accuracy (Figure 6A; kappa = 0.67). Plots that converted to grass, were more southwest facing ($p < 0.01$; effect size = 0.52), had more negative postfire precipitation anomalies ($p < 0.01$; effect size = 0.36), and larger percent covers of secondary vegetation in 1930 ($p < 0.01$; effect size = 0.46) than plots that maintained primary vegetation as chaparral (Table 4). Mean annual precipitation, percent silt and clay content, winter solar radiation, distance from roads, and maximum January VPD all had relatively large mean decreases in accuracy as well (Figure 6A). Plots that converted to grassland had lower mean annual precipitation normals ($p < 0.01$; effect size = -

0.45), higher percent silt ($p < 0.01$; effect size = 0.27) and clay ($p < 0.01$; effect size = 0.24), higher winter solar radiation ($p < 0.01$; effect size = 0.30), were closer to roads ($p < 0.01$; effect size = -0.40) and higher maximum January VPD's ($p < 0.01$; effect size = 0.59; Table 4).

Minimum fire return interval ranked in the lower half of variables (Figure 6A), yet the Pearson's chi squared test showed there was a significantly different distribution of values between plots with chaparral versus grass as their primary vegetation type in 2009 ($p < 0.01$; Table 2).

The decision tree generated from the conditional inference tree analysis split first on southwestness (Figure 6B; kappa = 0.58). For plots that were more northeast facing, the next split was on maximum January VPD (14.3hPa). Plots with higher January VPD's had no more splits and were approximately 75% likely to convert to grassland. Plots with lower January VPD's split next on percent secondary cover in 1930 (20%), with plots surpassing the 20% threshold having a 25% probability of converting. For plots with lower secondary cover, the next and final split was on percent clay content (22.5%). Plots with higher clay contents were approximately 25% likely to convert, whereas plots with lower clay contents were almost 0% likely to convert. Plots that were more southwest facing at the top node split next on mean annual precipitation (614mm/year). Plots with lower precipitation normals were approximately 90% likely to convert. Conversely, plots with higher precipitation normals had one final split on distance from roads (722m). Plots closer to roads had above 50% probability of conversion, whereas plots farther from roads had approximately 10% probability of conversion.

E. Discussion

Our results support loss of shrublands and conversion of chaparral to grassland in this region. Almost one third (27%) of plots originally chaparral in 1930 converted to grassland by 2009, while 75% of sage scrub plots had converted. Our analyses of chaparral loss demonstrated

that aridity factors and fire return interval interact to drive these changes. Specifically, within this region, short interval fires, postfire drought, and long-term site conditions (aspect, elevation, climate normals, and solar radiation) are key drivers in where chaparral cover declines and conversion to grassland occur. The long-term site conditions associated with chaparral loss are all associated with increased aridity (greater southwest aspect, lower elevation, higher VPD, lower mean annual precipitation, and higher solar radiation). Thus, as climate change drives increased aridity in these ecosystems, portions of the landscape will be vulnerable to conversion to non-native grassland.

Once formed, grasslands were very stable: approximately 86% of plots with grass as the primary vegetation type in 1930 maintained grass as the primary vegetation type in 2009. This observation highlights the importance of targeted management actions to prevent shrubland conversion to grassland. Restoration actions aimed at returning shrubs into grassland habitats have proven challenging (Allen et al., 2018; Eliason & Allen, 2008) thus underscoring the importance of management to avoid type conversion.

Role of fire: I demonstrate the importance of minimum fire return interval in two ways: (1) in random forest analyses for chaparral cover change and conversion (Figure 5A;6A). For cover change it was the 4th most important variable and the associated linear regression model showed that shorter fire return intervals, when subset to only include intervals ranging from one to 34 years, were significantly associated with negative changes in chaparral cover (Table 3). For conversion, minimum fire return interval was lower in importance, but there was a significantly different distribution between converted and non-converted plots (Table 2). (2) Analyses on the data subset into two groups (short to moderate fire return intervals and long fire return intervals; Appendix S5) led to markedly different rankings of variable importance, showing the interaction

of fire return intervals with other variables in leading to chaparral cover decline or conversion. Together these analyses support the literature showing minimum return interval as an important driver of shrub loss and conversion (Haidinger & Keeley, 1993; Keeley & Brennan, 2012; Syphard et al., 2019a, 2019b; Zedler et al., 1983).

When evaluating the distribution of plots across the minimum return interval classes, a site threshold of five to seven years stands out as a potential threshold resulting in chaparral conversion to grassland (Table 2). This adds an important data point to a latitudinal trend that Syphard et al. (2019b) suggest. They report a minimum return interval threshold for conversion of 15 years in San Diego county (the southernmost and more arid county in southern California; Syphard et al., 2019b), and 10 years in Malibu (a central and less arid county in southern California; Syphard et al., 2019a). I suggest that for Ventura county (a more northern and even less arid county in southern California), a minimum return interval of 5-7 years may be necessary for conversion. This coupled with the importance of site aridity (see below) reveal that what defines a short interval fire in chaparral communities is likely to be driven by regional aridity.

It is important to note that all our plots experienced at least one fire (Piru fire, 2003) during the study period, with the large majority experiencing two or more. By contrast, other studies showing fire with a high degree of importance in determining conversion, included areas that experienced zero fires in the entire period (Syphard et al., 2019a, 2019b). Thus, I cannot fully parse out the role a single fire has on cover change and conversion in our study. Yet, I do show how varied fire histories and other site factors (i.e. factors indicative of aridity and grass presence pre-fire) determine the heterogeneity of conversion when fire is present.

Site aridity and drought: In the presence of fire, our study shows that factors contributing to site aridity (i.e. lower elevation, more southwest facing aspects, lower mean annual precipitation

normals, higher winter and summer solar radiation exposure and vapor pressure deficits) are important determining factors in where chaparral communities are vulnerable to decline. More arid chaparral stands have been shown to experience shrub mortality and cover decline during drought events (Paddock et al., 2013). Drought leads to shrub mortality through carbohydrate limitation (associated with resprouters; Pausas et al., 2016; Pratt et al., 2014), hydraulic failure (associated with high intensity droughts and obligate seeders; Pausas et al., 2016), or through synergistic interaction with pathogens (Schultheis et al., 2019). It is likely that site aridity is affecting postfire recovery through several factors including a reduction in productivity (Pratt et al., 2014; Sims et al., 2006) and carbon reserves of resprouters (Pratt et al., 2014), reduced postfire regrowth (Pratt et al., 2014), and increased hydraulic failure for germinants of obligate seeding species postfire (Paddock et al., 2013). This likely leaves more canopy gaps available for grasses to invade and ultimately initiate a grass-fire cycle (D'Antonio & Vitousek, 1992).

Since our study only has images from the start and end years, I cannot directly attribute conversion to drought. The consistently high importance of minimum postfire precipitation anomaly in our random forest analyses, coupled with findings such as Paddock et al. (2013) point towards drought as a factor contributing to chaparral cover loss, however. Because long-term drought can limit carbon gain, it can make shrubs more vulnerable to a compounding disturbance such as pathogen invasion (Aguirre et al., 2018; Schultheis et al., 2019) or fire (Pratt et al., 2014). Additionally, drought conditions coinciding with fire make hydraulic failure and mortality more likely for species that recruit strictly during the first few years postfire (Jacobsen et al., 2014; Jacobsen & Pratt, 2018; Paddock et al., 2013; Pratt et al., 2007). Our analyses point towards the first four years postfire being the most vulnerable years to drought conditions (Appendix S1: Table S1). Future work testing whether this is a site-specific threshold, or if it

holds up throughout southern California is essential. Because climate change is expected to cause more arid conditions and more frequent and intense drought events, the breadth of chaparral communities vulnerable to both fire and drought is expected to expand (Molinari et al., 2018).

There is also an important seasonal dynamic to our results: summer aridity was not as strong a predictor as winter aridity. Perhaps this is because shrubs have evolved to tolerate the typical summer drought associated with Mediterranean climate regions (Burk, 1978; Gray, 1982; Jacobsen et al., 2014; Rundel et al., 2016). By contrast, periods of winter aridity occur during the active growing season (Burk, 1978; Gray, 1982). Such growing season droughts are increasing in frequency (Diffenbaugh et al., 2015) and may have important implications for chaparral persistence. Similarly, fire season has been expanding with climate change at least partially as a result of winter aridity (Brotons et al., 2013; Goss et al., 2020).

Role of edaphic variables: A higher percent of clay and silt were associated with both chaparral cover decline and conversion in our analyses. Causal relationships are difficult to entangle here but are potentially twofold: (1) these associations could be related to landscape position as lower elevation sites likely have more fine soil particles than higher elevation sites (Akumu et al., 2015; Taye et al., 2018; Wu et al., 2019) and chaparral loss is more often associated with low elevations. (2) Higher values of clay and silt are typically associated with higher soil moisture (Fernandez-Illescas et al., 2001; Saxton et al., 1986). Our soil metrics represent the top 150 cm of soil. Higher shallow soil moisture may disproportionately favor shallow rooted, annual non-native grasses in the post fire environment, allowing them to outcompete seedlings of deep rooted, perennial native woody shrubs (Allen et al., 2018; Eliason & Allen, 2008; Goldstein & Suding, 2014).

Grass dynamics: It has long been assumed that non-native grasslands in southern California are highly static and of low likelihood to convert back to native cover. Yet there is a surprising dearth of literature providing concrete support of this assumption at large spatial scales (but see (Callaway & Davis, 1993). Our findings show that throughout the landscape, grass cover trended upward and almost no plots with grass as their primary vegetation type in 1930 converted to woody vegetation regardless of site conditions. Thus, without direct intervention, grasslands will likely remain grasslands. Therefore, chaparral preservation should be focused on preventing type conversion from occurring.

I identified a cover threshold at which the presence of grass dramatically increases the likelihood of conversion (24%), even with a single fire and long fire return interval (80 plus years; Appendix S5; Figure S4B). This finding has important management implications. Shallow rooted, annual grasses have limited competitive effects on mature, deep-rooted chaparral shrubs (Keeley et al., 2005). They are however, able to quickly colonize gaps that open in the canopy and subsequently out-compete shrub seedlings, preventing their establishment (Allen et al., 2018; Eliason & Allen, 2008). Therefore, invasion of non-native grasses is largely believed to be initiated by their ability to opportunistically fill canopy gaps caused by disturbance (i.e. fire, drought or disease). Our results showed that higher shallow soil available water supply (high clay and silt) is correlated with higher rates of chaparral conversion and these may be locations that favor high annual grass cover and reduced shrub seedling growth. Once abundant (potentially 24% cover) annual grasses can trigger more frequent fire leading to a grass-fire cycle (D'Antonio & Vitousek, 1992), and type conversion.

Restoration implications: Our results have important implications for efforts aimed at the restoration of chaparral communities. Our study has confirmed that type conversion largely

occurs on more arid, southwest facing slopes, sites that will be challenging places to restore because of the aridity and exposure due to lack of a shrub canopy. Chaparral restoration in California has largely been unsuccessful, with plant establishment and woody seedling survival being substantial constraints (Allen et al., 2018). The lack of success seen to date is likely at least partially due to the challenging site conditions where restoration is desired. Yet a subset of degraded sites (e.g. higher elevation, more northerly aspects) might be easier to restore and these could be identified using guidance from the analyses I present here. Additionally, because chaparral species traits vary among taxa, the species used in restoration could be modified to take into consideration the conditions in the target degraded areas

Conclusions: While the geographic scale of this work is limited, it has important implications for Mediterranean ecosystems. Our findings add an important data point for understanding how topographic and disturbance variables interact to drive type conversion in shrubland ecosystems. The physiological similarities among Mediterranean climate shrublands, and the increasing occurrence of fire in them, make the insights discovered here applicable beyond California.

This study supports that increases in fire occurrence, drought, and site aridity are likely to lead to vegetation change and loss of California chaparral and that conversion of chaparral to exotic annual grasslands is a complex process. In our study area, this degradation process appears to be primarily driven by an interaction between long term site conditions (e.g. southwestness and elevation), short term drought (post fire precipitation anomaly) and fire. Additionally, our study suggests that what defines a minimum fire return interval threshold is dependent on geographic location (i.e. 5-7 years here, but 15 years in San Diego). This work also has important implications for land managers. Our results indicate that passive succession to chaparral once sites are in a grassland state rarely occurs: grasslands once formed,

are extremely stable. Management and restoration efforts may be more successful if focused on chaparral communities in the process of degradation. Efforts to preserve chaparral communities could focus on ignition prevention including non-native annual grass reduction and establishment of woody seedlings or other native species that are less ignitable than non-native grasses. While our identification of a grass cover threshold has management implications, more work focused on determining how that threshold varies with topography and environment is needed.

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G. Tables and Figures

Table 1: Description of images and variables used for vegetation classification, their source, spatial scale and units.

Variables	Units	Source	Spatial Scale
Percent Cover of Secondary Vegetation in 1930	Percent	Vegetation Classifications	–
Number of Fires	–	Fire and Resource Assessment Program (FRAP)	–
Minimum Fire Return Interval	years	FRAP	–
Elevation	meters	USGS National Elevation Dataset	1 arc second (~30m)
Slope	degrees	Derived from elevation	1 arc second (~30m)
Aspect	degrees	Derived from elevation	1 arc second (~30m)
Southwestness	–	Derived from aspect	1 arc second (~30m)

Summer, Equinox, and Winter Solar Radiation	Watt hours/ square meter	Derived from elevation	1 arc second (~30m)
30 year normal Mean Annual Precipitation	millimeters/year	Parameter-elevation Regressions on Independent Slopes Model (PRISM)	800 meter
30 year normal Minimum January Temperature	Celsius	PRISM	800 meter
30 year normal Maximum August Temperature	Celsius	PRISM	800 meter
30 year normal Mean Annual Temperature	Celsius	PRISM	800 meter
30 year normal Maximum January VPD	hectopascal	PRISM	800 meter
30 year normal Maximum August VPD	hectopascal	PRISM	800 meter
Minimum Precipitation Anomaly (sum of 0-4 years postfire)	Millimeters/year	PRISM	4000 meter
Percent Silt Content	Percent	Soil Survey Geographic database (SSURGO)	–
Percent Clay Content	Percent	SSURGO	–
Percent Sand Content	Percent	SSURGO	–
Bulk Density	gram/centimeter cubed	SSURGO	–
Available Water Supply (0-150 cm)	centimeter cubed	SSURGO	–
Organic Matter	Percent	SSURGO	–
Distance to Roads	meters	Derived from United States Census Bureau data	10 meter
1930 Aerial Images	–	Map and Image Laboratory at the University of California, Santa Barbara	1 meter
2009 OthoImage	–	USGS	1 meter

Note: USGS stands for United States Geological Survey and VPD stands for vapor pressure deficit.

Table 2: Contingency table showing the difference in plot level minimum fire return interval distribution between plots that remained chaparral (Non-converted) and plots that converted to grassland (Converted).

Minimum fire return interval	Non-converted	Converted
1	0% (0)	2.97% (3)
5	3.41% (9)	30.69% (31)
6	39.02% (103)	19% (19)
7	0.76% (2)	5.94% (6)
14	3.41% (9)	0% (0)
15	0.38% (1)	0% (0)
19	1.52% (4)	2.97% (3)
26	0.76% (2)	0% (0)
34	0% (0)	0.99% (1)
81	0.76% (2)	0% (0)
86	50% (132)	37.62% (38)

Note: Chi-squared $p < 0.01$. The percent represents the percent of plots with a given minimum fire return interval out of all the plots in that conversion category. Values in parentheses are the raw counts of number of plots in each category.

Table 3: Single variable linear regression results from chaparral cover change analysis.

Variable	Coefficient	r ²	p-value
Maximum January VPD	-5.88	0.161	<0.01
Minimum postfire precipitation anomaly	0.0376	0.0838	<0.01
Southwestness	-14.18	0.130	<0.01
Minimum fire return interval	0.037	0.00349	0.261
Minimum fire return interval (0-34 years)	0.9732	0.0202	0.0489
Percent silt	-1.108	0.0528	<0.01
Percent clay	-2.833	0.085	<0.01
Distance from roads	0.00464	0.0803	<0.01
Mean annual precipitation	0.118	0.124	<0.01
Maximum August VPD	-1.196	0.0275	<0.01
Summer solar radiation	0.01007	0.0376	<0.01
Winter solar radiation	-0.00228	0.00201	0.396
Available water supply	-1.348	0.0495	<0.01
Slope	-0.2348	0.00638	0.128
Percent organic matter	-9.152	0.00795	0.0889

Note: Coefficient shows the amount of chaparral cover change predicted with a one unit change in independent variable values. VPD stands for vapor pressure deficit.

Table 4: Central measures for plots with chaparral cover (non-converted) and grass cover (converted) and their differences from chaparral conversion to grass analysis.

Variable	Non-converted	Converted	Difference	Central measure	p-value	Effect size
Percent secondary cover in 1930	12	26	-14	median	<0.01	0.46
Southwestness	-0.39	0.44	-0.83	median	<0.01	0.52
Slope	20.66	23.00	-2.34	mean	0.035	0.25
Summer solar radiation	5908	5690	218	mean	<0.01	-0.47
Winter solar radiation	1268	1412	-144	mean	<0.01	0.30
Distance from roads	1137	289	848	median	<0.01	-0.40
Mean annual precipitation	684	591	93	median	<0.01	-0.45
Maximum January VPD	12.0	13.7	-1.7	median	<0.01	0.49
Maximum August VPD	38.1	40.5	-2.4	median	<0.01	0.22
Percent clay	20.8	22.5	-1.7	median	<0.01	0.24
Percent silt	27.2	34.0	-6.8	median	<0.01	0.27
Available water supply	9.2	9.2	0	median	0.13	0.10
Percent organic matter	0.65	0.75	-0.10	median	0.99	0.00
Minimum postfire precipitation anomaly	57.5	-48.5	106.0	median	<0.01	-0.36

Note: Central measure used indicates whether the variable was normally (mean) or non-normally (median) distributed. P-values show if the central measures for each variable are significantly different between chaparral and grass covered plots and effect size shows the strength of that difference. VPD stands for Vapor pressure deficit.

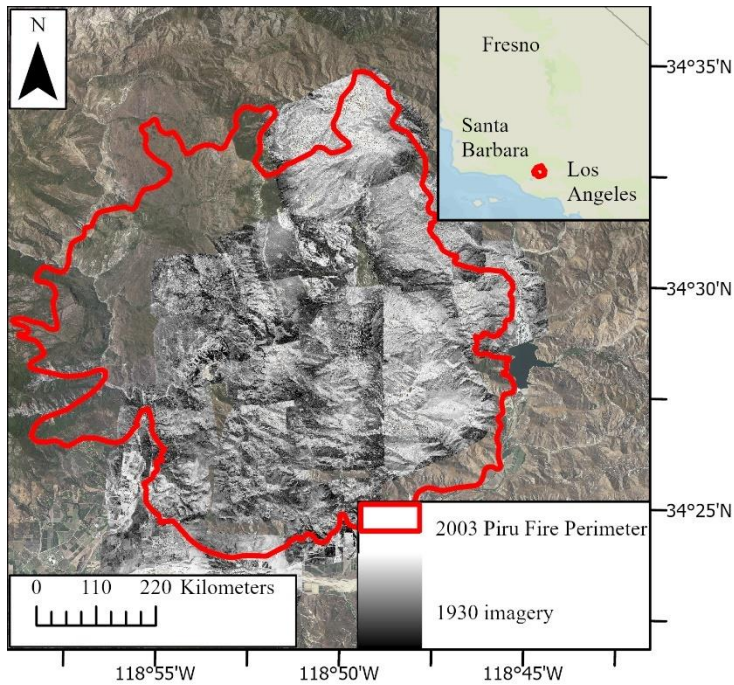


Figure 1: Map of study area with the fire scar outlined in red and coverage by our 1930 imagery in black and white. Inset shows the study site (red outline) in a larger geographic context.

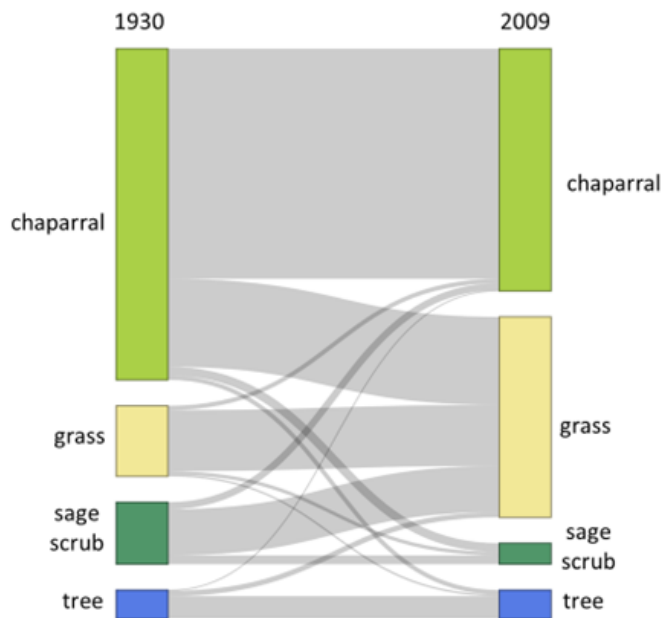


Figure 2: Sankey diagram showing vegetation fluxes from 1930 to 2009. Bars are proportional to the number of plots dominated by each vegetation type, with larger bars signifying more plots dominated by that vegetation type. Vegetation fluxes were calculated with the plot level data (n = 565).

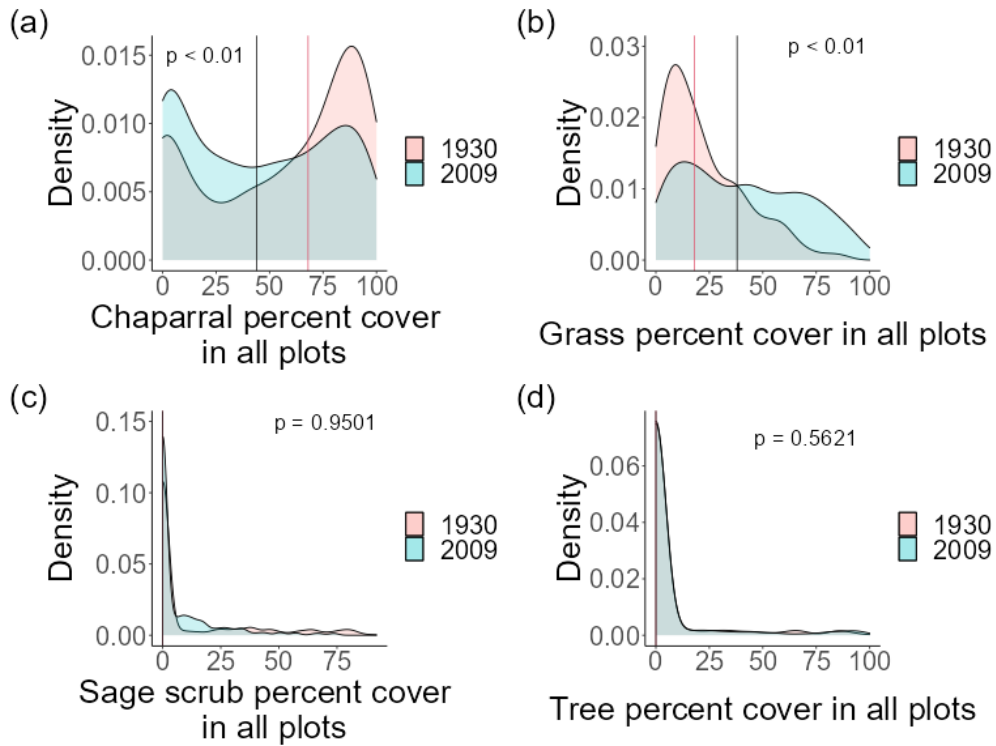


Figure 3: Density distribution of chaparral (A), grass (B), sage scrub (C), and trees (D) in all 565 plots in 1930 (pink) and 2009 (blue). Vertical bars represent the median percent cover that each vegetation community occupied in all plots in 1930 (pink) and 2009 (blue). The p-value is the result of a Mann Whitney test to see if those medians' values are significantly different.

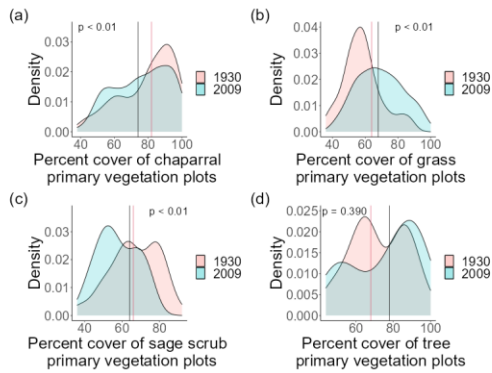


Figure 4: Density distribution of the percent cover for chaparral (A), grass (B), sage scrub (C), and trees (D) in plots they were the primary vegetation group in during 1930 (pink) and 2009 (blue). Vertical bars represent the median percent cover in 1930 (pink) and 2009 (blue). The p-value is the result of a Mann Whitney test to see if those medians' values are significantly different.

