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Invasive Species Impacts on Coastal Sage Scrub Recovery

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Invasive Species Impacts on Coastal Sage Scrub Recovery

THESIS

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for the degree of

Ecology and Evolutionary Biology M.S.

by

Emily Griffoul

Thesis Committee:
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ABSTRACT OF THE THESIS

Invasive Species Impacts on Coastal Sage Scrub Recovery

By

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Ecology and Evolutionary Biology M.S.

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Professor Travis Huxman, Chair

Significant resources are invested