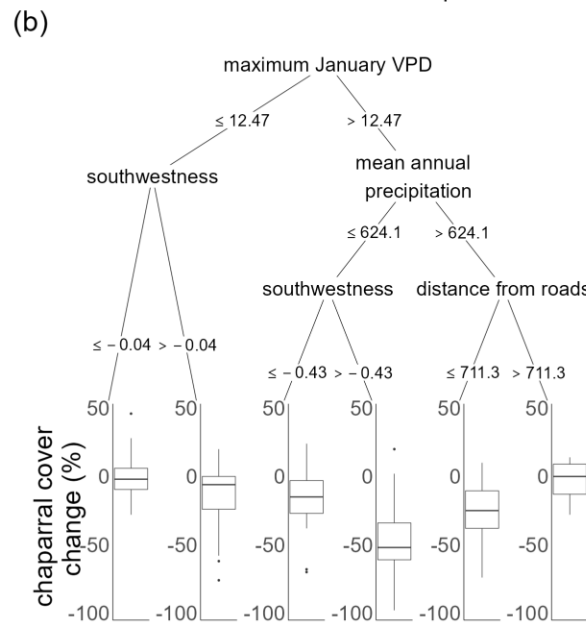
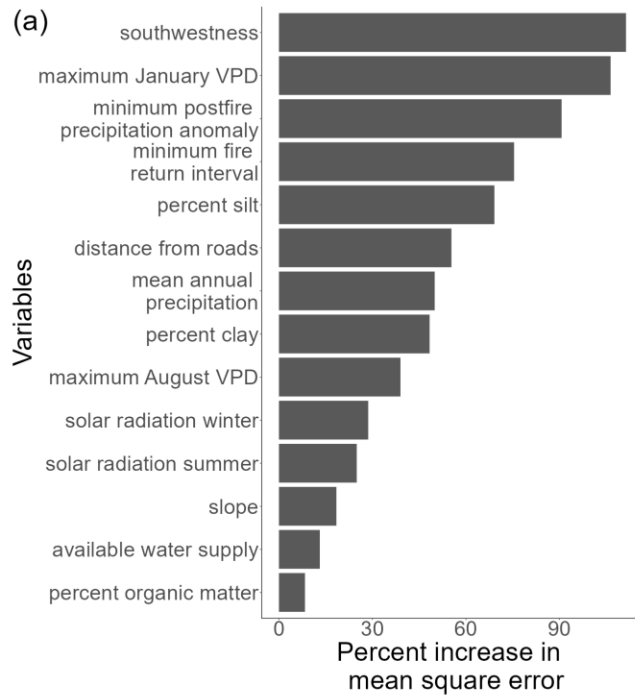


Figure 5: Results from random forest analysis (A) and hierarchical decision tree analysis (B) for **chaparral cover change** analysis. Variables with higher percent increase in mean square error have higher relative variable importance (A). In (B) the topmost node is the most important split.

Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the distribution of chaparral cover change values for those plots. VPD stands for vapor pressure deficit.

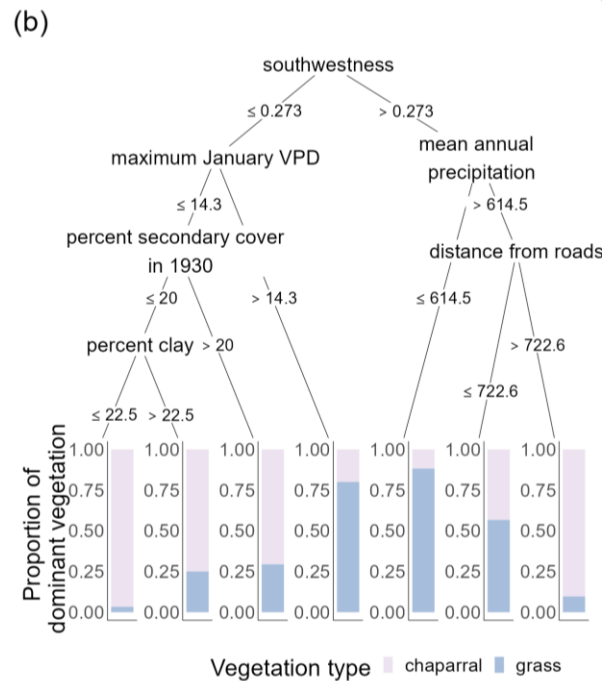
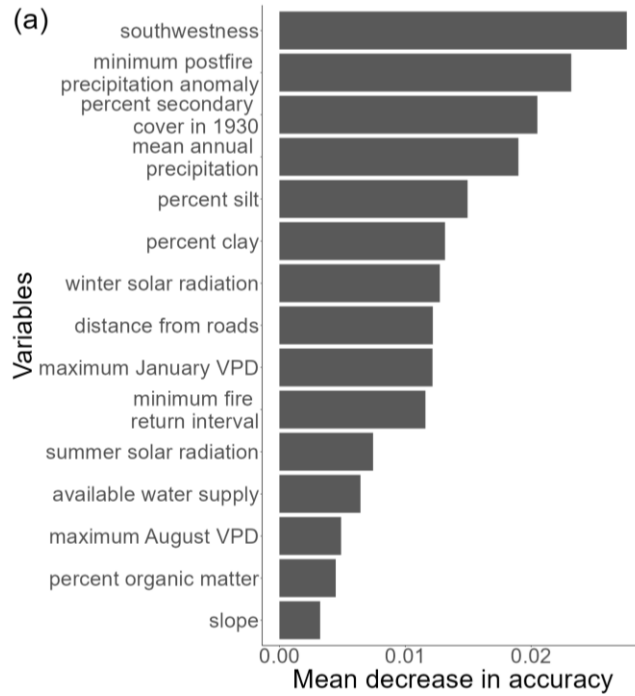


Figure 6: Results from random forest analysis (A) and hierarchical decision tree analysis (B) for **chaparral conversion to grass**. Variables with higher mean decrease in accuracy have higher relative variable importance in (A). In (B) the topmost node is the most important split. Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the proportion of plots (blue bar) that converted to grass. VPD stands for vapor pressure deficit.

H. Appendices

Appendix S1

Table S1: Random forest model accuracies from testing different combinations of years to use in calculating minimum postfire precipitation anomaly. For both chaparral cover change and conversion to grass, the variable that summer yearly precipitation anomalies from year of fire through four years after fire led to the most accurate predictive model.

Precipitation anomaly	Root mean square	Kappa
variable	error	
Year 0 (year of fire)	21.56	0.64
Year 0 – year 1	21.58	0.61
Year 0 – year 2	21.44	0.64
Year 0 – year 3	21.48	0.61
Year 0 – year 4	21.20	0.75
Year 0 – year 5	21.55	0.64

Appendix S2

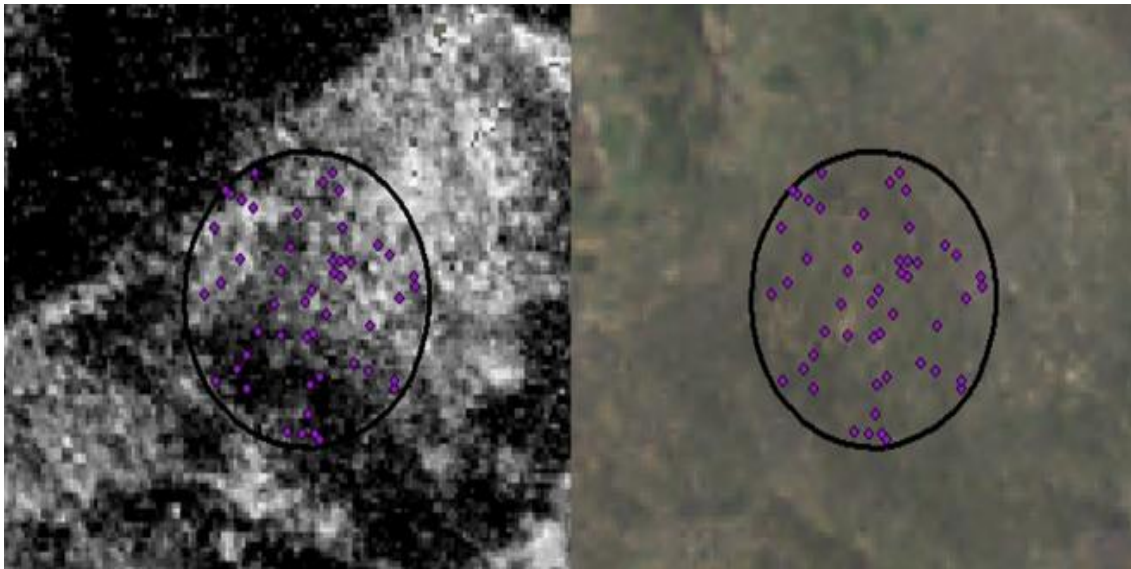


Figure S1: Example of study plots and 50 random points generated to classify vegetation.

An example plot (black circle) with 50 randomly generated classification points (purple dots). Shown both in 1930 imagery (left) and 2009 imagery (right). For each plot, vegetation type was determined based off color, pixel texture and canopy type. Since the images are from the summer, grasses tended to be light grey to white in the 1930 imagery and tan/brown to grey in the 2009 imagery. Grasses also had less pixel texture and no visible canopy. Sage scrub tended to be grey to light black in the 1930 imagery and grey to grey green to light green in the 2009 imagery. Sage scrub pixels also tended to have moderate texture and partial to closed canopies. Chaparral tended to be black to dark black in the 1930 imagery and green to dark green in the 2009 imagery. Chaparral pixels also tended to have the most texture and closed to very dense canopies. Trees tended to be black in the 1930 imagery and green in the 2009 imagery. Tree pixels also tended to be textured and closed canopies with circular or jagged canopies.

Some possible sources of error could come from mixed canopies of sage scrub chaparral, or plots with chaparral-forest transitions. Additionally, some chaparral species (i.e. *Heteromeles arbutifolia*, *Rhus ilicifolia*, *Sambucus nigra*) can appear very tree like, and since the imagery doesn't give the best impression of canopy height, might have led to some error in classifying certain chaparral plots as trees or vice versa. Additionally, since senesced grass in the imagery could at times look like bareground, some soil pixels could have been classified as grass. There is also likely a larger margin of error from the 1930's imagery, since it is of lower quality and lacks color.

Appendix S3

Table S1: Number of plots in each conversion class.

Conversion type	Number of Plots
Chaparral → chaparral	264

Chaparral → grass	101
Chaparral → sage scrub	10
Chaparral → tree	5
Grass → grass	70
Grass → chaparral	5
Grass → sage scrub	4
Grass → tree	2
Sage scrub → sage scrub	10
Sage scrub → chaparral	8
Sage scrub → grass	53
Sage scrub → tree	0
Tree → tree	26
Tree → chaparral	1
Tree → grass	6
Tree → sage scrub	0

Appendix S4

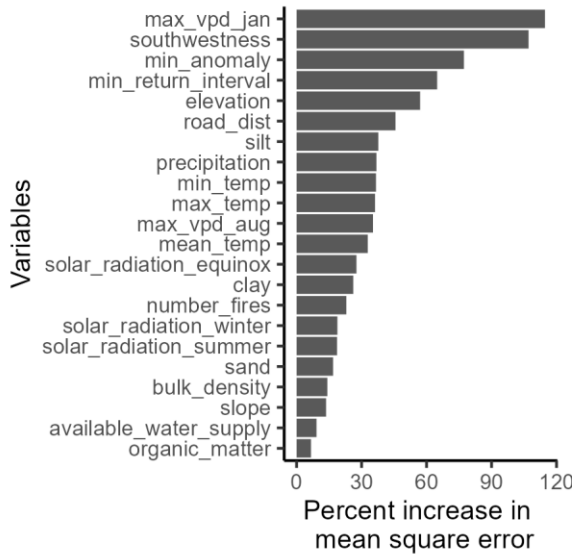


Figure S1: Random forest results from chaparral cover change analysis.

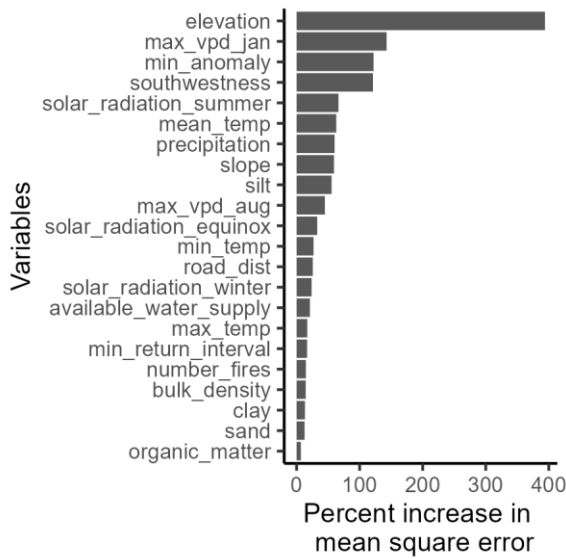


Figure S2: Random forest result from chaparral cover change analysis with data subset to only include minimum fire return intervals less than or equal to 34 years.

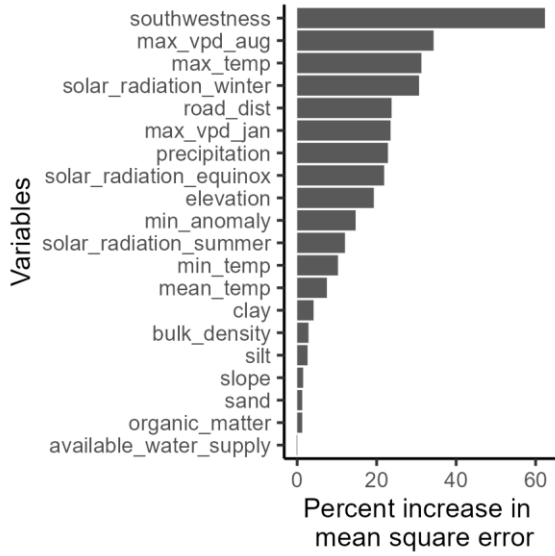


Figure S3: Random forest results from chaparral cover change analysis from data subset to only include minimum fire return intervals greater than or equal to 81 years.

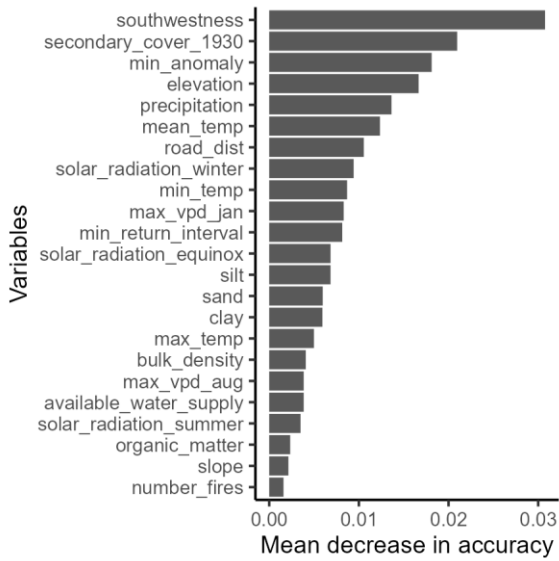


Figure S4: Random forest results from chaparral conversion to grass analysis.

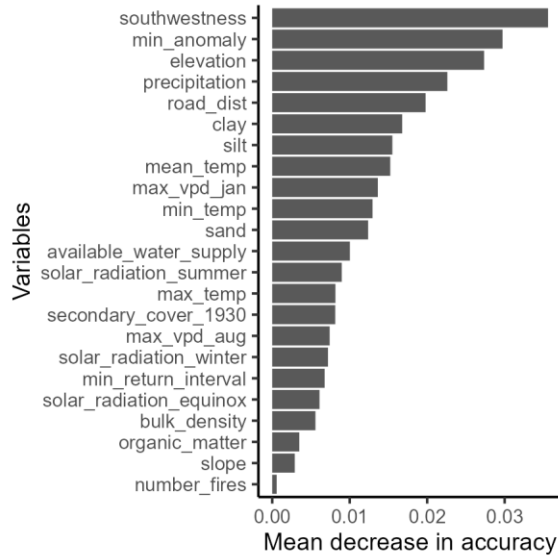


Figure S5: Random forest results from chaparral conversion to grass analysis with data subset to only include minimum fire return intervals less than or equal to 34 years.

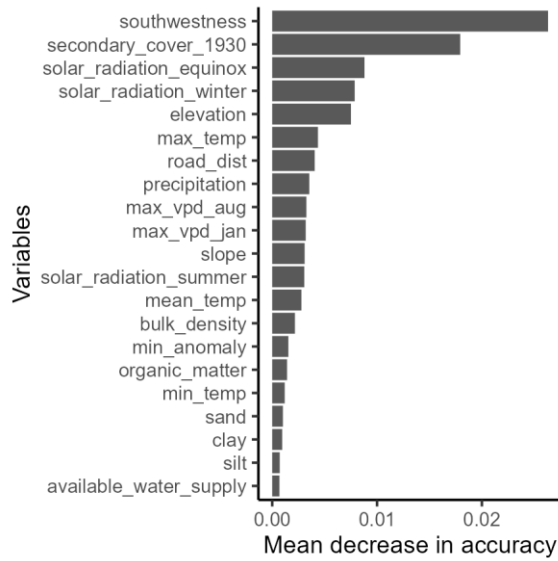


Figure S6: Random forest results from chaparral conversion to grass analysis from data subset to only include minimum fire return intervals greater than or equal to 81 years.

Appendix S5

Machine learning analysis on data subset to include short and moderate fire return intervals

≤ 34 years and only long intervals ≥ 81 years.

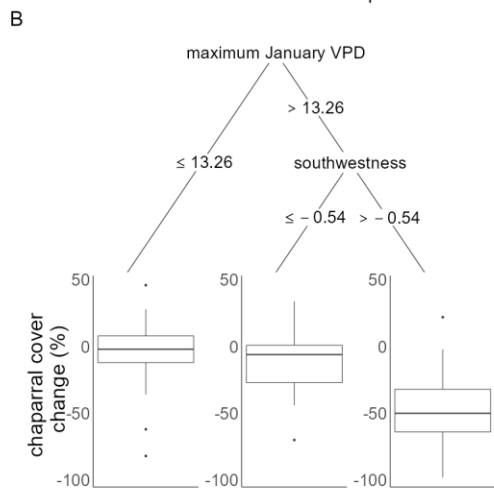
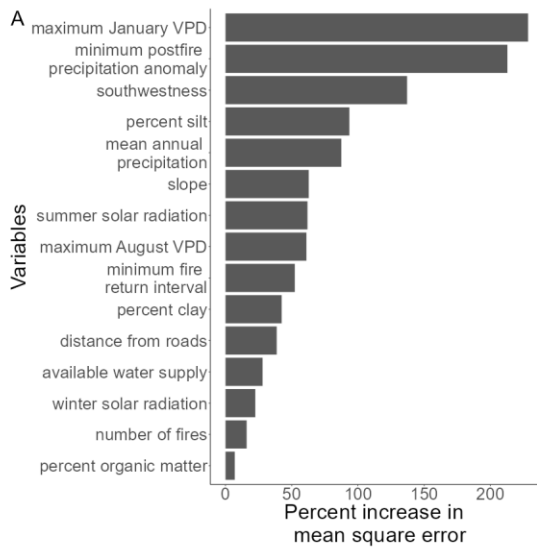


Figure S1: Results from random forest analysis subset to only include minimum fire return intervals ≤ 34 years (A) and hierarchical decision tree analysis (B) for chaparral cover change analysis. Variables with higher percent increase in mean square error have higher relative variable importance (A). In (B) the topmost node is the most important split. Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the distribution of chaparral cover change values for those plots.

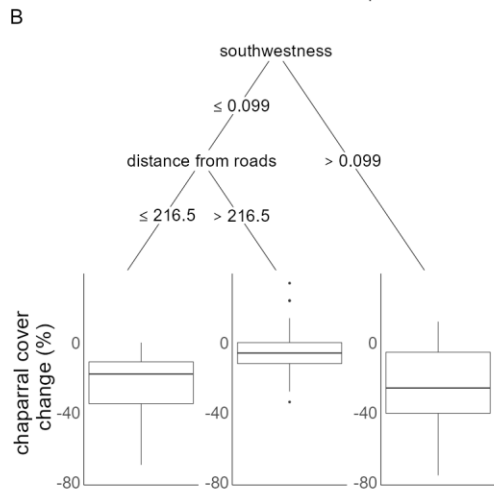
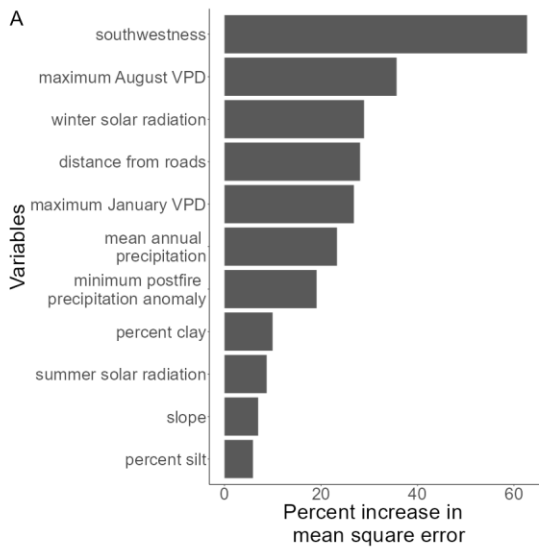


Figure S2: Results from random forest analysis subset to only include minimum fire return intervals ≥ 81 years (A) and hierarchical decision tree analysis (B) for chaparral cover change analysis. Variables with higher percent increase in mean square error have higher relative variable importance (A). In (B) the topmost node is the most important split. Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the distribution of chaparral cover change values for those plots.

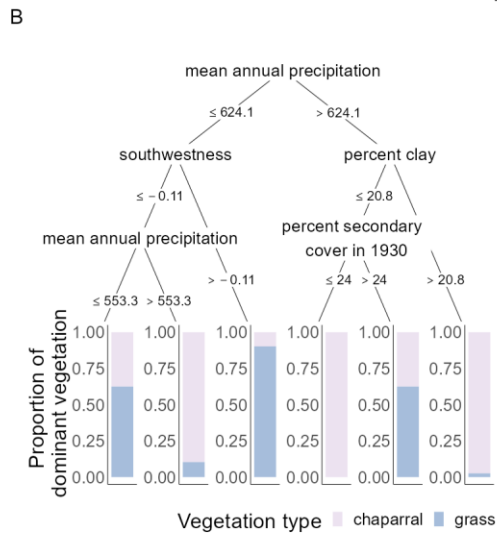
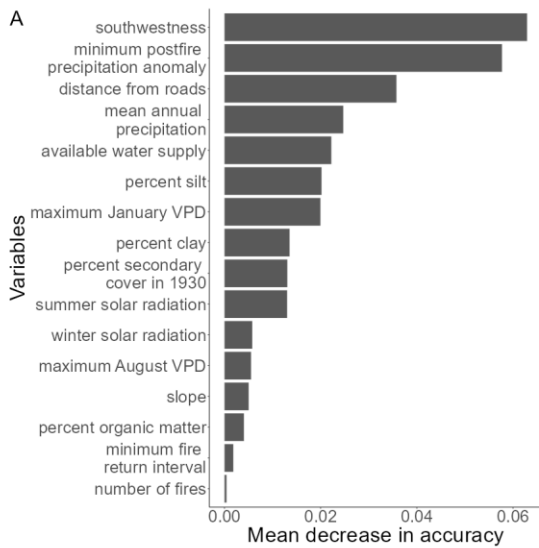


Figure S3: Results from random forest analysis on data subset to only include minimum fire return intervals ≤ 34 years (A) and hierarchical decision tree analysis (B) for chaparral conversion to grass. Variables with higher mean decrease in accuracy have higher relative variable importance in (A). In (B) the topmost node is the most important split. Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the proportion of plots (blue bar) that converted to grass.

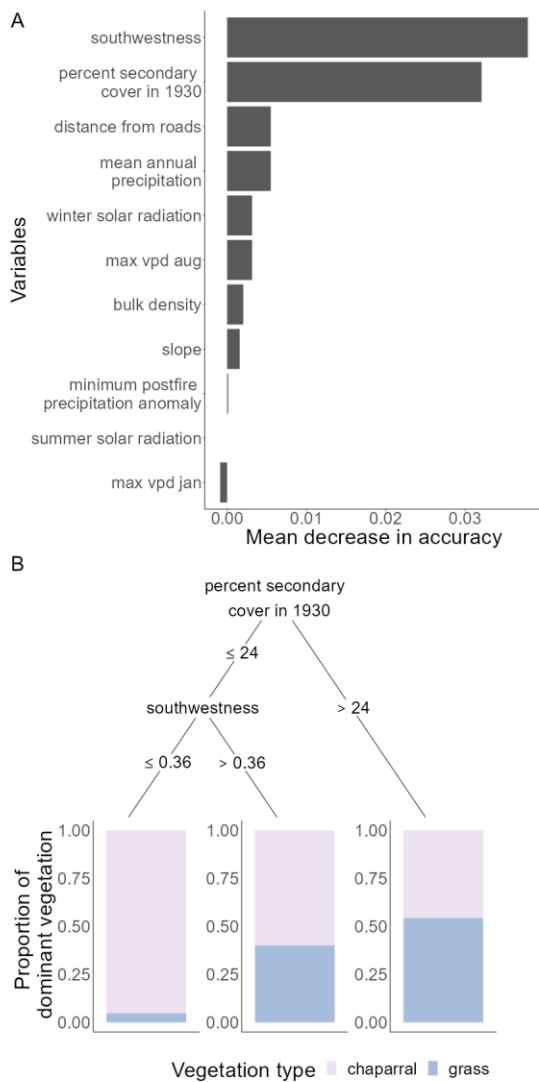


Figure S4: Results from random forest analysis on data subset to only include minimum fire return intervals ≥ 81 years (A) and hierarchical decision tree analysis (B) for chaparral conversion to grass. Variables with higher mean decrease in accuracy have higher relative variable importance in (A). In (B) the topmost node is the most important split. Values shown between nodes are threshold values the model found to best partition the data. Terminal nodes show the proportion of plots (blue bar) that converted to grass.

Appendix S6

Website and query details for all external datasets used in analysis.

Historical fire perimeters data was obtained from CALFIRE at <https://frap.fire.ca.gov/frap-projects/fire-perimeters/>

Elevation was obtained from the USGS National Map Viewer's data download application (<https://apps.nationalmap.gov/downloader/>) with the datasets query set to the spatial extent of the 2003 Piru fire (data in above layer). Data query was also set to "Elevation Products (3DEP)" sub category "1 arc-second DEM current", Data Extent "1 x 1 degree", File Formats "GeoTiff".

Slope was calculated from the Elevation dataset in ArcGIS's Surface toolset in the Spatial Analyst toolbox and run under default parameters for the slope tool.

Aspect was calculated from the Elevation dataset in ArcGIS's Surface toolset in the Spatial Analyst toolbox and run under default parameters for the Aspect tool. Southwestness was then calculated as $\cos(\text{aspect} - 225^\circ)$.

Solar radiation was calculated from the elevation dataset in ArcGIS's Solar Radiation toolset in the Spatial Analyst toolbox. The Area Solar Radiation tool was used and run under default settings, except for the time configuration option, which was set to "special days".

30-year mean annual precipitation normal was downloaded from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) website "normals" tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to "800m (18-350MB per data file; 5MB per full-size imagery)", climate variable set to "Precipitation", temporal period set to "annual values", then clicking the "Download Data (.bill)" button.

30-year minimum January temperature normal was downloaded from the PRISM) website "normals" tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to "800m (18-350MB per data file; 5MB per full-size imagery)", climate variable set to "Minimum

temperature”, temporal period set to “monthly values for January”, then clicking the “Download Data (.bill)” button.

30-year maximum August temperature normal was downloaded from the PRISM) website “normals” tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to “800m (18-350MB per data file; 5MB per full-size imagery)”, climate variable set to “Maximum temperature”, temporal period set to “monthly values for August”, then clicking the “Download Data (.bill)” button.

30-year mean annual temperature normal was downloaded from the PRISM) website “normals” tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to “800m (18-350MB per data file; 5MB per full-size imagery)”, climate variable set to “Mean temperature”, temporal period set to “annual values”, then clicking the “Download Data (.bill)” button.

30-year minimum January vapor pressure deficit (VPD) normal was downloaded from the PRISM) website “normals” tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to “800m (18-350MB per data file; 5MB per full-size imagery)”, climate variable set to “Minimum vapor pressure deficit”, temporal period set to “monthly values for January”, then clicking the “Download Data (.bill)” button.

30-year maximum August vapor pressure deficit (VPD) normal was downloaded from the PRISM) website “normals” tab (<https://prism.oregonstate.edu/normals/>), with spatial resolution needed set to “800m (18-350MB per data file; 5MB per full-size imagery)”, climate variable set to “Maximum vapor pressure deficit”, temporal period set to “monthly values for August”, then clicking the “Download Data (.bill)” button.

Minimum precipitation anomalies were calculated by downloading the mean annual precipitation normal as described above, but at 4km spatial resolution instead of 800m spatial resolution. Then yearly annual precipitation values for 1912-1980 were downloaded from the PRISM website “Historical Past” tab (<https://prism.oregonstate.edu/historical/>) by setting climate variable to “precipitation”, the blank box in temporal period each year in the span 1912-1980 and then clicking the “Download All Data for Year (.bil)” button. Of the downloaded files, the bil file ending with “just the year”_bil corresponds to annual precipitation. For example, the desired data file in the 1912 folder would be “PRISM_ppt_stable_4kmM2_1912_bil.bil”. For yearly precipitation values from 1981-2009, data were downloaded from the PRISM website “Recent Years” tab (<https://prism.oregonstate.edu/recent/>) by setting climate variable to “precipitation”, temporal period to “monthly data x” with x representing each year from 1981-2009, annual values, then clicking the “Download Data (.bil)” button. Precipitation anomalies were then calculated as yearly precipitation – 30 year normal for every year.

All soil data was downloaded from the USDA’s web soil survey interactive map (<https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx>). First, under the “Area of Interest (AOI)” tab and the “Area of Interest” subtab, the “Import AOI” option was selected and the “Create AOI from Shapefile” option was used to upload a shapefile of the 2003 Piru fire scar. Next, the “Soil Data Explorer” tab was selected and under the “Properties and Qualities Ratings” subtab the “Soil Physical Properties” option was selected. Then, for each “Available Water Supply (0-150cm)” “Bulk Density, One-Third Bar”, “Organic Matter”, “Percent Clay”, “Percent Sand”, and “Percent Silt” under “Advanced Options”, the “Aggregation Method” was set to “Weighted Average”, “Tie-break Rule” to “Higher”, and “Layer Options (Horizon Aggregation Method)” was set to “Depth Range (Weighted Average)” with Top Depth set to 0, Bottom Depth

set to 150 and “centimeters” selected. Lastly for each of the layers, the “View Rating” button was clicked and then “Add to Shopping Cart”. Once all of the layers are successfully added to the shopping cart, the “Download Soils Data” tab was selected and under the “Your AOI (SSURGO)” sub tab, the “Create Download Link” button was clicked. This then creates a download link for all the desired data. Once all the data is downloaded, some processing in ArcMap or Rstudio is required. In the Spatial tab, the “soilmu_a_aoi” shapefile must be joined to the appropriate “rating” file in the thematic tab. For each soil variable downloaded, there will be a ratingxxxxxx file in the thematic tab. The summary text document in the thematic folder provides a key to which rating file corresponds to which variable. Lastly, the rating file and soilmu_a_aoi shapefile must be joined by their “MapUnitKey” (or MUKEY in the shapefile).

The Distance from roads data set was created by calculating a distance raster in ArcGIS using the Euclidean Distance tool in the Distance toolset in the Spatial Analyst toolbox. The input feature source data was a primary and secondary roads shapefile obtained from the United States Census Bureau’s Tiger/Line roads shapefiles (<https://www.census.gov/cgi-bin/geo/shapefiles/index.php?year=2017&layergroup=Roads>) with the “primary and Secondary Roads” “Select a State” set to California. Then the “output cell size” was manually set to 10m.

III. Microclimate and plant trait interactions predict species’ survival and growth responses in a restoration context.

A. Abstract

Habitat degradation and conversion have become a ubiquitous problem globally and are expected to increase with climate change. In areas where degradation and conversion have

already occurred, ecological restoration provides a promising avenue to enhance biodiversity and ecosystem function. While studies have shown instances of restoration success, the applicability of such findings to new areas, let alone new species, is very limited. The burgeoning field of plant functional trait ecology posits, however, that there are fundamental relationships between plant functional traits and how species perform in their environment. Therefore, classifying species by their plant traits, instead of taxonomic identity, offers a promising way to expand the findings of restoration ecology research to new settings and species.

Here, I map seedlings survival and growth (fitness components which plant ‘functional’ traits are presumed to influence) across a variety of microsite environments in a Mediterranean climate shrubland restoration experiment. I then tested for the effect of plant traits as well as trait-by-environment interactions on growth and survival. In January 2020, approximately 1600 1-year old individuals of ten native shrub species were planted across a 6-acre, topographically heterogeneous field site in Ventura County, California, USA. Fine-scale mapping of the planting locations and hourly temperature, humidity and soil moisture measurements were used to model species survival probability as a function of microsite environmental differences. I found a significant relationships between all of our measured functional traits and survival, as well as between leaf traits associated with the leaf economics spectrum, water use efficiency and wood density and growth rate. These findings show potential for relatively easy-to-measure plant traits to be used to predict how different species respond to different microsite environmental conditions and survival across a landscape. I also found the slope and direction of the correlation between these traits and survival or growth was highly dependent on plant height and/or microsite environmental conditions indicating the necessity to include more nuance when describing the ‘function’ of plant traits.

B. Introduction

The restoration of degraded ecosystems has become a dominant focus of conservation efforts in the twenty-first century. As a result, the field of restoration ecology (the study of the relationships between organisms and their environment, specifically in a restoration context; Palmer et al., 2016) has blossomed, and a plethora of ecological theories have been studied and applied to restoration endeavors. The goal of ecological theories are to explain historical events, understand present observations, and predict future states (Scheiner & Willig, 2011). Therefore, the development of ecological theory specific to restoration ecology is especially imperative as ecological systems are increasingly altered and the successful outcome of restoration relies on the predictive accuracy of any guiding theory.

Restoration success is vexingly inconsistent, despite the growing use of ecological theory to inform restoration approaches (Christmann & Menor, 2021; Crouzeilles et al., 2016; Gómez-Aparicio et al., 2004; Nolan et al., 2021; Wortley et al., 2013). This holds true both across and within ecosystems, begging the question of how applicable any given study's findings are to new locations, and species.

The field of plant functional trait ecology posits that there are fundamental relationships and tradeoffs between plant traits (e.g. the leaf economics spectrum) and that these traits are functional in determining how species perform (i.e. survive, grow and reproduce) in their environment (Mcgill et al., 2006). Promising a way to transcend esoteric, species-by-species analyses, functional trait theory has been referred to as the 'holy grail' of community and functional ecology, because of its potential to make the findings of studies more easily applicable to new locations and species (Funk et al., 2017; Lavorel & Garnier, 2002). However, many plant functional trait studies focus predominantly on quantifying the relationship and trade-off

between traits and assume the “functional” aspect (i.e. that the traits in question mediate performance in a given environment). Additionally, in-depth studies that actually test the function of plant traits have mixed results and reveal an emerging theme of function being context dependent on intraspecific trait plasticity (Poorter et al., 2018), environmental variation (Rowland et al., 2021), and variation in plant size/age (Kitajima et al., 2002; Thorne, 1973). While several recent studies have suggested that plant trait theory can provide guidance to the field of ecological restoration (Balazs et al., 2022; Kimball et al., 2016; Merchant et al., 2023), empirical tests have been limited in their geographic and species palette scopes (Merchant et al., 2023, but see Gornish et al., 2023). Therefore, in this study, I aim to describe the function, in a restoration context, of a myriad of plant traits across a diverse range of species and how that function may change with environmental and plant size.

Our study addresses these question in southern Californian shrublands, which are comprised of two main vegetation communities: sage scrub and chaparral (Barbour et al, 2007). The sage scrub community is characterized by partially closed canopies of shrub and sub-shrub species 0.5-2m in height, most species of which are fully or partially drought deciduous and have whitish green leaves often with some degree of reflective trichomes or glaucous surface. Representative species include *Salvia leucophylla*, *S. apiana* and *Artemisia californica* (Rundel, 2007; Westman, 1981). Additionally, the sage scrub community is identified as threatened, with only an estimated 10% of its historic distribution remaining due largely to human development and altered disturbance regimes (Rundel, 2007). By contrast, the chaparral vegetation community is characterized by an extremely dense and closed canopy of evergreen shrubs 1.5-3m in stature. Chaparral typically occurs higher on the mountain slopes than sage scrub with a mix of sclerophyllous leaved dominants such as *Adenostoma fasciculatum*, *Heteromeles arbutifolia*,

Malosma laurina, *Ceanothus species* and *Arctostaphylos species*. (Gray, 1982; Keeley, 1998; Parker et al., 2016). The chaparral community has lost an estimated 70% of its historic southern California distribution due to direct human development and shortened fire return intervals in the last 50 years (Syphard et al., 2018). Both vegetation communities are adapted to the Mediterranean environment (i.e. hot-dry summers and cool-wet winters). Sage scrub and chaparral vegetation form discrete communities and naturally co-occur or intermingle on the same slopes, especially in years following fire (Westman, 1981). Sage scrub species are often viewed as early successional in disturbed chaparral (Hanes, 1971).

While there is a solid foundation of ecological research on the restoration of the sage scrub vegetation community (Bowler, 2000; Cox & Allen, 2008; DeSimone, 2011; Quon et al., 2019; Michael F. Allen, 1998), there is an absence of published research on chaparral restoration (Allen et al., 2018), with a dearth of reporting on chaparral restoration activities in general (but see VinZant, 2013). Under the right circumstances (i.e. close enough to intact stands for seed dispersal to occur), passive restoration of sage scrub has been shown to lead to establishment after removal of non-native cover (DeSimone, 2011). Additionally, where passive restoration does not lead to establishment, active restoration via both direct seeding and transplanting of seedlings has shown to be a feasible alternative (Cox & Allen, 2008; Quon et al., 2019). Conversely, the few reported chaparral restoration endeavors find no shrub establishment from the direct seeding for chaparral shrubs (Allen et al., 2018; Ma unpublished) and post-transplant survival only with intensive watering efforts that are likely unsustainable at large scales and in complex terrain (VinZant, 2013).

In this study, I link the holy grail of functional traits with plant performance through a large-scale restoration experiment in a degraded southern California shrubland. I first evaluate the

above- and below-ground environmental conditions that facilitate growth and survival of transplanted seedlings. I then use a suite of plant functional traits to test for significant relationships between these traits and plant survival as well as the interaction of traits with measured above- and below-ground conditions.

C. Methods

Study area: The study area consists of approximately 8 acres of a heterogenous landscape in the Los Padres National Forest, Ventura County, California (Figure 1). Climate normals from the Temescal (LPF; TCLC1) weather station covering the years of 2000 to 2020 characterize this region as having hot-dry summers and cool-wet winters, with winter lows of 0.6°C, summer highs of 41°C and highly variable season and interannual rainfall. The site is currently dominated by non-native annual species (i.e. *Avena fatua*, *Bromus sp.*, *Rapistrum rugosum*) with a few isolated patches of remnant native-shrubs (*Rhus ovata*, *Sambucus nigra*, *Salvia leucophylla*, *Artemisia californica*, and *Hesperoyucca whipplei*), but historically it was shrub dominated (Deweese et al., 2022). This landscape represents a type converted southern California shrubland. The study site is arid, low elevation, on a southwest facing slope, and close to roads- all of these characteristics have been identified as being in great need of restoration and represent some of the most challenging conditions to restore (Deweese et al., 2022). Therefore, this study location presents an ideal area for investigating the effect of topographic and environmental microsite conditions on seedling growth and survival in a restoration context.

Experimental Design: Our restoration planting community consisted of 1653 seedlings comprised of 10 shrub species (Table 1) common to the chaparral and sage-scrub vegetation communities and found in the area surrounding our study site. They were selected based on the desire to include species representing a wide array of functional traits. Functional traits of nearly

30 species were collected for this region and the species for this study were selected from within these 30, as determined by availability of germinable seeds. Seed for 8 of the 10 species were collected from mature individuals within 5 miles of the study site and grown for approximately 1-year at the UCSB Biological greenhouses in D40H 2.5” x 10” containers (Stuewe and Sons Inc.). Seeds for *Malosma laurina* and *Adenostoma fasciculatum* were not collected from within 5 miles of the study site because the limited number of mature individuals didn’t allow for responsible seed collection. *Malosma laurina* seeds were collected from within the Los Padres National Forest at a similar elevation to the west of the site and grown as stated above. Due to difficulty with successful germination and growth, *Adenostoma fasciculatum* seedlings were purchased from the Tree of Life Nursery in San Juan Capistrano, California, in a mix of 1- and 2-gallon pots. All seedlings were moved from greenhouses to raised tables outside by June of 2019, ensuring they had over 6 months of “hardening-time” prior to field transplantation.

The study site was selected because it represented a landscape with a wide range of microhabitats and elevations, all of which had been degraded by introduced grasses and short interval fire. Prior to planting, each seedling had a randomly selected planting location assigned, with a minimum of 1-meter distance from any other planting location. Each planting location had a half-meter by half-meter square weeded of all other vegetation and then covered with weed cloth. The planting locations were also labeled with a unique number, using tree coins, and 1535 (delays related to COVID-19 led to a small number unable to be relocated to GPS) had their location mapped to sub-meter resolution using a Trimble Geo 7x GPS device (Trimble Inc.). Each plant was then out planted to the field from January to early March of 2020. The species and locations planted on a given day were randomized to minimize the influence of planting time on our results. During outplanting, a small square was cut into the center of the weed cloth and a

hole as deep as the roots extended was dug. Each plant was then planted with a 50-50 mixture of their potting soil and native soil from the aforementioned hole and watered with 500ml of water. Additional watering of 500ml per plant was also performed halfway through planting in February because of a lack of rain, and then again in May, because of extended rain-free periods during the normal wet season. Survival of all individuals was then recorded in May 2020, July 2020, late October-early December 2020 (hereafter referred to as fall 2020) and December 2021, with height also measured at time of planting and all but the May 2020 census dates.

Environmental and Topographic Measurements: Microsite temperature and humidity differences were measured through deploying 115 temperature-measuring ibuttons (a subset of 39 also measured humidity; IbuttonLink) to record hourly data across a representative topographic range of the planting locations. Additionally, 30 soil moisture probes (ECH20 10HS, Meter Environment) were inserted parallel to the soil surface at 15cm depths and logged hourly (resampled to mean daily) soil moisture across a similarly representative topographic range of planting locations. The soil moisture probes were installed by digging a 15cm trench at the edge of the weed cloth directly across from the plant. This allowed the insertion of the probe into the active rooting zone underneath the weed cloth. Additionally, a depth of 15cm was selected because most seedlings had roots extending 10-20 cm (data not shown) at time of planting. A one-meter digital elevation model was also obtained from the United States Geological Survey National map viewer and used to calculate the elevation, southwestness (Beers et al., 1966), slope, summer- winter- and spring solar radiation (ArcGIS Pro, ESRI), diurnal heat, heat load index, solar-radiation aspect index, terrain ruggedness (Rstudio 4.2.2 *spatialEco* package), topographic wetness index and SAGA wetness index (SAGA GIS) for all of the mapped planting locations (n = 1535).

Limitations in the number of environmental sensors made it impossible to measure soil moisture, temperature and VPD at all 1535 locations. Therefore random forest models, using date, maximum daily temperature from the nearby Temescal (LPF; TCLC1) weather station and the above topographic variables, were developed to predict maximum daily temperature, maximum daily vapor pressure deficit (VPD), and scaled to mean, daily soil moisture for each planting location. The models were trained on the sensor collected data with a random subset of 80% of the data and tested on the remaining 20%. Model accuracy was then evaluated through calculating both the r^2 and root mean square error (RMSE) of the predicted values versus the sensor measured values from the testing dataset (temperature: $r^2 = 0.95$ and RMSE = 3.19, VPD: $r^2 = 0.93$ and RMSE = 0.529 and soil moisture: $r^2 = 0.9785$ and RMSE = 0.139; Appendix 1). These models were then used to predict maximum daily temperature, VPD and soil moisture for all planting locations with mapped locations.

Plant traits: Our analysis also included a variety of measured plant traits (detailed in Appendix 2). Measured traits included leaf petiole length, leaf width, leaf dry matter content, leaf carbon per unit area, leaf nitrogen per unit area, leaf carbon to nitrogen ratio, leaf thickness, leaf lamina length, specific leaf area, and $\delta^{13}\text{C}$ (photosynthetic fractionation of carbon-13 isotopes) for integrated water use efficiency, wood density and plant height (Appendix 2). All measured traits, except plant height, were collected from a minimum of 5 mature individuals within 5 miles of our restoration site during winter/spring 2016-17. I measured plant height at time of planting and periodically through the study, as described above, on all individuals. Species averages for all traits except plant height were then used for subsequent analyses. Plant height values were used at the individual level.

I acknowledge that the measured trait values from mature individuals may vary from the actual values of our out-planted seedlings due to the potential of ontogenetic shifts and environmentally induced trait plasticity. Additionally, I recognize that there is a fundamental difference between taking a species-based approach as done here from an individual-based approach (i.e. measuring the trait values for every individual used in the study; Poorter et al., 2018). One of the main differences common to the species-based approach is that traits and function (i.e. survival and growth) are measured under standardized and “optimal growth conditions” (Pérez-Harguindeguy et al., 2016; Poorter et al., 2018). In contrast, I measured plant traits on a subset of individuals across a landscape during an unprecedented multi-year drought, not optimal conditions, and function (i.e. survival and growth) across time and space, not standardized conditions. It was not feasible, both logistically and because of the impact of tissue removal from small plants, to measure traits other than plant height on each individual.

I believe our trait approach represents a balance between providing important mechanistic ecological insight and being applicable to practitioners and land managers. It is likely that the application of plant trait theory would be done at the planning stage, potentially before seedlings have been germinated and fully grown, therefore, using pre-existing or adult trait values is likely more akin to the approach a restoration practitioner may take.

The methods I used to measure each trait are detailed in Appendix 2, but briefly, multiple leaves from each individual were collected and then rehydrated overnight. The following day, wet weights were measured and then leaves were scanned and placed in a drying oven at 65C for three days. Following oven drying, dry weight was measured. Dry leaf samples were then ground in a Wiley benchtop mill and Wig-L-Bug, dried again at 65C and then had 2mg portions wrapped in tin capsules. Measured trait values were then obtained from the leaf scans and

weights and leaf chemistry (leaf carbon, nitrogen and $\delta^{13}\text{C}$) were measured by the University of California, Santa Barbara Marine Analytical Lab.

All of the leaf traits except for integrated water use efficiency (photosynthetic discrimination against carbon-13) were highly correlated. To address this, and because most are key traits in the commonly referenced leaf economics spectrum (hereafter LES; Wright et al., 2004), these traits were combined into a principal components analysis and the axis scores from the first two principal components (which captured 72% of total variation) were then used as predictors.

Data Analysis: All data analysis was performed under a survival analysis, also known as time-to-event, framework using the *survival* package in R. Survival was analyzed from planting through December 2021. However, the abiotic factors and influence of plant traits on survival were only analyzed on mortality data through the fall 2020 census point, for two main reasons: (1) The first summer was identified as the period where most mortality occurred, so I wanted to isolate the environmental drivers specific to that important period, and (2) the 2021 growing season (January to May) was abnormally dry (Figure 2), leading to very high mortality for virtually all species. Additionally, all plants that succumbed to mortality due to gopher kill (plant missing with obvious gopher hole at planting location or dead plant with no root system intact) were treated as right censored data. Right censored data means that the survival data for these individuals up to the interval in which they were killed, was used in the models, but then removed, or censored, from the dataset instead of analyzed as a death. This prevented gopher activity from biasing the analysis of environmental drivers of mortality.

Overall plant survival on all of our individuals ($n = 1653$) was analyzed by constructing Kaplan-Meier survival curves for each species. Survival differences between species were analyzed by creating a cox-proportional hazards model, which allowed us to look at species-

specific mortality rates over time and compare the overall survival of species. While creating this model, I set the highest surviving species (*Hesperoyucca whipplei*) as the reference. This means that the modeled hazard rate for each species is the ratio of hazards between that species and *Hesperoyucca whipplei*. For example, a hazard ratio of two for *Salvia apiana* means that twice as many *Salvia apiana* individuals are dying as *Hesperoyucca whipplei* individuals, at any given time.

Survival: The influence of temperature, soil moisture, VPD, seedling height and plant traits on survival for nine of the ten species was analyzed using cox-proportional hazards models (n=1264). I dropped *Hesperoyucca whipplei* from this analysis because it is the one species that is not a shrub and is fairly distinct from the other 9 species in terms of trait values (Figure 3): as it does not have wood and its leaf structure is dramatically different (long narrow basal rosette) from all others. Because the effect of the predictor variables changed over time, I partitioned the time axis, which is a common established approach to address this issue (Therneau & Grambsch, 2000). I partitioned time into two intervals: (1) planting-July (early drought) and (2) July -fall (late drought). This led to the assumption of proportional hazards to remain true for both time periods and allowed us to identify season specific effects of the three environmental variables. I further analyzed three possibilities for how environmental variables were calculated for each of the two time periods in order to capture season-specific effects. To explain the first survival period, I calculated the environmental predictor variables as the means for three different time periods: whole early growing season (planting through July), spring (early drought, planting through May) and early summer (June through July). For the second survival period, I calculated full late growing season (July through fall census), late summer (July through September) and fall (October and running through to the fall census date).

Final model selection was determined by AIC selection. Initial models were set including the LES 1, LES 2, integrated water use efficiency, wood density, temperature, soil moisture, VPD, and height at the beginning of the survival interval (either planting or July). I was then interested in potential trait-environment interactions and interactions between height and all other variables, so models with a single interaction (all possible variable combinations but only one interaction term per model) had their AIC values computed (Appendix 3). I selected the most parsimonious model for each time period as the least complex model that was within two AIC units (ΔAIC) of the lowest AIC model (Zuur et al., 2009). From there, I developed models with one additional interaction, from all the single interaction models that led to an AIC decrease of 2 or more. I iterated this process until either there were no more interactions to add, or AIC did not decrease by 2 or more. Once I had this full model, I performed single variable removal, once again testing for AIC decreases of 2 or more and iterated this process until there was no longer an AIC decrease of 2 or more. To evaluate seasonal importance of environmental variables, this process was repeated six times: three times for the planting to July time period either averaging daily environmental variables across the whole time period, or shortening the variable window to planting through May or from June through July to predict July outcomes; and three times for the July-fall time period with daily environmental variables averaged across the whole time period, or July through September, or October through fall census date (Appendix 3).

Growth: I also developed generalized linear models to analyse the influence of microsite environment and traits on growth rate. Growth rate was calculated as:

$$(\text{height}_{\text{end}} - \text{height}_{\text{start}})/(\text{time interval}) \text{ Equation 1}$$

where $\text{height}_{\text{end}}$ is the height at the end of the time interval, $\text{height}_{\text{start}}$ is the height at the start of the time interval, and time interval is the length of time in days. Growth rate was calculated

and analysed for the same two time intervals that survival was analysed (planting to July and July to fall). In contrast to the survival analysis, environmental variables were averaged across the whole time period, not partitioned seasonally. Final model selection via AIC selection was then carried out identical to described above.

D. Results

Microsite Environmental Modeling: As mentioned above, the random forest models developed to predict daily temperature, VPD, and soil moisture all had high r^2 (0.95, 0.93 and 0.9785 respectively) and reasonable RMSE (3.19, 0.529, and 0.139 respectively) values. Additionally, examination of variable importance and how the predicted values varied in both space and time are reassuring that the models are capturing the appropriate amount of variation due to topography and day of year respectively (Appendix 1). Therefore, while I might hesitate to use the predicted values to identify specific values of environmental threshold, I believe our modeled environmental values are appropriate for comparing the relative effect of soil moisture, temperature and VPD over space and time.

General Survival: Species specific survival curves, with plants lost to gopher activity included as right-censored data, showed the same general trend of minimal to moderate die-off by early summer (July) and then significant die-off through the rest of summer and fall (Figure 4). The two species that showed some deviation from this trend were *Malosma laurina* and *Sambucus nigra*. *Malosma laurina* had relatively high die-off between planting and May, likely due to the fact that there were multiple below freezing nights and this species has been documented as frost-intolerant (Pratt et al., 2005). *Sambucus nigra* had similar rates of die-off during the early summer and late summer to fall.

Hesperoyucca whipplei had the highest survival, and a cox-proportional hazards test evaluating the hazard ratio of switching from *Hesperoyucca whipplei* to any other species revealed that to be a significant difference for all species but *Encelia californica*, *Adenostoma fasciculatum*, and *Rhus ovata* when looking at survival through the first year (Figure 5A). By December 2021, all species had significantly higher hazard rates than *Hesperoyucca whipplei* (Figure 5b). Meanwhile, *Heteromeles arbutifolia* had the highest hazard rate during both the first year (13 surviving individuals) and by December 2021 (0 surviving individuals; Figure 5). These hazard rates for *Heteromeles arbutifolia* were significantly higher than all species but *Malosma laurina*'s by the end of the first year (Figure 5A) and significantly higher than all species by December 2021 (Figure 5B).

All species but *Heteromeles arbutifolia* had surviving individuals at the end of the study (Table 1). Additionally, many of the *Encelia californica*, *Salvia apiana*, and *Salvia mellifera* individuals flowered and set seed during both 2020 and 2021 (data not shown). *Sambucus nigra* individuals that survived to the 2021 summer also flowered and set seed (data not shown).

Seasonal Models Selected: AIC model selection for seasonal effects of environmental factors (i.e. temperature, soil moisture, and VPD), for both the planting to July time period and July to fall time period, suggests that sub-setting the environmental data to June-July and October-fall leads to the best predictive models for both July and fall survival respectively (Appendix 3).

Influence of Microsite Environment on Survival: Survival from planting to July was significantly influenced by microsite differences. As soil moisture increases, survival increases (hazard rate = 0.15, $p < 0.01$) and while VPD did not have a significant effect in isolation (hazard rate = 1.31, $p = 0.6$) it did have a significant interaction with wood density (hazard rate = 8.71, $p = 0.042$) indicating that as VPD and wood density increased survival decreases at increasing

rates. However, model selection led to temperature being excluded from the final model (Table 2). Additionally, there was a significant interaction between soil moisture and VPD (hazard rate = 1.61, $p < 0.01$; Table 2). While all wood density values had lower survival at higher VPD's, VPD moderated the effect of wood density on survival: at lower VPD values, there was no significant changes in survival with wood density. However, as VPD increased, wood density became increasingly negatively correlated with survival (Figure 6D). Generally, survival probability increased as soil moisture increased and decreased as VPD increased (Table 2; Figure 6E). Yet the interaction between soil moisture and VPD revealed that increasing soil moisture amplified the negative influence of VPD, with higher VPD's having a lower survival probability at wetter microsites (Table 2; Figure 6F).

Survival from July through the fall was significantly influenced by microsite differences in temperature and soil moisture, but not VPD (Table 3). Generally, as temperature increased survival decreased; Table 3). However, there was also a significant interaction between temperature and wood density (Table 3): for species with lower wood densities (i.e. *Sambucus nigra*, *Salvia apiana*, *Malosma laurina*, *Rhus ovata*, and *Salvia mellifera*), increasing temperatures led to lower survival, whereas moderate to high wood density species (i.e. *Ceanothus oliganthus*, *Heteromeles arbutifolia*, *Encelia californica*, and *Adenostoma fasciculatum*) showed no response to temperature (Table 3; Figure 7D).

Plant traits and Survival: The first two axis of this PCA explained a cumulative 72% of the variation in the data. The first axis (hereafter LES 1) was most strongly associated with specific leaf area, leaf carbon per unit area, leaf nitrogen per unit area and leaf carbon to nitrogen ratio. It showed a strong negative correlation between specific leaf area and leaf carbon to nitrogen ratio, driven by larger decreases in leaf carbon than in leaf nitrogen. In the context of the leaf

economics spectrum this means that more negative LES 1 values are more akin to the conservative strategy, whereas more positive values are more akin to the acquisitive strategy. Alternatively, the second axis (hereafter LES 2) was strongly associated with petiole length, leaf width and leaf lamina length. Both axes were moderately associated with leaf dry matter content and leaf thickness.

Including plant traits in our predictive models consistently explained more variance than models not including plant traits. When comparing the amount of explained variance of our final early summer cox proportional hazards model to a model including only planting height and environmental factors, the early summer trait model explained 17% more variation in the data. Additionally, the early summer trait model explained 18.2% more variation than a model including planting height, environmental factors and species id, but not traits. Similarly the fall model explained 7.9% more variation than a model using only planting height and environmental factors and 8.2% more variation than a model using planting height, environmental factors, and species id, but not traits.

All of the functional traits included in the analysis had a significant effect on early summer survival (Table 2). Both of the PCA axes representing the leaf economic spectrum were positively correlated to survival (as they increased, the hazard rate decreased; Table 2 and Figure 6A/B). This means that species (i.e. *Encelia californica*, *Sambucus nigra*, *Ceanothus oliganthus*, *Salvia mellifera*, and *Salvia apiana*) with higher SLA values and lower leaf C:N (i.e. higher values on LES 1) generally had higher survival during this period. Similarly, plants (i.e. *Malosma laurina*, *Rhus ovata*, *Heteromeles arbutifolia*, and *Encelia californica*) with thinner and wider leaves, longer petioles and smaller leaf lamina lengths (i.e. higher values on LES 2), were generally more likely to survive. However, there was also a significant interaction between LES

2 and the height of an individual at time of planting that confounded this effect (Table 2). When plants were smaller at time of planting, they were more likely to survive if they had higher values on LES 2, but plants that were larger at time of planting had no response to LES 2 values (Table 2 and Figure 6B). Water use efficiency had a positive correlation with survival probability (Table 2, Figure 6C). Lastly, wood density also had a significant interaction with microsite VPD—at low VPD's wood density did not functionally affect survival, but as VPD increased, survival probability dropped more dramatically with higher wood densities. (Table 2 and Figure 6D).

Fall survival was significantly affected by all of the functional traits (Table 3). Similar to early summer survival, both PCA axes representing the LES (more acquisitive leaf traits at higher PC values) and water use efficiency had positive correlations with survival, (Table 3 and Figure 7A/B/C). Wood density again had a significant interaction, this time with microsite temperature (Table 3). Species with less dense wood (i.e. *Sambucus nigra*, *Salvia apiana*, *Malosma laurina*, *Rhus ovata*, and *Salvia mellifera*) were more likely to die as temperature increased, whereas species with denser wood (i.e. *Ceanothus oliganthus*, *Heteromeles arbutifolia*, *Encelia californica*, and *Adenostoma fasciculatum*) were unaffected by fall temperatures (Table 3 and Figure 7D).

Influence of Height on Survival: The height of an individual at time of planting significantly influenced July survival, with bigger plants more likely to survive (Table 2). Additionally, as mentioned above, height at time of planting also moderated the correlation between LES 2 and survival (Table 2; Figure 6B). Briefly, if plants were large enough at time of planting, LES 2 appeared to not affect survival, but smaller plants showed a strong positive correlation between LES 2 and survival. Similarly, height in July had a significant effect on fall survival (Table 3),

with larger plants being more likely to survive (Figure 7F). The moderating effect of height on the correlation between LES 2 and survival disappears during this time period.

Factors Affecting Growth: Growth from planting through July (growing season) was shown to be significantly affected by three different interactions: microsite temperature and LES 1 (Figure 8A), wood density and height (Figure 8B), and microsite VPD and water use efficiency (Figure 8C). Alternatively, growth from July through the fall was influenced by LES 1 and microsite temperature (Figure 9A) and LES 2 (Figure 9B). The microsite temperature and LES 1 interaction showed contrasting results depending on the time interval analyzed. During the spring and early summer, species with lower LES 1 values were unaffected by temperature and while increasing LES 1 values consistently meant more growth, the slope of that relationship increased with increasing microsite temperature (Figure 8A). Conversely, through the summer and fall species with lower LES 1 values experienced more growth at hotter microsite temperatures whereas higher LES 1 values were unaffected by microsite temperature, with the steepness of the LES 1 to growth rate relationship decreasing at cooler microsites (Figure 9A). The interaction between planting height and wood density showed that individuals that were small at time of planting experienced similar amounts of growth regardless wood density, but moderate and large individuals had less negative growth rates, or less dieback, if they had higher wood density (Figure 9B). Whereas the interaction between microsite VPD and water use efficiency showed that species with lower water use efficiencies had lower growth rates at higher microsite VPD's, but species with higher water use efficiencies were unaffected by VPD (Figure 8C). Lastly, during the summer through fall time period, species with higher LES 2 values experienced higher growth rates (Figure 9B).

E. Discussion

Our study supports that plant traits can help to explain variation in survival in species outplanted during restoration. I found that all ten of our restoration species had the same general survival trend, with the highest die-off during the summer and fall after planting (Figure 4). A finding consistent with previously observed demographic trends of natural post-fire recruitment in this vegetation community (Frazer & Davis, 1988; Guo, 2001; Keeley, 1991; Keeley & Keeley, n.d.; Keeley & Zedler, 1978). Importantly, while the same general trend was observed for all study species, the inclusion of plant traits in survival models substantially increased the amount of explained variation compared to either models with just environmental factors or environmental factors and species as a categorical descriptor. I also demonstrated that the plant traits included in this study were functional in terms of survival and growth. Furthermore, the function of multiple traits was context dependent on the microsite environmental conditions (i.e. temperature, soil moisture and VPD), a finding that is novel in the context of restoration ecology and has important implications to plant trait theory.

General survival: Our expectation that the highest die-off would occur during the dry season, informed by natural post-fire recruitment studies, bore out as valid. Additionally, our expectation that the faster-growing, mainly drought deciduous, sage scrub species would have higher survival rates than the slower-growing, evergreen chaparral species was supported when comparing survival curves of the species grouped by community type (Appendix 4). However, when species were ranked by their hazard ratio, compared to the highest surviving species *Hesperoyucca whipplei*, the chaparral and sage scrub species did not separate strongly (Figure 5). Chaparral species are commonly further differentiated into three post-fire functional groups by reproductive strategy, physiological attributes and drought response (Ackerly, 2004;

Jacobsen et al., 2007; Jacobsen & Pratt, 2018; Paddock et al., 2013; Pratt et al., 2007). While our chaparral species sample size was small, I did find suggestive demographic differences between these three groups. Two of the three facultative resprouters (i.e. *Rhus ovata* and *Adenostoma fasciculatum*), species that can recruit in exposed post-fire landscapes and have the potential for lignotuberous carbon storage and resprouting, have comparable survival to the sage scrub species (*Encelia californica*, *Salvia apiana*, *Salvia mellifera*, and *Sambucus nigra*) and significantly higher survival than both the obligate seeder (*Ceanothus oliganthus*) and obligate resprouter (*Heteromeles arbutifolia*) species (Figure 5). An obligate resprouter having very low survival is not unexpected as these species generally recruit in mature chaparral stands with shaded canopies and seedlings have been found to have higher mortality and show signs of sun-scalding through the dry season in sun-exposed environments (Pratt et al., 2008). Significantly lower survival in an obligate seeding species, however, a functional group that is generally very drought tolerant (Ackerly, 2004; Jacobsen et al., 2007; Pratt et al., 2008) and necessarily recruits in high-exposure environments (Keeley, 1991), was unexpected. However, *Ceanothus oliganthus* has been shown to be one of the more cavitation susceptible species in that functional group (Davis et al., 1999). Therefore, the actually surprising finding was the relatively high survival rates of the facultative resprouters (Frazer & Davis, 1988; Keeley & Zedler, 1978) *R. ovata* and *A. fasciculatum*. Our findings suggest that the combination of drought tolerance and carbon storage potential via lignotubers (indeed individuals were seen to have developed lignotuber organs at the time of planting) is critical for survival of out planted evergreen species through the hot-dry summer.

Environmental microsite effects: Early summer survival was shown to be significantly affected both by microsite soil moisture and VPD. Microsites that were drier, either below

ground or at the leaf level, had broadly more mortality. Furthermore, the interaction between soil moisture and VPD suggests that the effects of soil moisture may overpower any VPD effects at drier microsites. Analyses looking at the combined effect of soil moisture and VPD on plant productivity have shown that while VPD determines the level of plant productivity at moderate and high soil moistures, soil moisture is the main determinant at drier soil moistures (Fu et al., 2022). Therefore, it is possible I am observing a similar influence on seedling survival here.

Fall survival was shown to be significantly affected by October and November temperature and soil moisture, but not VPD. The influence of temperature on survival also interacted with wood density—species with higher wood density were generally not affected by differences in microsite temperature, whereas species with lower wood density were significantly less likely to survive through the fall in hotter microsites. Wood density is hypothesized to inversely correlate with respiration demands both directly (Larjavaara & Muller-Landau, 2010) and indirectly through its relationship to growth, with growth being higher in lower wood density species (Baraloto et al., 2010; Larjavaara & Muller-Landau, 2010). Assuming this is true for our study species, those with lower wood density, could reach the end of fall suffering from or close to carbon depletion either because they are wholly or partially drought deciduous (*S. nigra*, *S. apiana*, and *S. mellifera*) and have had no leaves for photosynthesis for several months, or because of the low soil moisture/high VPD of summer limiting carbon assimilation. Higher temperatures can also directly increase respiration rates and metabolic demand (Atkin et al., 2005; Bunce, 2007; Wright et al., 2006). Hence the interaction between wood density, fall temperature and survival may be that microsite differences in temperature are determining whether individuals become carbon depleted and die, or are able to support their carbon budget through the end of the dry season.

The above interpretation on the interaction between fall temperatures and wood density is further supported when put in the context of a study looking at how stomatal closure of shrub species responds to decreasing soil water potentials (Pivovarovoff et al., 2018). Our overlapping species (*Salvia apiana*, *Salvia mellifera*, *Sambucus nigra*, *Heteromeles arbutifolia*, and *Malosma laurina*) match one-to-one when ordering them from least dense to most dense wood (our study) and least negative to most negative water potential at which they close their stomata (Pivovarovoff et al., 2018). In other words, the species with the least dense wood and that I found to be most negatively affected by higher fall temperatures are also the species found to close their stomata at less dry soil moistures, or earlier in the growing season to dry season transition, and thus have a longer net negative carbon budget time to survive.

In addition to the above environmental effects on fall survival, temperature and VPD also had an indirect effect on fall survival through their influence on growing season (planting to July) growth rates. July height was found to significantly correlate with fall survival, with taller plants having a higher survival probability (Figure 7F). The interaction between temperature and LES 1 suggests that cheaper and shorter-lived leaves, which likely have higher carbon assimilation rates at any given moment in time than their longer-lived counterparts (Wright et al., 2004), have a significant positive carbon assimilation response to increasing temperatures (Berry & Bjorkman, 1980; Medlyn et al., 2002), under the range experienced during the growing season (i.e. January through May). Alternatively, during the growing season, the upper range of VPD's experienced are enough to limit growth for the less water efficient species. This is likely through VPD's influence on stomatal opening (Brodribb & McAdam, 2011; Darwin, 1898; Franks & Farquhar, 1999; Lange et al., 1971; Mott & Peak, 2013; Oren et al., 1999; Turner et al., 1984) being more impactful to carbon assimilation, and thus growth, for the less water efficient species.

A note of seasonality: Our analyses suggest distinct periods of stress during both our planting-July and July-fall time periods. Higher die off in the June-July time period as summer temperatures start to increase and soil moisture decreases (Pivovarov et al., 2014, 2018; Pratt et al., 2007) matches post-fire demographic studies (Frazer & Davis, 1988; Guo, 2001; Keeley, 1991; Keeley & Zedler, 1978). The highlighted importance of fall conditions over the late summer, especially under the context of the fall season during this study having higher than average temperatures and extremely late first-rains (Figure 2), has some important management implications. This suggests that individuals that survive through the early summer may be fairly likely to survive into the next winter if the rainy season begins in October to early November, which was not the case during the period of this study but has been the case historically (Figure 2). This is simultaneously reassuring and concerning: it is reasonable to expect that under a more normal growing year I should expect higher survival rates. However, under the advent of climate change, seasons like the one experienced here might be the “new-normal”, suggesting restoration efforts are only going to increase in difficulty.

Physiological insights for plant traits: Our inclusion of a variety of plant traits in our survival analysis identified two key strategies—acquisitiveness (higher SLA, lower C:N ratio, ‘faster’ LES traits) and/or tolerating (higher WUE) water stress—in surviving through the first-year dry season. The consistent relationship between LES 1 and survival and WUE and survival point towards two separate strategies for surviving the hot-dry season: avoidance or tolerance. Higher survival among species with higher specific leaf area and a lower leaf carbon-to-nitrogen ratio (captured by LES 1) represents the success of an avoidance strategy. These LES traits are characteristic of “cheaper”, flashier, and shorter-lived leaves (Wright et al., 2004), which in the context of our study allows the plants to avoid the worst of the dry-season water stress in two

ways: 1. Most of these species with shorter lived leaves are wholly or partially drought deciduous, with the curling or dropping of leaves at the onset of water stress halting evapotranspiration and the resulting water stress much more completely than the mere closing of stomata (Gill & Mahall, 1986) and 2.) These flashier leaves with lower carbon-to-nitrogen ratios, likely represent leaves with more photosynthetic material versus structural investment, allowing them to assimilate carbon for growth (specifically root growth) more quickly than leaves on the other end of the LES spectrum. This quicker growth likely leads to deeper root development in spring and thus potentially access to water later into the summer. This second mechanism is further supported by the finding that growing season (planting – May) growth rate, is highly responsive to growing season temperature in these flashier leaves (i.e. *E. californica*, *S. nigra*, *C. oliganthus*, *S. mellifera*, and *S. apiana*), but not the longer-lived counter parts (*R. ovata*, *A. fasciculatum*, *M. laurina*, and *H. arbutifolia*; Figure 8A) and it is well established that carbon assimilation can increase with temperature up to a certain point (Berry & Bjorkman, 1980; Medlyn et al., 2002).

Alternatively, higher survival among species with a higher water-use-efficiency represents the success of a water stress tolerance strategy. Species that are more water efficient assimilate carbon with lower rates of stomatal conductance to water, are likely able to meet their metabolic and growth demands with less open stomata and/or during fewer hours of the day performing photosynthesis. This is further supported by the interaction between WUE and VPD in influencing growing season growth rate (Figure 8C). While less efficient species (*E. californica*, *M. laurina*, *S. nigra*, *S. apiana*, *C. oliganthus*, and *S. mellifera*) that experienced the upper end of growing season (January-July) VPD had the lowest growth rate, the more water efficient species (*R. ovata*, *H. arbutifolia*, and *A. fasciculatum*) showed no response of July height to VPD (Figure

8C). It is also worth noting that despite these two strategies being, at least in part, conflicting (i.e. species with high PC1 values mostly did not also have high WUE values), they showed a similar range of hazard values (data not shown), suggesting one strategy isn't necessarily better than the other across this heterogeneous site.

Adding Function to Traits: Our inclusion of a variety of plant traits in our survival analysis led to two critical findings: 1.) I show significant correlations between plant traits and survival or growth, explicitly defining the function of said traits and 2.) I find that the function of a trait can be context dependent on plant height, microsite environmental conditions, and potentially the value of other traits.

Often, research grounded in plant trait theory focuses on defining trait-to-trait correlations/relationships and assumes the function of traits. However, recent studies have shown that the assumption of consistent trait function across any scale is not necessarily valid. Here, I explicitly test the function (i.e. survival and growth) of a variety of traits in a Mediterranean shrubland restoration context. Using the survival models I developed, I show how predicted survival probability changes across the range of a single trait or trait spectra (LES), with all other trait values held constant. Namely, our analysis shows that moving across the LES spectra from conservative to acquisitive and having a higher water use efficiency both functionally provide a higher survival probability. Additionally, when using the generalized linear models developed to analyze the function of various traits on growth, our analysis shows that again moving across the LES spectra from conservative to acquisitive and having a higher water use efficiency both functionally provide a higher growth rate, as does having a higher wood density. Explicit tests of trait function like this are essential to the application of plant trait theory. However, a deeper

examination of our results reveals that defining plant trait function is not as straightforward as the idyllic ‘holy grail’ would have us believe.

While the above identified functions of plant traits are supported by our findings, our analysis shows that the degree, and even direction, of a given trait’s correlation to survival and growth is not always consistent. How a trait appears to influence survival and growth can vary depending both on the value of other traits and the microsite environmental conditions an individual was planted in. When modeling the effect of a given trait on survival or growth, I held all other trait values constant. However, in reality, traits don’t vary in isolation (no species had the same value for any of our measured traits). Let’s take, for example, two species: *Rhus ovata* and *Heteromeles arbutifolia*. Based only off the LES 1 values, both species should have low survival, whereas based only off integrated water use efficiency, both species should have relatively high survival. In reality *Rhus ovata* had one of the highest survival rates, whereas *Heteromeles arbutifolia* had the lowest survival rate. This shows that there are trait-trait interactions and/or hierarchies that are likely affecting the survival function of any given trait. Unfortunately, our study is missing these interactions and/or missing important traits determining survival in our context.

While our experiment was not equipped with enough species to model most of these interactions, without the risk of overfitting our model, I was able to model plant height-other trait interactions. Since I measured plant height on every individual, I was able to look at how this trait interacts with other traits on the individual, instead of species, scale. I found that plant height significantly interacted with LES 2 to influence survival probability and wood density to influence growth rate. These interactions led to both intraspecific differences in trait function (i.e. different survival probabilities for individuals within a species depending on height), for

both interactions, and change in the direction of a trait's correlation with survival for the height-LES interaction. Two potential interpretations of these interactions are that 1.) trait function varies with plant size and/or 2.) intraspecific differences in plant height are also indicative of intraspecific differences in LES 2 and wood density, which in turn affect survival and growth rate function. Importantly, these interpretations are not mutually exclusive, and both plant size and intraspecific trait differences have been shown to affect function. Additionally, both of these interactions disappearing in the fall analyses could indicate environmentally driven trait plasticity causing a reduction in intraspecific trait variation in all three traits.

Microsite environmental conditions are also shown to affect both the degree and direction of traits' survival and growth function. For survival, the function of wood density is environmentally dependent during both of our analysis time points (Figure 6D and 7D). Whereas, for growth, the function of LES 1 is environmentally dependent during both of our analysis time points (Figure 8A and 9A), but water use efficiency is only environmentally dependent during the first time point (planting – July; Figure 8C). Importantly, I see a consistent effect of seasonality (i.e. growing season versus dry season) affecting the context dependency for all 3 of these traits. Depending on the season, the survival function of wood density becomes dependent on different environmental factors (i.e. VPD during the growing season and temperature in the fall). Further compounding the complexity of these interactions, I see that the function of wood density in the fall can range from a slightly negative correlation with survival at more mild temperatures to strongly positive at higher temperatures (Figure 7D). While water use efficiency is also significantly interacting with VPD in the growing season time period, but to affect growth (Figure 8C), this interaction disappears for the dry season. The consistent loss of importance for VPD at the onset of the dry season likely supports the above discussed hypothesis

that at a certain low soil moisture threshold, low soil moisture overrides any VPD effects. Lastly, while LES 1's influence on growth is significantly dependent on temperature during both the growing (Figure 8A) and dry season (Figure 9a), the direction of this relationship flips across seasons. I see that in the growing season, species with lower LES 1 values are unaffected by temperature and species with higher LES 1 values grow more at higher temperatures (Figure 8A). Conversely, in the dry season, species with lower LES 1 values grow more at higher temperatures and species with higher LES 1 values are unaffected by temperature (Figure 9A).

Overall, I show at times drastic changes in function due to both trait-trait interactions and trait-environment interactions. This shows that the metaphorical 'holy grail' of plant trait theory—identifying fundamental functions of traits—is likely too simple of a framework for the ecological complexity present. Our study includes a relatively narrow range of trait values and environmental conditions and still finds a consistently context dependency of trait function, so how realistic is it to expect consistent trait-function relationships globally?

Conclusion: The findings from our study further the field of plant trait theory with a detailed field experiment that provides novel insights into restoration of southern California shrublands, while providing a foundation for the application of plant trait theory to restoration ecology. I showed that a key barrier to the restoration of southern California shrublands is survival during the first-year dry season, with two distinct periods of die-off. The first is during the early summer as the soil dries, and the second is in the late fall as the summer drought persists. Additionally, I found that there appear to be two distinct strategies, tolerance or avoidance, that may dictate where on a landscape to plant particular species: more tolerant species (i.e. *A. fasciculatum*, *R. ovata*, and *H. arbutifolia*) may benefit from microsites that are less arid, whereas more avoidant species (i.e. *E. californica*, *S. nigra*, and *C. oliganthus*) might be able to survive in more arid

microsites if the growing season temperatures allow for more growth. However, these ‘avoidant’ species appear more vulnerable to an extended dry season, a weather trend which could become pronounced with climate change. Our findings also have important contributions to plant trait theory, both by demonstrating significant relationships between traits, environment, survival and growth and providing concrete data highlighting the context dependency of function for most of the traits included in our analyses. This indicates that the function of a given trait cannot be taken for granted, and the field of plant trait ecology might be better served by redefining the ‘holy grail’ as fundamental relationships between traits and other traits and/or environmental conditions in determining function.

In addition to the above intellectual impacts of this study, I believe that the models developed here also provide the foundation for future applications. For example they demonstrate the potential to create survival probability maps prior to a restoration project, at new locations and with new species, using available or easy-to measure plant traits, freely available digital elevation models and nearby weather station data. While more data needs to be collected to provide out of sample model validation and refinement, this application could help bridge the divide between trait theory and its usefulness in restoration. So did I find the metaphorical holy grail? No... but what is that glimmer in the shrub over there?

F. References

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G. Tables and Figures

Table 1: Table of species used in outplanting experiment and number of surviving individuals, and percent in parentheses, by December 2020 and 2021.

Species	Community	Leaf Persistence	Number Planted	December 2020 Survival	December 2021 Survival
<i>Adenostoma fasciculatum</i>	Chaparral	Evergreen	144	26 (18%)	6 (4%)
<i>Ceanothus oliganthus</i>	Chaparral	Evergreen	254	11 (4%)	1 (0.4%)
<i>Heteromeles arbutifolia</i>	Chaparral	Evergreen	110	3 (3%)	0 (0%)
<i>Malosma laurina</i>	Chaparral	Evergreen	88	6 (7%)	2 (2%)
<i>Rhus ovata</i>	Chaparral	Evergreen	196	24 (12%)	7 (4%)
<i>Encelia californica</i>	Sage scrub	Drought deciduous	204	34 (17%)	17 (8%)

<i>Hesperoyucca whipplei</i>	Sage scrub	Evergreen	248	67 (27%)	46 (19%)
<i>Salvia apiana</i>	Sage scrub	Drought deciduous	98	9 (9%)	5 (5%)
<i>Salvia mellifera</i>	Sage scrub	Drought deciduous	128	23 (18%)	10 (8%)
<i>Sambucus nigra</i>	Sage scrub	Winter deciduous	154	21 (14%)	14 (9%)

Table 2: Outputs from the early summer cox proportional hazards model.

Characteristic	HR¹	95% CI¹	p-value
PC1	0.87	0.77, 0.98	0.026
PC2	2.29	1.32, 3.98	0.003
height	0.97	0.96, 0.98	<0.001
wue	0.89	0.79, 1.00	0.045
wood_density	0.45	0.15, 1.37	0.2
vpd	3.86	2.91, 5.12	<0.001
soil_moisture	0.18	0.07, 0.48	<0.001
PC2:height	0.98	0.96, 0.99	0.008
wood_density:vpd	1.25	0.94, 1.65	0.13
vpd:soil_moisture	1.55	1.21, 1.99	<0.001

¹ HR = Hazard Ratio, CI = Confidence Interval

Table 3: Outputs from the fall cox-proportional hazards model.

Characteristic	HR¹	95% CI¹	p-value
PC1	0.87	0.78, 0.96	0.009
PC2	1.40	1.10, 1.80	0.007
wue	0.84	0.76, 0.92	<0.001
wood_density	41,321	454, 3,759,762	<0.001
temperature	1.10	0.97, 1.24	0.13
soil_moisture	0.82	0.73, 0.92	<0.001
vpd	1.99	0.76, 5.25	0.2
height	0.99	0.98, 1.00	0.022
wood_density * temperature	0.89	0.84, 0.93	<0.001

¹ HR = Hazard Ratio, CI = Confidence Interval

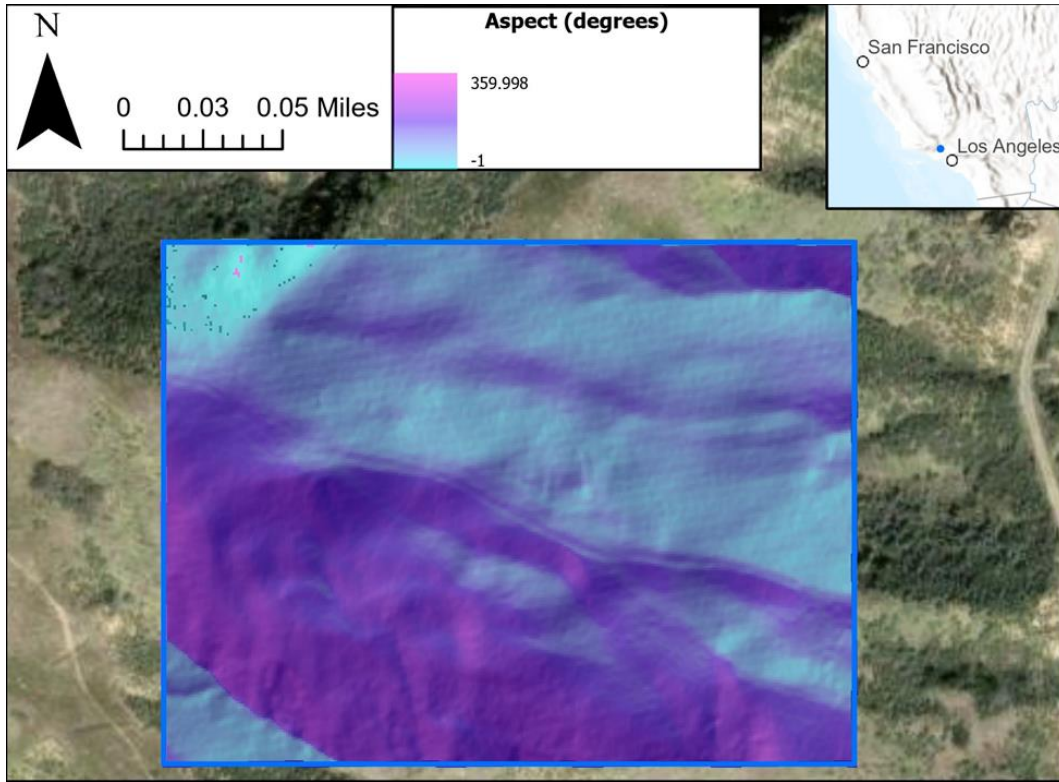


Figure 7: Map of study site with an opaque aspect layer overlaid on a hill shade elevation model to show topographic heterogeneity across study area.

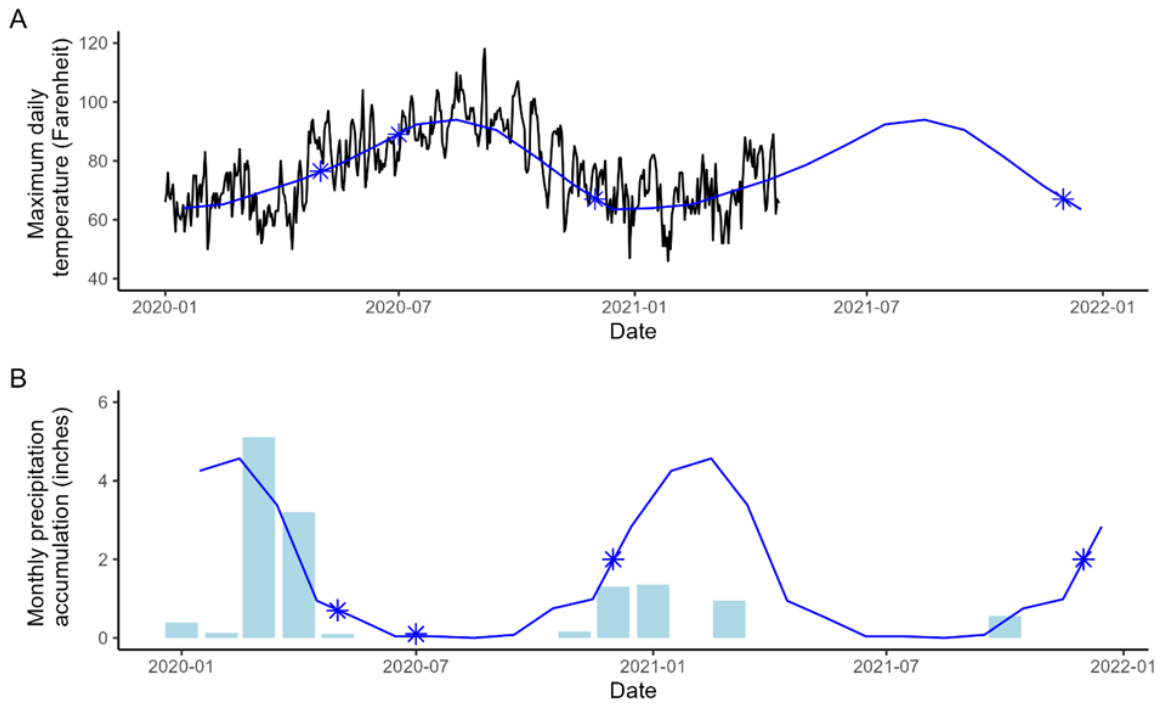


Figure 8: Time series of maximum daily temperature (A) and monthly precipitation (B) for the study period. Data from nearby Temescal weather station are shown in black lines for maximum daily temperature (A) and light blue bars for monthly precipitation (B). The station had a sensor malfunction and stopped recording temperature in mid-March 2021. Blue lines are the 30-year normal monthly maximum temperature (A) and total monthly precipitation (B). Blue stars represent approximate census dates.

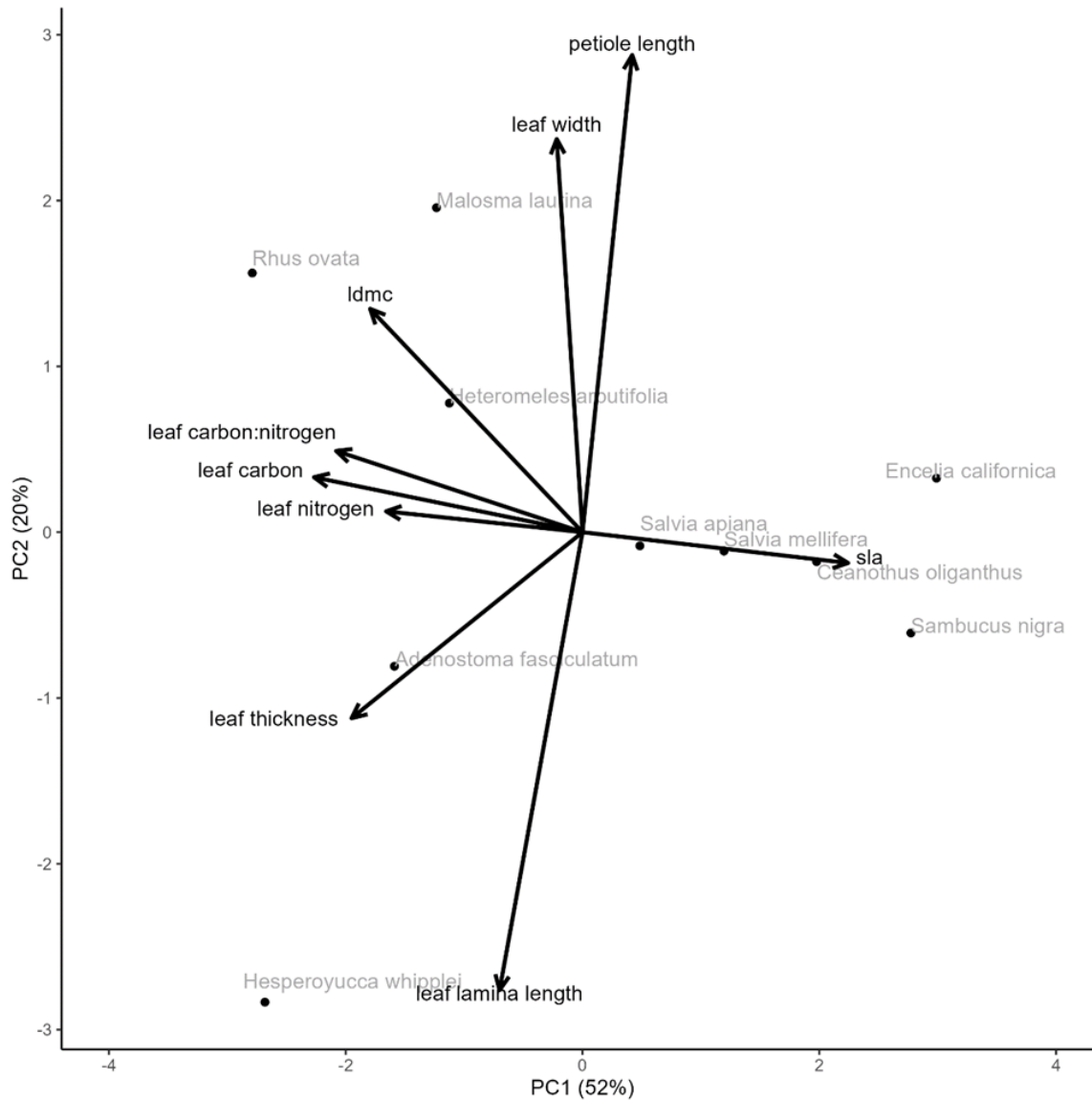


Figure 9: Biplot of a principal components analysis developed to represent the leaf economic spectrum (Wright et al., 2004). Nine traits were included in the PCA. Arrows show the trait loadings (multiplied by 5 for better visualization) on the first two axis and black dots and labels show where each species falls on the biplot. Black dots are the actual PC1 and PC2 values, but the labels are artificially moved to increase interpretability. Numbers in the parentheses are the percent of variance explained by each axis. Abbreviations are for specific leaf area (sla) and leaf dry matter content (ldmc).

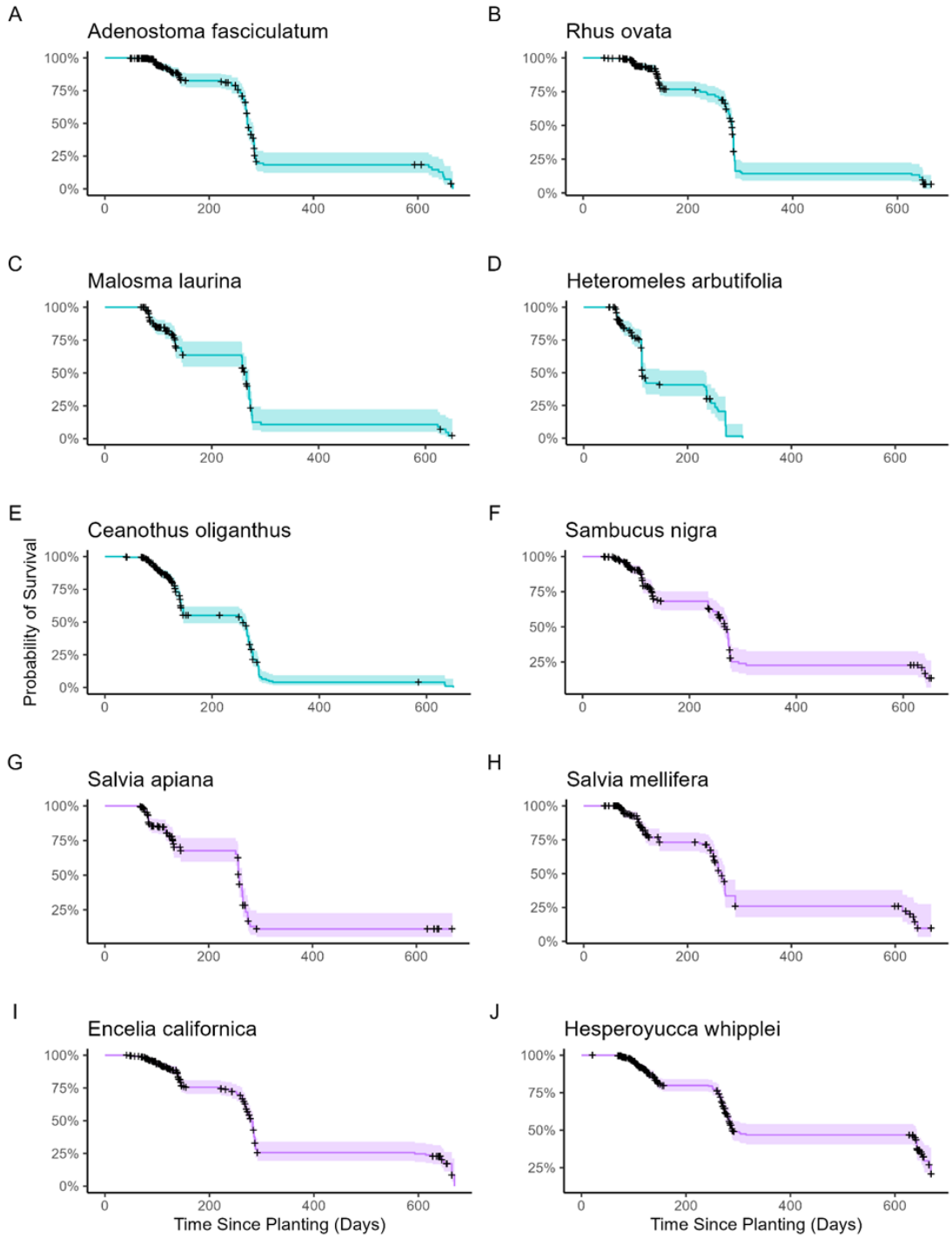


Figure 10: Kaplan-Meier survival curves for all ten restoration species. Transparent ribbons are 95% confidence intervals and black pluses are right censored data. Data was censored either due to gopher kill or still being alive at the end of the study period. Species survival curves are colored by the community type where they tend to be most dominant: either chaparral (blue) or sage scrub (purple).

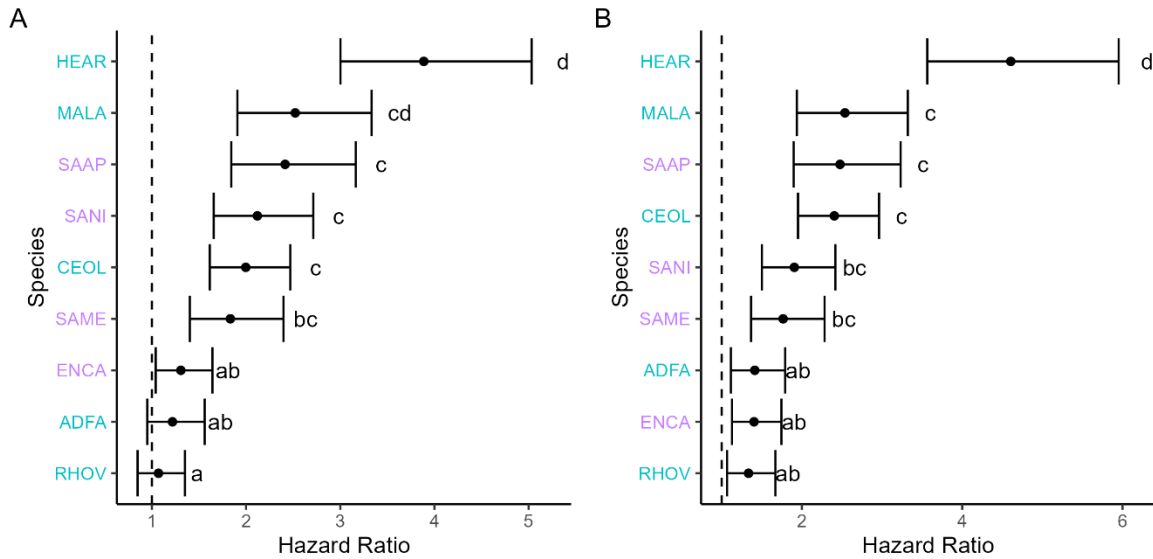


Figure 11: Hazard ratio of each species in comparison to our best surviving species *Hesperoyucca whipplei* from planting to December 2020 (A) and planting to December 2021 (B). Dots represent the mean hazard ratio and error bars are 95% confidence intervals. Non-matching letters indicated significant differences in hazard rates from non-overlapping 95% confidence intervals. Species whose error bars do not cross 1 (dashed line) are significantly more likely to die at any given time than *Hesperoyucca whipplei*. The hazard ratio can be interpreted as the number of individuals for a given species that are dying for every *Hesperoyucca* that dies at any given point in time. The higher the number, the greater the number of individuals dying. Species are colored by the community type where they tend to be most dominant: either chaparral (blue) or sage scrub (purple).

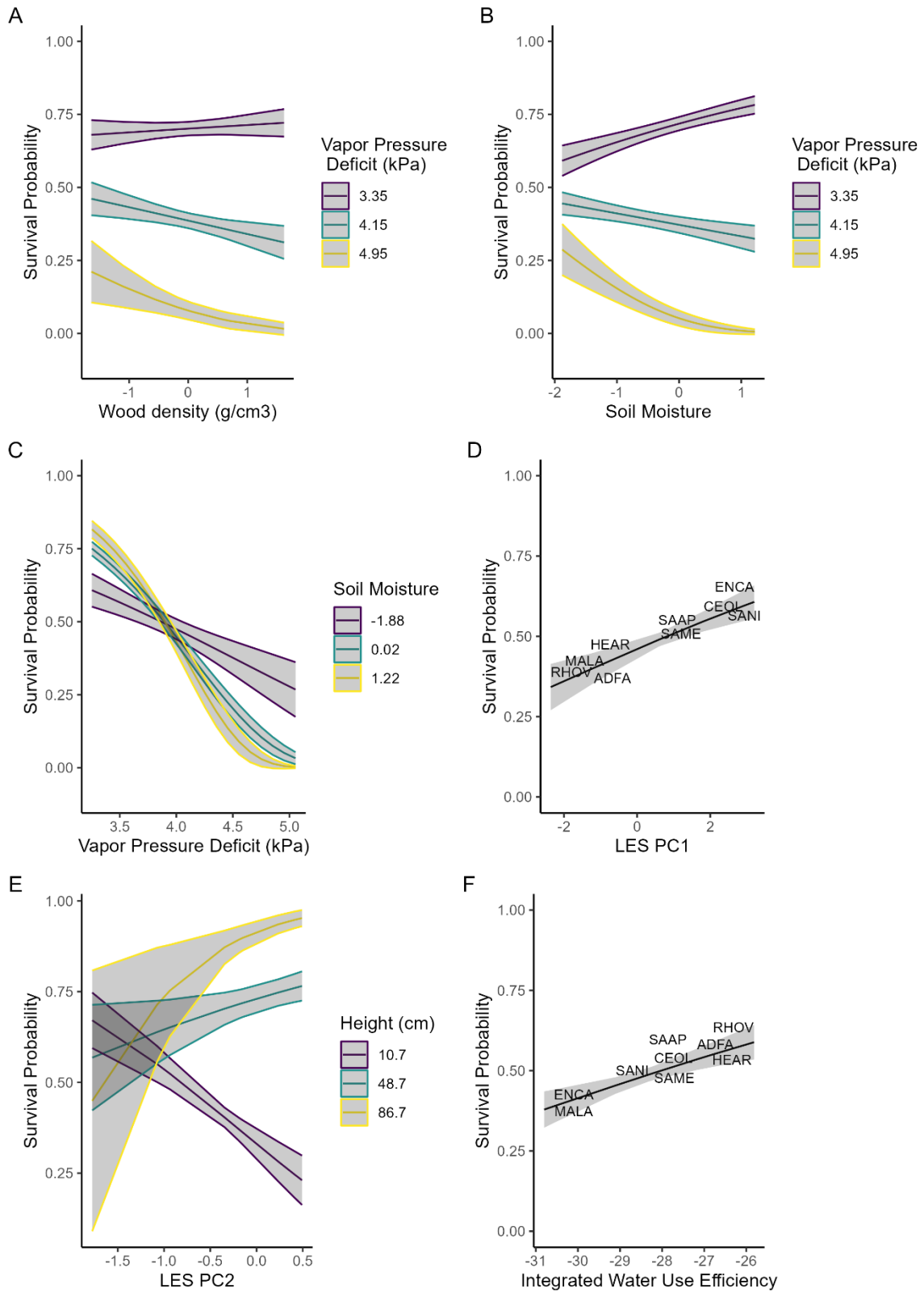


Figure 12: Partial dependency plots for the planting to July cox-proportional hazard model, showing how changing one, or two for interactions, variables while holding all other independent values at the mean value, affects survival probability. The ranges shown at the x-axis are spanning from the minimum to maximum values represented in our data set. For interaction plots, the three values chose for modeling are the 10th quantile, median and 90th quantile values in our data. Ribbons on the line graphs are 95 % confidence intervals. For single variable panels with species, species are shown on their x-axis value for that trait, but are modeled all having the median trait values for all other traits, not their true values. Abbreviations: *Adenostoma fasciculatum* (ADFA), *Ceanothus oliganthus* (CEOL), *Encelia californica* (ENCA), *Heteromeles arbutifolia* (HEAR), *Malosma laurina* (MALA), *Rhus ovata* (RHOV), *Salvia apiana* (SAAP), *Salvia mellifera* (SAME) and *Sambucus nigra* (SANI).

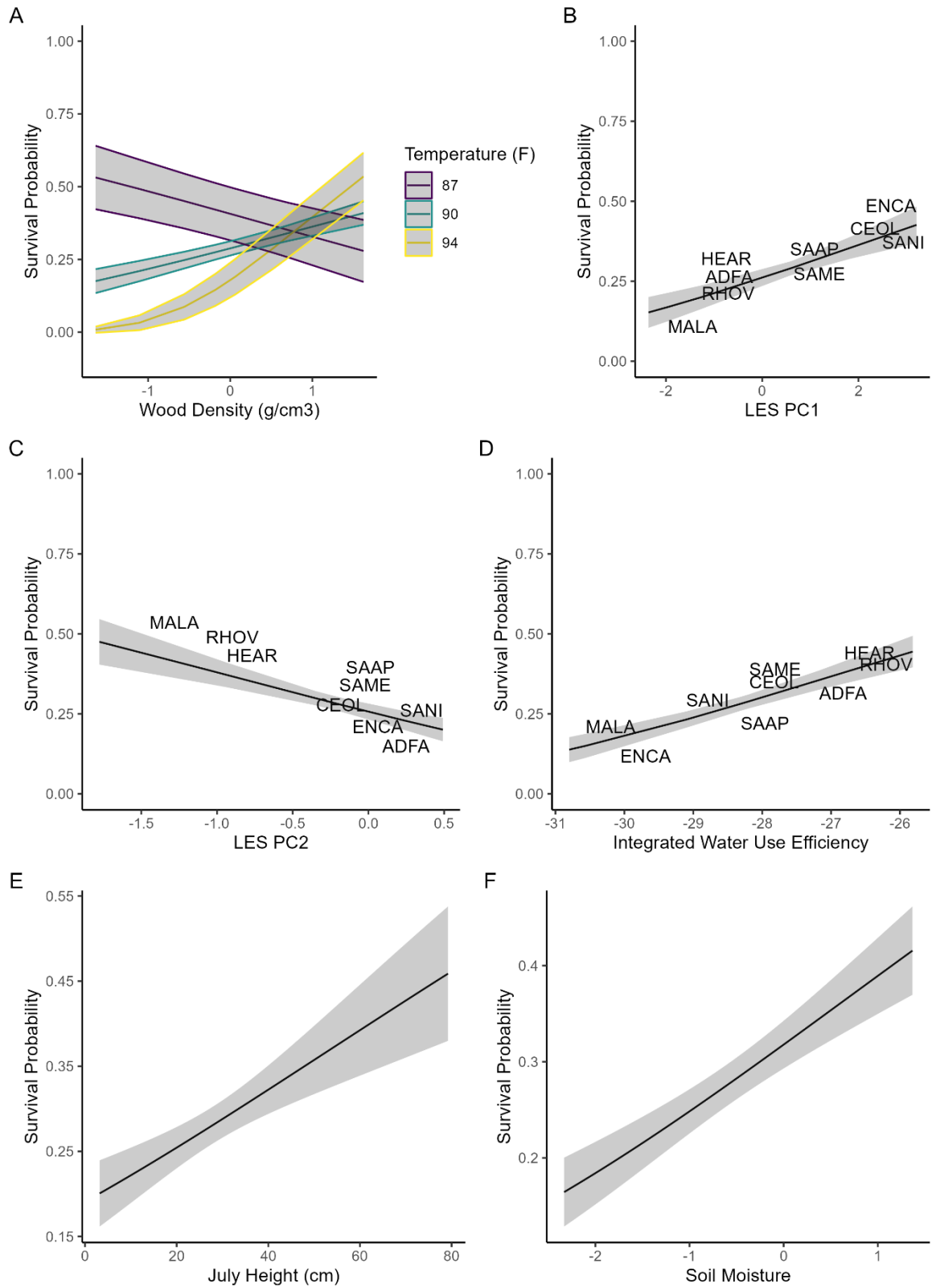


Figure 13: Partial dependency plots for the July to fall cox-proportional hazard model, showing how changing one, or two for interactions, variables while holding all other independent values at the mean value, affects survival probability. The ranges shown at the x-axis are spanning from the minimum to maximum values represented in our data set. For interaction plots, the three values chose for modeling are the 10th quantile, median and 90th quantile values in our data. Ribbons on the line graphs are 95 % confidence intervals. For single variable panels with species, species are shown on their x-axis value for that trait, but are modeled all having the median trait values for all other traits, not their true values. Abbreviations: *Adenostoma fasciculatum* (ADFA), *Ceanothus oliganthus* (CEOL), *Encelia californica* (ENCA), *Heteromeles arbutifolia* (HEAR), *Malosma laurina* (MALA), *Rhus ovata* (RHOV), *Salvia apiana* (SAAP), *Salvia mellifera* (SAME) and *Sambucus nigra* (SANI).

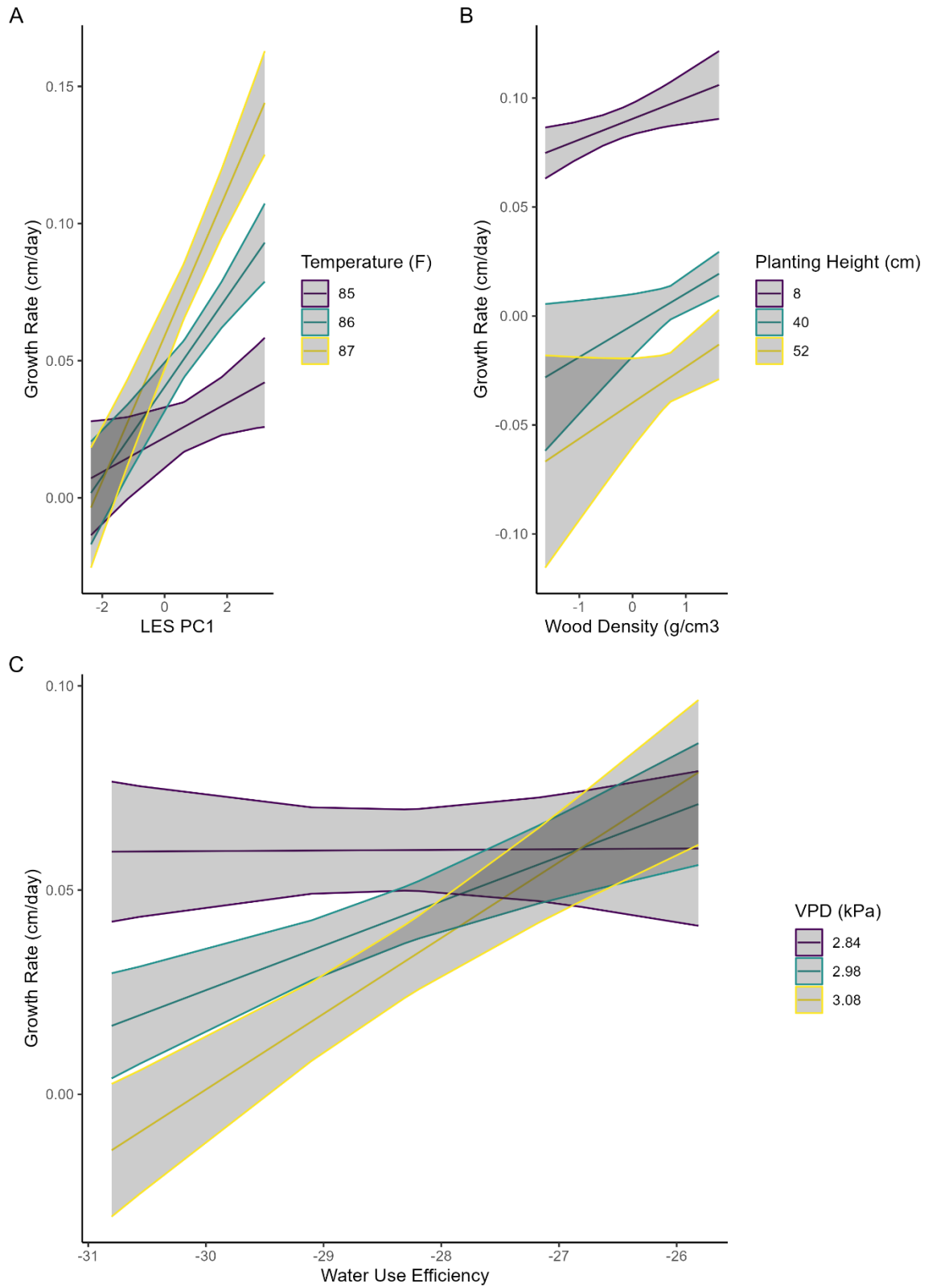


Figure 14: Partial dependency plots for the planting to July growth model, showing how changing one, or two for interactions, variables while holding all other independent values at the mean value, affects growth rate. The ranges shown at the x-axis are spanning from the minimum to maximum values represented in our data set. For interaction plots, the three values chose for modeling are the 10th quantile, median and 90th quantile values in our data. Ribbons on the line graphs are 95 % confidence intervals.

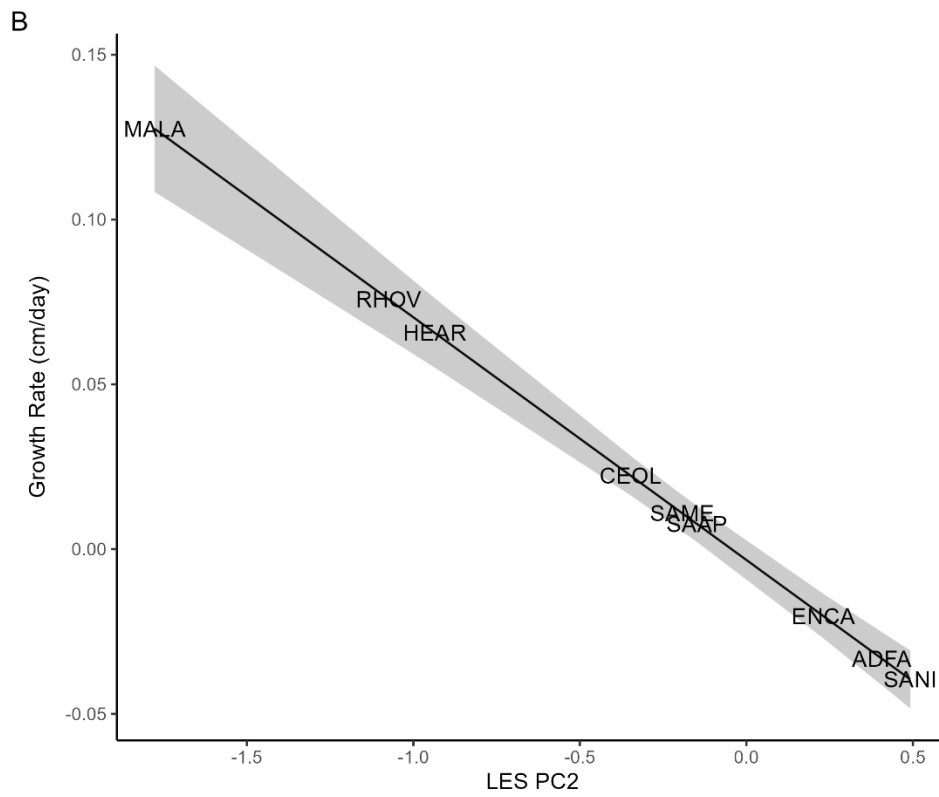
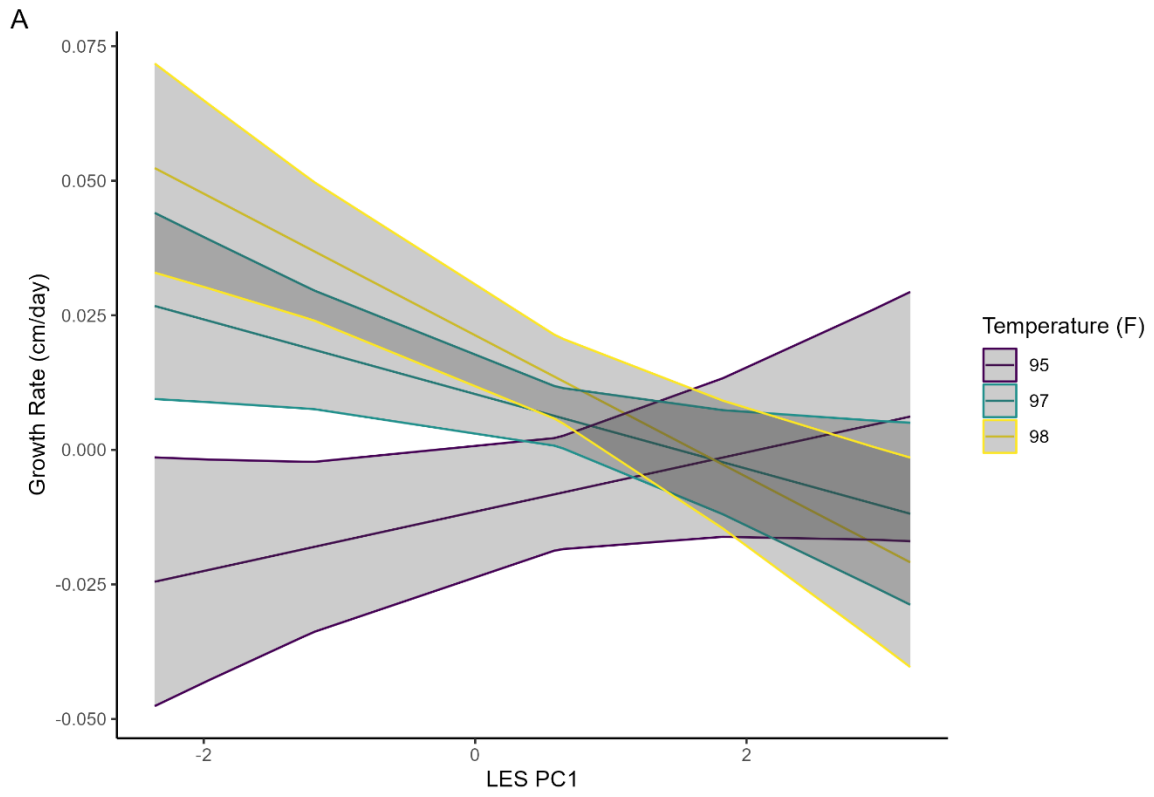


Figure 15: Partial dependency plots for the July to fall growth model, showing how changing one, or two for interactions, variables while holding all other independent values at the mean value, affects growth rate. The ranges shown at the x-axis are spanning from the minimum to maximum values represented in our data set. For interaction plots, the three values chose for modeling are the 10th quantile, median and 90th quantile values in our data. Ribbons on the line graphs are 95 % confidence intervals. For single variable panels with species, species are shown on their x-axis value for that trait, but are modeled all having the median trait values for all other traits, not their true values. Abbreviations: *Adenostoma fasciculatum* (ADFA), *Ceanothus oliganthus* (CEOL), *Encelia californica* (ENCA), *Heteromeles arbutifolia* (HEAR), *Malosma laurina* (MALA), *Rhus ovata* (RHOV), *Salvia apiana* (SAAP), *Salvia mellifera* (SAME) and *Sambucus nigra* (SANI).

H. Appendices

Appendix 1: Environmental Random Forest Models

Random forest models were developed to predict each of the three environmental variables (i.e. soil moisture, temperature and vapor pressure deficit (VPD)) across the planting landscape. Each model was tuned to the number of variables to try at each split (mtry input) to optimize the out of bag error rate (tuneRF function in randomForest package). The models were then trained on a random subset of 80% of the data and tested for accuracy on the remaining 20% of the data. Model performance was evaluated by the amount of variation it explained in the training dataset and then calculating the root mean square error when tested with the testing dataset.

The soil moisture model was developed using all 13 of the topographic variables and the date of measurement. Additionally, the soil moisture data measured from our soil moisture probes were grouped by day and then mean centered prior to input. This means that instead of predicting raw soil moisture values, we are predicting the relative moisture of a location at a given day compared to the mean value measured that day. The 80% training data was selected at the plot plus day level, not just the plot level. This may have the downside of leading to no true out-of-sample testing data (i.e. a plot that doesn't have any values in the training dataset) but helped address the issue of our limited sample size. Additionally, because we are mainly interested in a

plot's relative wetness to other locations across the landscape and this did change over time (e.g. the plot that was the wettest at the start of measurement wasn't necessarily the wettest for the whole time period), we believe this approach still creates a valid testing dataset. Additionally, evaluation of variable importance showed that the saga wetness index, topographic position value and date were the three most important values with similar increases in mean square error and node purity when removed. This shows that our model is accounting for both spatial and temporal differences to an equal degree.

The temperature model was developed using all 13 of the topographic variables, the maximum daily temperature from the nearby Temescal weather station, and the date of measurement. Additionally, because we had some abnormally high temperature recordings due to radiation effects, the ibutton measured temperatures were first filtered to exclude measurements greater than 10F of the daily maximum temperature measured at the Temescal weather station. Again the 80% training data was selected at the plot plus day level, not just the plot level. Evaluation of the variable importance showed that the maximum weather station temperature and date explained by far the most variation in the data. This was initially concerning that we were only predicting temporal, not spatial, changes in the data. However once considering that the vast majority of the variation in the data occurs temporally, an average of 72F difference between the minimum and maximum measured daily maximum at our plots, not spatially, an average of only 14F difference between minimum and maximum measured temperature at any given day, this becomes more reasonable. Especially, when looking at the predicted values show that the model is still predicting spatially different temperatures at any given day.

Lastly, VPD was calculated using the same filtered temperature data as above. Then the svp was calculated as $610.78 * \exp(\text{temperature}/(\text{temperature} + 237.3) * 17.2694)$ and vpd was calculated as $(\text{svp} * (1-\text{humidity}/100))/1000$. The model was then developed using all 13 of the topographic variables and the date of measurement. Again, the 80% training data was selected at the plot plus day level. Evaluation of variable importance once again showed date being the most important variable, but we again confirmed that our model was predicting differences in both space and time.

Appendix 2: Model selection

Table comparing AIC of best model from each season

Season	AIC
Plating – July	6283
Planting-May	6275.625
June-July	6228.853
July-December	4892.442
July-September	4940.952
October-December	4886.983

Appendix 3: Additional Survival Analyses

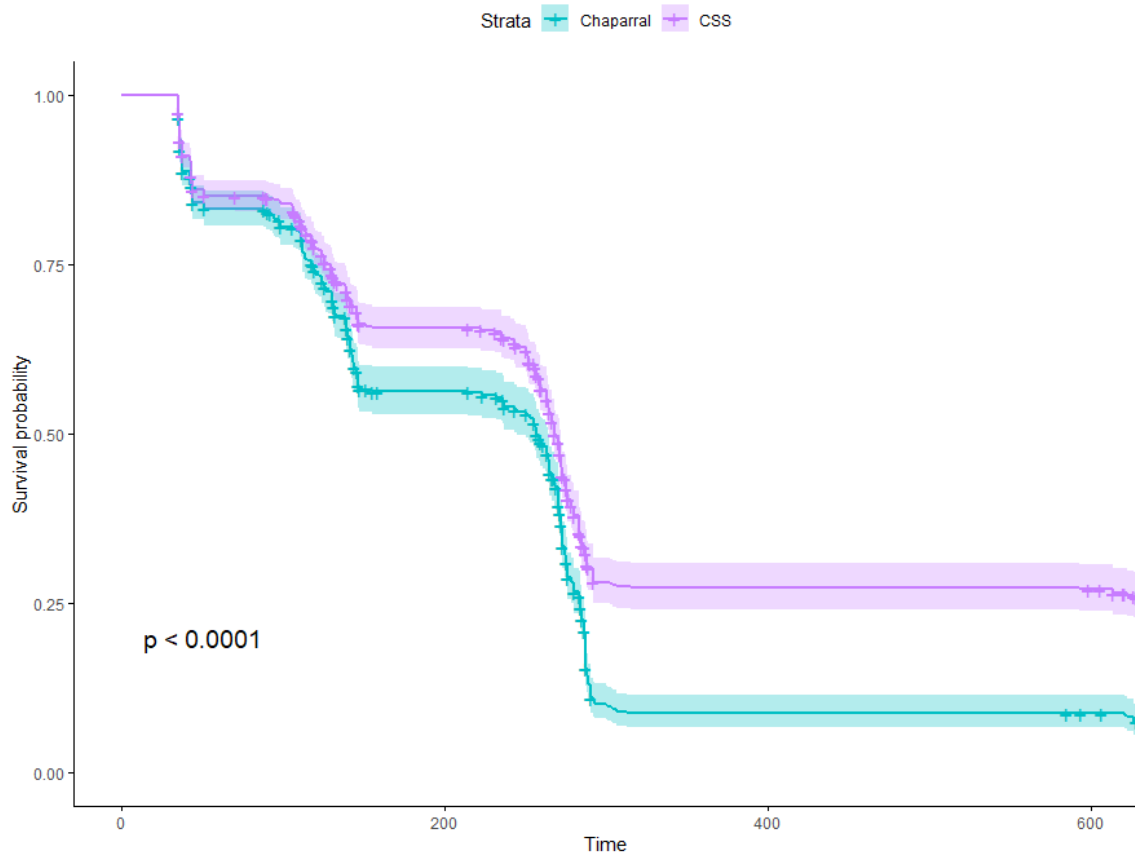


Figure S1: Kaplan-Meier survival curves for sage scrub (purple) and chaparral (blue) species grouped together. Transparent ribbons are 95% confidence intervals and pluses are right censored data. Data was censored either due to gopher kill or still being alive at the end of the study period.

IV. Lord of the Flies or Neverland? Testing the efficacy of ‘restoration islands’ in southern California shrubland restoration.

A. Abstract

Habitat degradation and conversion have become a ubiquitous problem globally and are expected to increase with climate change. In areas where degradation and conversion have already occurred, ecological restoration – defined by the Society for Ecological Restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed – provides a promising avenue to conserve biodiversity and ecosystem function. Influenced by competition and niche partitioning theory, single plant plantation and/or random style planting has been the restoration status quo for decades. Recent focus on plant facilitation, however, has led to the introduction of promising new techniques. One such technique introduced in the last decade and a half is the idea of planting restoration islands that can then nucleate out. Here, we test this approach in a southern California shrubland restoration experiment through the establishment of fifteen, twenty-five square meter plots with eighty plants each. We obtained a range of planting densities after natural transplant shock and then monitored monthly survival, soil moisture, and plot and ambient photosynthetically active radiation. We find that there is a consistent positive influence of higher planting density on seedling survival. Additionally, we find that by year 2, plots planted at higher density have exerted more of a plot-level influence on environmental conditions. These findings suggest that future restoration efforts in southern California shrublands might have more success if they adopt a restoration island approach.

B. Introduction

Throughout the history of plant restoration, plantation and/or random style planting of a single individual at any given location has been the status quo of active restoration (Barbier et al., 2008; Golet et al., 2008; Lamb et al., 2005; Nolan et al., 2021; Rodrigues et al., 2009;

Stapleton et al., 2023). This approach is steeped, whether intentionally or unconsciously, in classical competition theory. It is often assumed that any two individuals planted close enough together to influence each other will likely negatively impact each other's performance (Craine & Dybzinski, 2013; Ford & Sorrensen, 2018; Park et al., 2003; Tilman & others, 1990). While the theory of niche partitioning suggests that it is possible for two individuals to coexist with little adverse effects (Finke & Snyder, 2008; Kitajima & Poorter, 2008; Roughgarden, 1976), overall it still supports the restoration status quo. However, traditional ecological knowledge has also recognized the concept of facilitation in plant communities for centuries. While ecological literature on facilitation dates back to the early twentieth century (Clements, 1916) and has been continuously investigated since (i.e. Bormann, 1966; Compton, 1929; Harris & Brock, 1972; Muller & Muller, 1956; Polunin, 1936; Shreve, 1931; Watt, 1947; Went, 1942; but see Callaway, 1995 for detailed chronology), it was largely overshadowed by the ecological paradigms of competition and allelopathy. However, thanks in large part to the championing of a few dedicated ecologists (Brooker et al., 2008; Callaway, 1995, 1997; Callaway & Pugnaire, 2007; Callaway & Walker, 1997) facilitation in plant communities has become a much more widely acknowledged phenomenon that commonly occurs (Brooker et al., 2007; Bruno et al., 2003; Callaway & Pugnaire, 2007; Michalet & Pugnaire, 2016; Soliveres et al., 2015; Van der Merwe et al., 2021; Zhang & Shao, 2013). Following suite, restoration practitioners started to incorporate facilitation into accepted practices, primarily through the use of already existing nurse plants (Filazzola & Lortie, 2014; Franco & Nobel, 1989; Padilla & Pugnaire, 2006). Yet the practice of using established nurse plants is not viable in degraded ecosystems where there are no pre-existing woody plants to act as 'nurses'. Planting high-density restoration islands (i.e.

nucleation restoration) has also become a predominant focus of restoration research in woody plant dominated landscapes (Albornoz et al., 2013; Corbin & Holl, 2012; Reis et al., 2010).

Nucleation theory was originally developed in physical chemistry to describe how during phase transitions of materials, materials can expand when they exceed a critical size above which further growth reduces the free energy in the system (Lothe & Pound, 1962; Oxtoby, 1992). A similar phenomena was observed in ecological succession, where an early establishing individual, or group of species, form a foci that cause changes in surrounding environmental conditions (Clements, 1916; Connell & Slatyer, 1977), allowing for the establishment of other species that eventually replace the initial foci species (Yarranton & Morrison, 1974). Nucleation as an ecological theory has since been applied to restoration ecology, with the idea of establishing native clusters that then alter abiotic conditions and provide new seed input (both directly and indirectly by creating habitat for animal dispersal) allowing for subsequent passive expansion of the native cluster (Albornoz et al., 2013; Corbin & Holl, 2012; Reis et al., 2010).

Tested primarily in tree- and grass-dominated ecosystems, plants in a nucleated planting have been shown to have comparable, if not higher, levels of individual survival than non-nucleated planting, and be more cost-effective (Corbin & Holl, 2012). These studies primarily compare the nucleation approach to passive restoration or plantation style restoration, holding planting density constant (Corbin & Holl, 2012; De Oliveira Bahia et al., 2023, 2023; Reis et al., 2010). However, as restoration ecology moves towards accepting the nucleation planting approach as a viable restoration option, research should start focusing on how to optimize this approach. Previous studies have investigated optimizing aspects such as island size (Cole et al., 2010; Zahawi & Augspurger, 2006), natural versus artificial structure to ameliorate environmental conditions and encourage seed dispersal via fauna (De Oliveira Bahia et al., 2023), and

hypothesized a benefit of increasing nuclei edge effects through closer arrangement of multiple nuclei (Hulvey et al., 2017). However, a key tenant of nucleation planting—higher planting density—has had much less attention, but begs a key question: Is denser always better, or is there a density threshold at which competition outweighs any facilitation?

There have been recent calls to apply nucleation theory to dryland ecosystems to test its more widespread efficacy (Hulvey et al., 2017). Southern California shrublands represent an excellent dryland ecosystem to apply nucleation restoration theory and specifically address the planting density question posited above. Southern California shrublands occur in a Mediterranean environment with hot-dry summers that have been shown to cause widespread mortality of restoration species (Allen et al., 2018; VinZant, 2013, Dewees et al., In prep). Additionally, these shrublands are comprised of two main vegetation assemblages as characterized by Barbour et al (2007): sage scrub and chaparral. The sage scrub community is characterized by partially closed canopies of shrub and sub-shrub species 0.5-2m in height, that are also fully or partially drought deciduous, and often have whitish green leaves often with some degree of reflective trichomes or a glaucous surface (Rundel, 2007; Westman, 1981). The chaparral vegetation community is characterized by an extremely dense and closed canopy of evergreen, sclerophyllous shrubs 1.5-3m in stature (Gray, 1982; Keeley, 1998; Parker et al., 2016). Chaparral shrub assemblages tend to be taxonomically and physiologically diverse. Sage scrub and chaparral species can form discrete communities and intermingle on the same slopes, especially in years following fire (Westman, 1981). Sage scrub species are often viewed as early successional in disturbed chaparral (Hanes, 1971).

As mentioned above, benefits of a nucleation approach are primarily through facilitation (via both creating more favorable abiotic conditions and allowing for more seed dispersal) by the

individuals planted in the initial cluster. In applying nucleation theory to southern California shrubland restoration, we might expect a secondary density benefit on survival of the planted individuals, especially for the co-planted chaparral species. This is because passive restoration of chaparral species has been shown to have very low potential (Allen et al., 2018; Ma unpublished), a good portion of chaparral species have low dispersal ranges (Keeley, 1991), and many species have fire dormant seeds (Keeley, 1991). This, coupled with previous findings of moderate to high sage scrub survival, but low chaparral survival in a non-nucleation restoration context (Deweese et al., In prep), suggests that high-density plantings, could facilitate higher growth and survival of chaparral seedlings where the faster-growing, successional sage scrub individuals create less arid microsites as they establish. This reasoning leads us to ask the following questions: 1.) Does increasing nuclei planting density lead to competition, facilitation, or no interaction and how does that differ for sage scrub versus chaparral species? And 2.) As foci establish, do they create more favorable environmental conditions that allow for further establishment and expansion? Furthermore, given that a major constraint to restoration of woody species in degraded chaparral is the high density of invasive grasses (Allen et al., 2018; Eliason & Allen, 2008; Ma unpublished), we also asked (3) How does the density of planting influence cover of invasive grasses? Lastly, because, previous work (Deweese et al, In prep) found there to be a correlation between plant functional traits and interspecific survival differences in a nearby restoration study, we asked (4) Do functional traits of sage scrub and chaparral species influence the effect of planting density on species survival?

C. Methods

Study site: The study area is a topographically homogenous, southwest facing slope ranging from 480m -508m in elevation (approximate co-ordinates of 118.7601°W 34.4984°N) and

located in the Los Padres National Forest, Ventura County, California (Figure 1). Climate normals from the nearby Temescal (LPF; TCLC1) weather station covering the years of 2000 to 2020 characterize this region as having hot-dry summers and cool-wet winters, with winter lows of 0.6C, summer highs of 41C and highly variable rainfall averaging 326 mm/yr during the period. Currently dominated by non-native annual species (i.e. *Avena fatua*, *Bromus* sp., *Rapistrum rugosum*) and a few isolated native-shrubs (*Rhus ovata*, *Salvia leucophylla*, *Artemisia californica*, and *Hesperoyucca whipplei*), but historically shrub dominated (Deweese et al., 2022), this landscape represents a southern California shrubland converted to invasive annual grassland by fire and drought. Additionally, this study site is representative of chaparral microsites that are the most challenging for restoration—arid, low elevation (for chaparral), southwest facing slopes that are close to roads where invasive species proliferate (Deweese et al., 2022; Deweese et al., In prep). Thus it presents an ideal area for investigating the potential for restoration nuclei to ameliorate stressful abiotic conditions and the biotic stress of competition with nonnative grasses.

Experimental design: We planted 15 5x5m plots with a mix of chaparral and sage scrub species as listed in Table 1. Species combinations were based on evaluating if sage scrub differentially influenced different groupings of chaparral species (Table 1, community 1 versus community 2) and if facilitation of chaparral survival is specific to sage scrub species (Table 1, communities 1 and 2) or just a higher planting density in general (Table 1, community 3). Seeds for 10 of the 13 species were collected from mature individuals within 5 miles of the study site. They were grown for approximately 1-year at the UCSB Biological greenhouses in D40H 2.5” x 10” containers (Stuewe and Sons Inc.). Seeds for *Malosma laurina* and *Adenostoma fasciculatum* were not collected from within 5 miles of the study site because the limited number of mature

individuals didn't allow for responsible seed collection. *Malosma laurina* seeds were collected from within the Los Padres National Forest at a similar elevation to the west of the site and grown as stated above. Due to limited germination success and high seedling mortality in the greenhouse, *Adenostoma fasciculatum* seedlings were purchased from the Tree of Life Nursery in San Juan Capistrano, California, in a mix of 1- and 2-gallon pots. Additionally, because we missed the seed collection window for *Artemisia californica*, seedlings were purchased from the Santa Barbara Natives plant nursery in Santa Barbara, California, in 2-inch pots. All seedlings were moved from greenhouses to raised tables outside by June 2021, ensuring they had over 6 months of "hardening-time" prior to field transplantation. The seedlings did not receive an additional "hardening-time" at the field site prior to field transplantation.

Prior to planting, plots were weeded and had weed cloth secured over them in fall of 2019. They were then planted in January-February of 2022 with 80 individuals each, for a total of 1200 individuals planted. Before outplanting the weed cloth was removed from the plots. Each plant was then planted with a 50/50 mix of greenhouse soil and native soil from the holes dug for planting and watered in with 500ml of water. All surviving plants were also given an additional 500ml of water in both late February and May 2022 because of a lack of rainfall. Any non-native plants that recruited into the plots were weeded out on a monthly basis through May 2022 so that competition was not initially affecting outplant survival. One final additional weeding was performed March 2023.

Plots were randomly assigned one of three planting communities, with each community having 5 replications (Table 1). However, between planting and the first census date in April, all plots experienced varying levels of mortality due to transplant-shock. This led to each plot having a unique planting density (Table 2), going into the stressful summer where widespread

mortality was expected. Therefore, we were able to test nucleation effects as a function of differences in initial ‘foci’ density.

Data collection: Starting in April 2022, we measured soil moisture to 30 cm until the soil was too dry to penetrate with a time domain reflectometry (TDR) probe and then down to 15cm (Table 3). We also measured photosynthetically active radiation (hereafter PAR), at the ground and above all plants in five random locations of each plot. These measurements were taken monthly, as site access and equipment functionality allowed, through November 2022, then again in March and September 2023 (Table 3). A road closure in winter 2023 due to a large landslide, limited site access in spring/summer 2023.

Seedling survival was censused during the same periods as soil moisture and PAR mentioned above. Additionally, percent cover of all species present in the plots, as well as by group (i.e. sage scrub, chaparral, native herbaceous species, and non-native species) was recorded in March and May 2023 and January 2024. However, the non-native percent cover in March 2023 is not used in any of the analyses, because percent cover data was collected after the March 2023 weeding was performed. Due to an extensive seedbank and 2023 winter precipitation, there was strong non-native germination and growth after the March 2023 weeding. Therefore, we used the May 2023 and January 2024 non-native percent cover in analyses. Natural recruitment within the plot, as well as into half-meter by half-meter weeded plots, installed in May 2023 adjacent to each plot, was surveyed in January 2024. These adjacent plots were installed to evaluate the potential of nuclei to spread outside of the main planted area when non-native grass competition was removed. They were created by hand weeding all cover (living and thatch) to create half-meter by half-meter plots of bare ground. These plots were hand weeded in May of 2023 and then monitored for the remainder of the study. Weeding was necessary in these adjacent plots

because of the very dense growth of non-native grasses in the surrounding ‘degraded’ area. All native seedlings present were recorded.

Shrub Traits: Our analysis also included a variety of measured plant traits, described in detail elsewhere (Deweese et al., In prep), including leaf petiole length, leaf width, leaf dry matter content, leaf carbon per unit mass, leaf nitrogen per unit mass, leaf carbon to nitrogen ratio, leaf thickness, leaf lamina length, specific leaf area, wood density, and delta 13 carbon (photosynthetic fractionation of carbon-13 isotopes) for integrated water use efficiency (Appendix 1). All traits, were measured on a minimum of 5 mature individuals within 5 miles of our restoration site during winter/spring 2016-17. Species averages for all traits were then used for subsequent analyses. Additionally, because most of the leaf traits were highly correlated (i.e. specific leaf area, leaf dry matter content, leaf thickness, petiole length, leaf lamina length, leaf width, leaf carbon to nitrogen ratio, leaf nitrogen per unit mass and leaf carbon per unit mass) they were dimensionally reduced into a principal components analysis. The first two axes of this PCA were then used in our trait analyses (henceforth LES 1 and LES 2 [leaf economic spectrum]; Figure 2).

Statistical Analysis: Analysis of measured factors contributing to survival was performed with a survival analysis framework, using the survival and coxme packages in R. Specifically, we used cox-proportional hazards models to analyze the effect of April density, soil moisture, PAR, and plant traits on monthly survival. The outputs of the cox-proportional hazards models is a hazard ratio that shows the effect of increasing the independent variable one standard deviation from the mean. For example, a hazard ratio of 0.9 for April density means that when a plot’s April density was one standard deviation higher than the mean, that plot had 0.9 times the amount of mortality. First, we ran single variable cox-proportional hazards models to test the

influence of April density on whole plot survival from April 2022 to November 21st, 2022, survival for sage scrub individuals only and survival for chaparral individuals only. Next, we ran multivariable cox-proportional hazards models testing the combined influence of April density, soil moisture and proportion of ambient PAR hitting the plot. To isolate the effect of plot-level differences in soil moisture and PAR at any given time, they were both mean scaled at each measurement time point. Again, these models were run for whole plot survival, sage scrub survival and chaparral survival. Additionally, the effect of predictor variables changed over time, so we included a PAR-time interaction to meet the proportional hazards' assumption. All cox-proportional hazards models had plot included as a random intercept.

To test if plant traits contribute to how a given species responded to the differences in post-transplant shock densities, additional cox proportional hazards models were created.

Additionally, to prevent overfitting of our data, individual trait models were conducted for LES 1, LES 2, wood density and water use efficiency. Each of these models included the trait, April density and an interaction between the trait and April density as fixed effects and then plot as a random intercept.

The suppressive effect of restored native cover on non-native cover was tested with a generalized linear model using a gamma distribution. This model used the May 2023 and January 2024 timepoints that percent cover was measured. Additionally, the effect of both nonnative and restored native cover on natural recruitment was tested with binomial logistic regressions using the percent cover data from January 2024. Lastly, the potential environmental conditions favoring natural recruitment were tested with single variable binomial logistic regressions for both September 2023 soil moisture and PAR.

D. Results

When considering April density as the only explanatory factor, the cox-proportional hazards models showed a significant benefit of higher density both on overall plot seedling survival and sage scrub individual survival through 2022, but not on chaparral survival (Figure 3). Including mean scaled plot differences in soil moisture and PAR as additional explanatory factors revealed that April density conferred a significant benefit to survival for all three survival plant groupings (Figure 4). Additionally, soil moisture was shown to not have a significant influence on survival in any of the models. By contrast, PAR had a significant and strong negative effect on survival when looking at whole plot and sage scrub survival, but not chaparral survival. All three models showed a significant interaction between PAR and time, where the negative effect of PAR lessened over time (Figure 4).

The trait models showed all traits except LES 2, significantly affected survival (Figure 5). Both LES 1 (Figure 5A) and wood density (Figure 5C) had a negative effect on survival, whereas water use efficiency (Figure 5D) had a positive effect on survival. Additionally, April density again had a significant positive effect on survival in all four trait models (Figure 5). Lastly, April density significantly interacted with traits in all four models, with a negative interaction with water use efficiency and a positive interaction with the other three traits.

The analysis of natural recruitment was significantly correlated both to native (positive; Figure 6A) and nonnative (negative; Figure 6B) cover. Additionally, natural recruitment was significantly negatively correlated to September 2023 PAR (Figure 6C), but not to soil moisture (Figure 6D). We also found a significant and strong suppressive effect of restored native cover, primarily sage scrub, on non-native cover one year after planting (Figure 7). Additionally, none of the adjacent weeded plots had any native shrub recruitment (data not shown).

E. Discussion

Overall, our study found strong support for the importance of initial planting density in affecting shrub seedling survival in a southern California shrubland restoration context. We found support for key tenants of nucleation theory, as it has been developed in forest restoration: 1.) There was a consistent positive effect of higher planting density on survival across all of our models investigating influences on plant survival; 2.) We found that these higher planting densities, and the associated higher plot-level survival, led to higher planted native percent cover which created shading and suppressed non-native species; and 3.) As a result of the increased native cover and its plot-level amelioration of biotic and abiotic limitations, we observed seedling recruitment of multiple native shrub species in years two and three of the project. Lastly, we found partial support for our hypothesis that higher density of sage scrub would facilitate higher chaparral survival.

Planting density facilitates higher survival overall: Ecological theory predicts that co-planting can lead to adverse effects through competition for resources (Aarssen & Epp, 1990; Connell, 1983; Craine & Dybzinski, 2013; Fowler, 1986; Gleason, 1926; Schoener, 1983), co-existence via niche partitioning (Kitajima & Poorter, 2008), facilitation through an influence on the surrounding biotic and abiotic conditions (Brooker et al., 2007), or some combination of the above. Our findings offer evidence that increasing planting density in degraded southern California shrublands primarily leads to facilitative effects on survival of out planted individuals. The primary facilitative effect we identified appears to be through providing shade: April density was negatively correlated with measured plot-level PAR throughout the summer (Appendix 2). In other words, higher density creates more shade which aids individual survival. This, combined with our models showing a consistent negative correlation between high PAR and survival

(Figure 4), points towards a primary mechanism of facilitation via shading. Shading likely offers some degree of amelioration on the harsh summer vapor pressure deficit (VPD) and soil, air and leaf temperatures, abiotic conditions previously shown to influence southern California shrubland seedling survival and recovery post fire (Deweese et al., 2022; Frazer & Davis, 1988; Storey et al., 2021; Dewees et al, In prep).

The lack of relationships between planting density and soil moisture, and soil moisture and survival (Figure 4) were surprising. Yet, previous studies in sage scrub restoration have shown that planted sage scrub seedlings do not influence shallow soil moisture until the year after their establishment (Eliason & Allen, 2008). Therefore, it is possible that had road closures not prevented us from measuring soil moisture more consistently during the second year of our study (Table 3), we would have detected an effect of planting density on soil moisture. We would have expected higher density to reduce soil moisture. As far as our results showing no relationship between plot level differences in soil moisture and survival, we posit a few possible explanations. First, it is possible that the relatively homogenous spatial conditions over which this study took place over (Figure 1) did not allow for enough plot-to-plot variation in soil moisture to explain differences in survival. Second, we were restricted to only measuring soil moisture down to 30cm, and at times 15cm, depth (Table 3). Most of the seedlings were planted with roots extending down to at least 20 cm below the soil surface. It is also safe to assume that most individuals surviving to May had at least some level of additional root growth. Therefore, it is possible that we were not measuring soil moisture at the soil depth the plants were experiencing, particularly as the study progressed. Lastly, it is possible that the out planted seedlings developed mycorrhizal networks that aided in accessing water not traditionally

accessible to roots alone (Fernández-Lizarazo & Moreno-Fonseca, 2016; Kakouridis et al., 2022).

We also hypothesized that there would be a facilitative benefit of planting density specific to chaparral seedlings because they are slower growing and more difficult to establish. Yet our results only partially support this hypothesis: the April density-only model showed no significant effect of density on chaparral seedling survival (Figure 3). The model including soil moisture, PAR and the interaction between PAR and time however, did show a significant positive effect of April density (Figure 4C). One interpretation of this is that while April density doesn't significantly explain the total variance in survival, it does significantly explain the reduced variance of survival that occurs after including soil moisture and PAR, which can be substantial even for two non-significant variables. Therefore, we believe that we are seeing some facilitative effect of planting density on chaparral survival, but that facilitative effect was not strong enough to completely offset the abiotic stressors, both measured and unmeasured, driving mortality.

Plant traits predict facilitation via density: Our examination of how, plant traits influence a given species' response to planting density unearthed that, in general, traits that make a plant more vulnerable to environmental stress (e.g. high SLA and leaf N per unit mass), predict facilitation by increased density, whereas traits that infer higher resistance to environmental stress (e.g. higher water use efficiency) predict negative effects of increased density. We found that, in general our LES 1 index, largely indicating higher specific leaf area and leaf N per unit mass, is in general harmful for survival in the arid setting we studied, and thus plants with these traits benefit from high planting density (Figure 5B). This is consistent with the abundance of plant functional trait literature on specific leaf area. It is generally accepted that higher specific leaf area is well adapted for partial to full shading (Liu et al., 2016; Lusk, 2002), and as a result

akin to a foliar strategy maximizing photosynthetic rates (Wright et al., 2004), sometimes at the expense of water-use efficiency (Hoffmann et al., 2005). Therefore, our results are likely showing the maladaptation of higher specific leaf area in low cover plots on our arid slope, and its positive response to the partial shading associated with higher planting density.

Similarly, the significant finding that increasing wood density is, in general, harmful to survival (Figure 5C), builds off previous findings (Deweese et al, In prep). In a prior study (Deweese et al, In prep), we found that species with higher wood density are much more vulnerable to higher values of VPD. Therefore, the wood density interaction with planting density, that showed higher survival in denser plots (Figure 5C), could indicate a facilitative effect through the reduction of plot level VPD. VPD is influenced both by temperature and relative humidity and it is likely that the increased shading in denser plots is lowering the within plot air temperature a given individual is experiencing (Breshears et al., 1998; Von Arx et al., 2012). Additionally, it is possible that denser plots, with more leaf area, are also increasing the within-plot relative humidity, as has been shown with other species (Pickering et al., 2021; Von Arx et al., 2012). In combination, this could explain how higher planting densities, and the resulting higher cover, reduce plot-level VPD and increase the survival of species with higher wood density.

Lastly, we found that water use efficiency, measured here as delta 13 carbon (photosynthetic fractionation of carbon-13 isotopes), a trait that confers higher resistance to environmental stress caused both by soil moisture and VPD, predicted lower survival in higher planting densities (Figure 5D). Therefore, having a higher water use efficiency likely negates some of the facilitative effects of reducing temperature and VPD. Additionally, we, as well as others, have found that water use efficiency is, at least partially antagonistic to specific leaf area (Hoffmann et

al., 2005), maximum rates of carbon assimilation (Tomeo & Rosenthal, 2017) and growth rates (Dixit et al., 2022; Valliere, 2019). Therefore, it appears that in our study, the higher resistance to water stress that water use efficiency confers is making an individual less receptive to facilitative processes while simultaneously making it more susceptible to the negative impacts shading has on photosynthesis and growth.

Nucleation occurs through within plot natural recruitment: Another key part of nucleation restoration theory, is the actual ‘nucleation’ of plots through natural recruitment within and outside of the plot (Corbin & Holl, 2012; Reis et al., 2010; Yarranton & Morrison, 1974). While we did not find evidence of our plots expanding their influence outside of where they were established yet, our study showed strong evidence for the facilitation of natural recruitment as a function of plant density. Previous studies found that sage scrub recruitment in grasslands is often limited to small, grass-free gaps created by micro disturbances such as gopher mounds (DeSimone & Zedler, 1999). Additionally, non-native grasses have been shown to exclude native shrub recruitment, likely through depletion of shallow soil moisture (Cox & Allen, 2008; DeSimone & Zedler, 1999; Goldstein & Suding, 2014) and potentially shading (Gray, 1983). Our findings of natural recruitment strongly correlating to native cover (Figure 6A), and native cover strongly suppressing non-native cover (Figure 7), support that some form of competitive release might be necessary for sage scrub seedlings to re-establish in non-native grasslands. However, our combined findings of no influence of soil moisture and lack of natural recruitment in the adjacent weeded sub plots suggest more than just a competitive release is required. We hypothesize that a potential mechanism explaining this is that the stand structural change with planted native shrubs provides a few secondary facilitative effects.

One key difference between our planted and weeded only plots was in stand structure/complexity. The weeding of both plot types removed the competitive inhibition of non-native grass on natural recruitment. However, there are a few secondary facilitative effects the added stand complexity of our planted plots may have provided that prove necessary for successful recruitment. First, the added stand structure may have led to a higher density of seeds present for germination through direct addition of seeds from our planted individuals and more stand structure to trap windblown seeds (personal observations, Figure 8). Second, while late season soil moisture has been shown elsewhere to have no influence on the survival of drought-deciduous sage scrub seedlings (DeSimone & Zedler, 1999), there could still be a soil moisture and shading effect that is facilitating higher post-germination survival during the growing season. It has been shown that foliar fog drip/moisture capture, which should increase with stand structure, can have influential additions to shallow soil moisture (Fischer et al., 2016; Vasey et al., 2012). Additionally, while the sage scrub seedlings are less affected by the summer dry season, because of their drought deciduous nature, the enhanced moisture status of the plot via shading and moisture capture may allow them to excise their leaves later into the summer thereby experiencing a shorter period in which they cannot assimilate carbon. While our data can't speak directly to the mechanisms at play here, the lack of natural recruitment in these adjacent weeded plots suggests more than just competitive release is required. The significant relationship to shading (Figure 6C) sheds, or should I say shades, light on one potential mechanism.

Conclusion: Our study shows the first successful application of nucleation restoration to southern California shrublands and adds credence to the widespread efficacy of this approach. We demonstrate that high density plantings ameliorate stressful abiotic conditions and exclude

non-native species, allowing for successful natural recruitment. Additionally, we identify a secondary benefit of the nucleation restoration approach, increased survival of the planted individuals. Lastly, our findings show that plant traits can not only predict the abiotic conditions under which a species can survive as demonstrated elsewhere (Balazs et al., 2020; Clark et al., 2012; Pywell et al., 2003; Sandel et al., 2011; Dewees et al., In prep), but also predict what species will benefit from high density plantings. This suggests that the nucleation restoration approach may allow for successful plant establishment in microsites too harsh for the traditional plantation style approach.

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G. Tables and Figures

Tables:

Table 1: Planting groups

Planting Community 1:		Planting Community 2:		Planting Community 3:	
Species	Number planted	Species	Number planted	Species	Number planted
<i>Salvia leucophylla</i>	10	<i>Salvia leucophylla</i>	10	<i>Adenostoma fasciculatum</i>	13

<i>Salvia apiana</i>	10	<i>Salvia apiana</i>	10	<i>Malosma laurina</i>	12
<i>Salvia mellifera</i>	7	<i>Salvia mellifera</i>	7	<i>Rhus ovata</i>	13
<i>Artemisia californica</i>	10	<i>Artemisia californica</i>	10	<i>Ceanothus oliganthus</i>	13
<i>Eriogonum fasciculatum</i>	7	<i>Eriogonum fasciculatum</i>	7	<i>Ceanothus cuneatus</i>	5
<i>Encelia californica</i>	10	<i>Encelia californica</i>	10	<i>Heteromeles arbutifolia</i>	12
<i>Adenostoma fasciculatum</i>	9	<i>Ceanothus oliganthus</i>	7	<i>Rhamnus ilicifolia</i>	12
<i>Malosma laurina</i>	8	<i>Ceanothus cuneatus</i>	5		
<i>Rhus ovata</i>	9	<i>Heteromeles arbutifolia</i>	7		
		<i>Rhamnus ilicifolia</i>	7		

Table 2: April densities:

Plot	Number of Plants Alive
11	53
12	50
13	70
14	71
15	59
2401	60
2402	46
2403	74
2404	71
2405	58
2458	57
2459	60
2460	66
2461	68
2462	59

Table 3:

Date	Soil Moisture	PAR	Survival	Height	Percent Cover	Natural Recruitment
02-17-2022	30 cm	Yes	No	No	No	No

04-05-2022	30 cm	Yes	No	No	No	No
04-29-2022	No	No	Yes	No	No	No
05-06-2022	30 cm	Yes	No	No	No	No
05-17-2022	No	No	Yes	No	No	No
06-09-2022	30 cm	Yes	Yes	No	No	No
07-15-2022	30 cm	Yes	No	No	No	No
08-05-2022	No	Yes	Yes	No	No	No
09-08-2022	15 cm	Yes	Yes	No	No	No
10-19-2022	15cm	Yes	Yes	No	No	No
11-21-2022	15 cm	No	Yes	No	No	No
03-09-2023	No	No	Yes	Yes	Yes	No
05-17-2023	No	Yes	Yes	Yes	Yes	No
09-25-2023	Yes	Yes	Yes	Yes	No	No
1-24-2024	No	No	Yes	Yes	Yes	Yes

Figures:

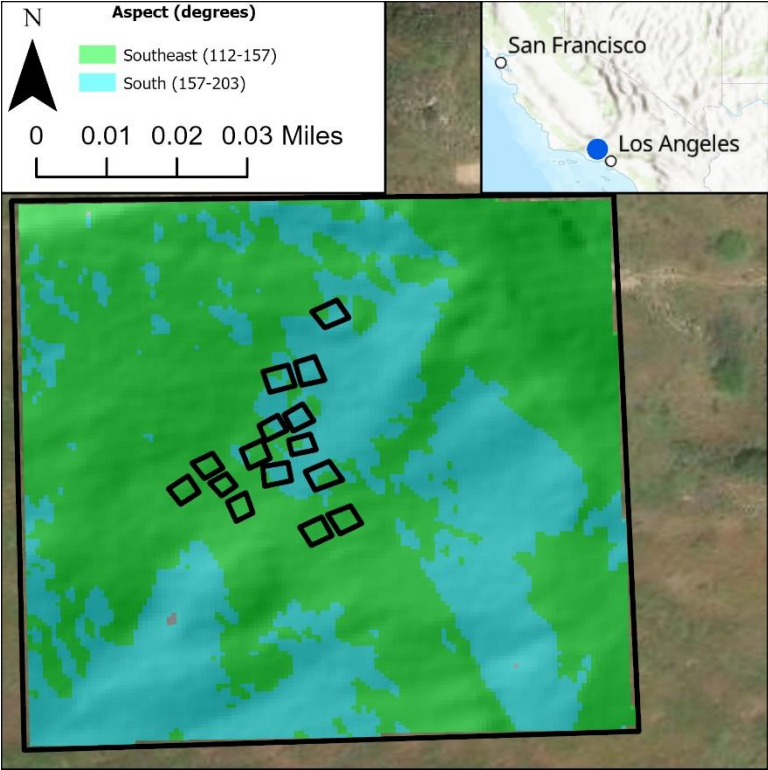


Figure 16: Map of study site with an opaque aspect layer overlaid on a hill shade elevation model to show topographic heterogeneity across study area.

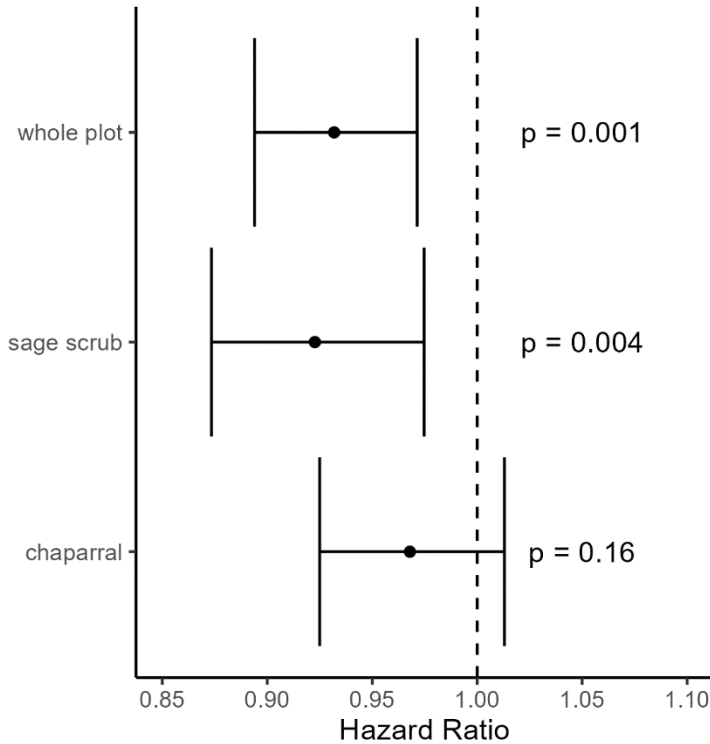


Figure 18: Hazard ratios from the single variable cox proportional hazards models, looking at the effect of April density on the rest of 2022 survival. The three models are using all individuals (whole plot), only sage scrub individuals (sage scrub), and only chaparral individuals (chaparral) as the input data. Dots represent the mean hazard ratio and error bars are 95% confidence intervals. P-values are from the cox proportional hazards models. The hazard ratio can be interpreted as the number of individuals for a given group that are dying for every one standard deviation increase from the mean of April density. The higher the number, the greater the number of individuals dying. All models have plot included as a random intercept.

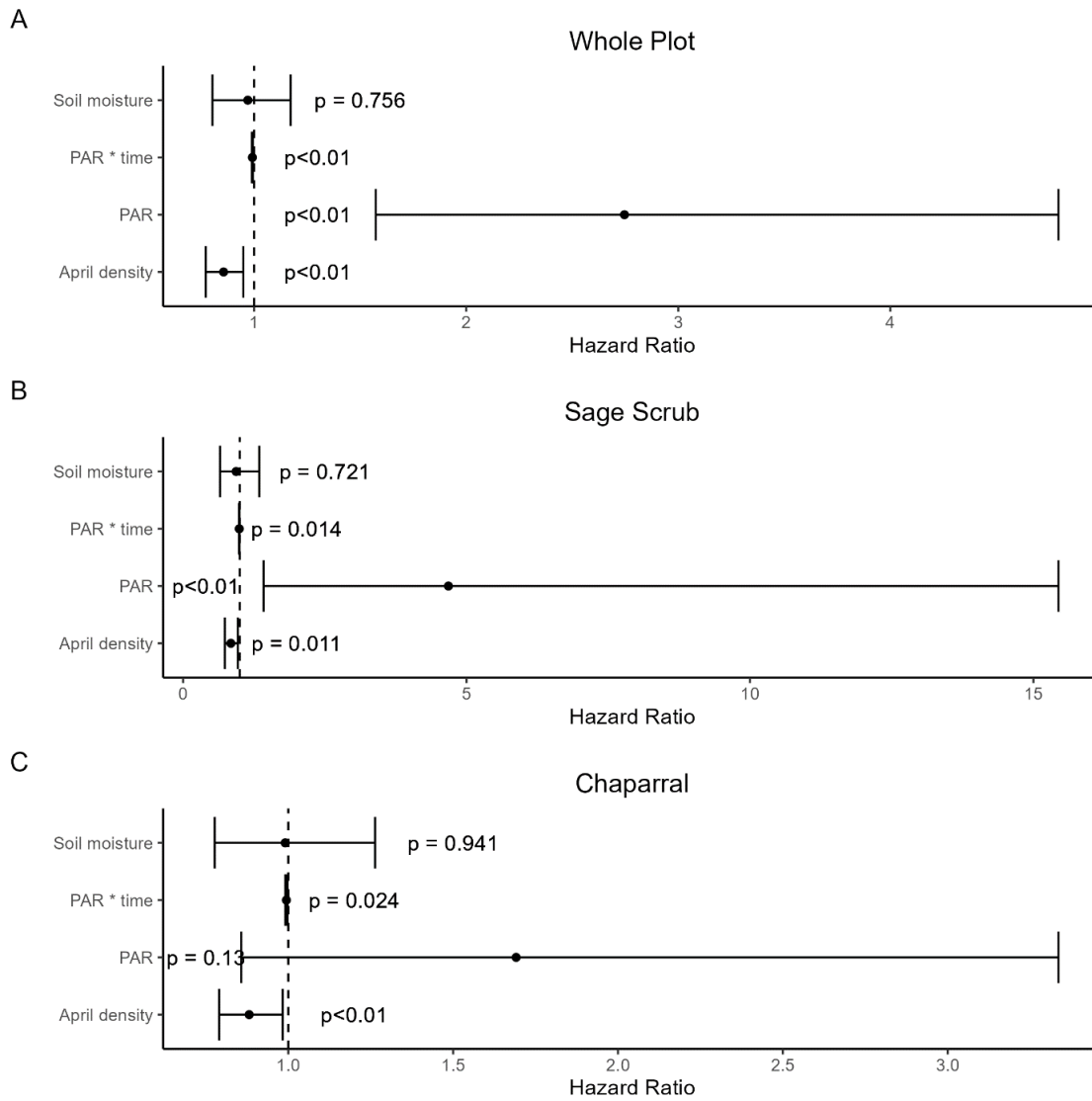


Figure 19: Hazard ratios from the multi-variable cox proportional hazards models, looking at the effect of April density, soil moisture and PAR on the rest of 2022 survival. The three models are using all individuals (A), only sage scrub individuals (B) and only chaparral individuals (C) as the input data. Dots represent the mean hazard ratio and error bars are 95% confidence intervals. P-values are from the cox proportional hazards models. The hazard ratio can be interpreted as the number of individuals for a given group that are dying for every one standard deviation increase from the mean of April density, soil moisture or PAR. The higher the number, the greater the number of individuals dying. All models have plot as a random intercept.

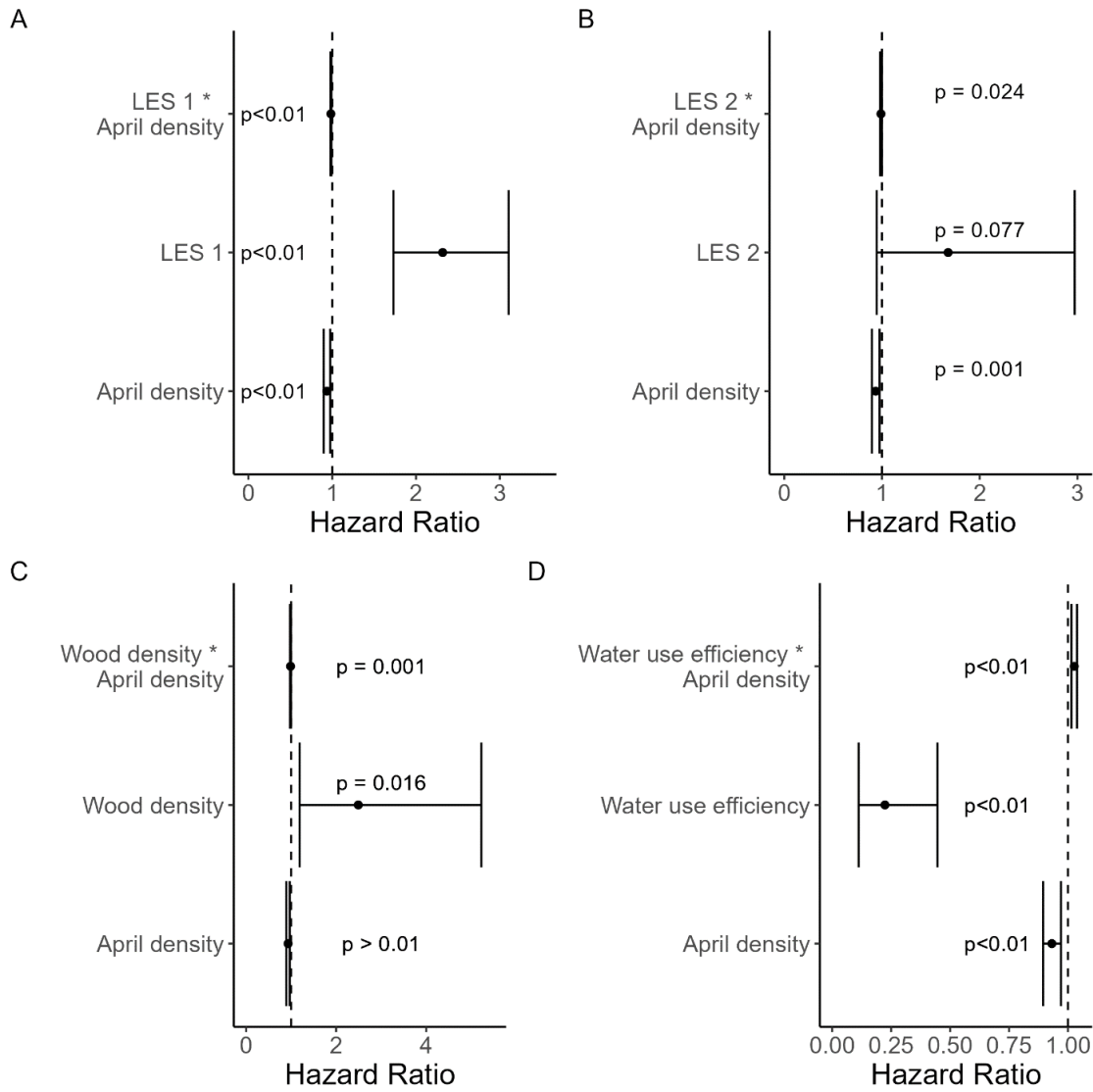


Figure 20: Hazard ratios from the multi-variable cox proportional hazards models, looking at the effect of April density and a single trait on the rest of 2022 survival. Dots represent the mean hazard ratio and error bars are 95% confidence intervals. P-values are from the cox proportional hazards models. The hazard ratio can be interpreted as the number of individuals for a given group that are dying for every one standard deviation increase from the mean of April density or trait value. The higher the number, the greater the number of individuals dying.

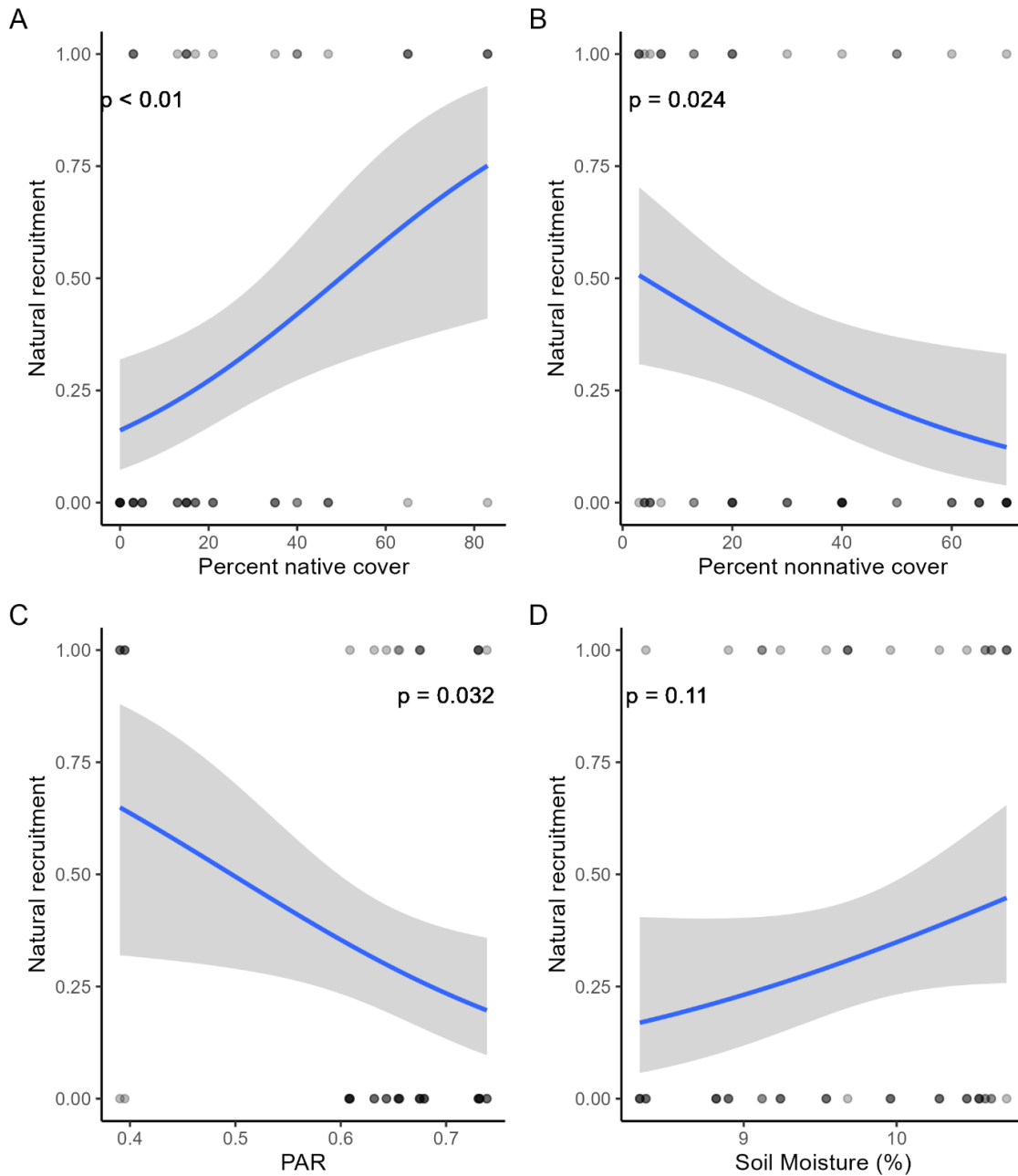


Figure 21: Graphs of natural recruitment versus percent native cover (A), percent non-native cover (B), proportion of ambient par reaching the plot (C) and soil moisture (D). The blue lines, grey confidence intervals, and p-values are from separate binomial logistic regressions and the grey dots are the actual data points. For the actual data, a y-axis value of 0 means no natural recruitment was observed and a y-axis value of 1 means that natural recruitment did occur. The natural recruitment and percent cover data are all from January 2024, whereas the PAR and soil moisture data are from September 2023.

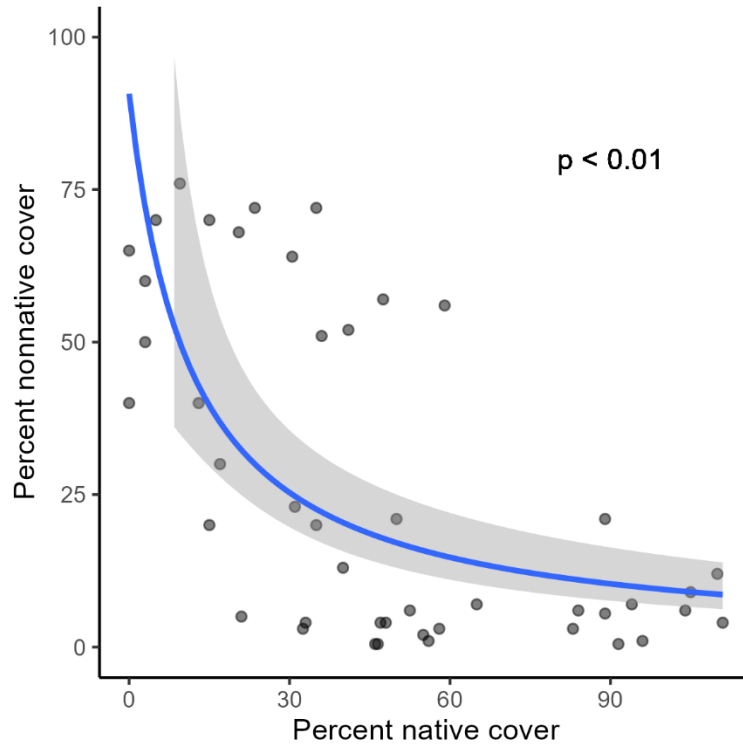


Figure 22: Native cover suppresses nonnative cover during year 2 of restoration. The blue line and grey confidence intervals are from a generalized linear regression of percent non-native cover as a function of percent native cover, using a gamma distribution. The gray points are the actual data that went into the model. P-value is from the generalized linear model.

H. Appendices

Appendix 1: Plant traits

Table S1: Mean value for all plant traits used in analysis.

Species	Specific leaf area	Leaf dry matter content	Leaf thickness	Petiole length	Leaf lamina length	Leaf width	Leaf Carbon: Nitrogen	Leaf Nitrogen percent mass	Leaf Carbon percent mass	Wood density	Water use efficiency
<i>Adenostoma fasciculatum</i>	4152.48	0.49	0.00049	0	0.7	0.12	35.28	1.44	50.30	0.75	-27.17
<i>Aremisia californica</i>	10913.71	0.40	0.00023	0	5.5	0.075	19.95	2.27	45.05	0.69	-27.24
<i>Ceanothus cuneatus</i>	5581.84	0.43	0.00042	0.23	1.8	1.05	31.79	1.52	48.21	0.68	-27.70
<i>Ceanothus oliganthus</i>	12373.41	0.40	0.00020	0.56	2.05	1.50	19.94	2.42	47.73	0.61	-28.19
<i>Encelia californica</i>	13994.11	0.21	0.00034	1.12	4.5	4.50	16.17	2.32	37.47	0.64	-30.80
<i>Eriogonum fasciculatum</i>	9100.45	0.35	0.00031	0.36	1.05	0.23	24.32	1.90	45.36	0.63	-28.35
<i>Heromeles arbutifolia</i>	4534.60	0.54	0.00041	1.36	7.5	1.95	38.36	1.33	50.43	0.62	-26.81
<i>Malosma laurina</i>	4469.91	0.48	0.00046	2.5	6.5	3.25	57.55	0.90	50.89	0.48	-30.56
<i>Rhamnus ilicifolia</i>	5288.98	0.49	0.00039	0.46	3.0	2.34	30.62	1.57	46.95	0.63	-27.43
<i>Rhus ovata</i>	3223.01	0.52	0.00060	1.18	5.5	5.5	50.35	1.03	50.68	0.52	-25.82
<i>Salvia apiana</i>	7359.02	0.32	0.00042	1.14	6.0	1.81	24.45	2.04	49.40	0.41	-28.31
<i>Salvia leucophylla</i>	10355.78	0.34	0.00028	0.70	5.0	1.61	25.26	1.95	46.40	0.50	-29.37
<i>Salvia mellifera</i>	9039.66	0.37	0.00030	0.95	4.75	1.19	31.31	1.54	46.91	0.56	-28.19

Appendix 2: Planting density – Par relationships.

Table S1: P-values from single variable regression with soil moisture or PAR as the dependent variable and April density as the independent variable.

Date	Soil moisture	PAR
05-06-2022	0.296	0.118
06-09-2022	0.730	0.120
07-15-2022	0.284	0.0606
08-05-2022	-	0.180
09-08-2022	0.906	0.0911
10-19-2022	0.655	0.0302
11-21-2022	0.961	-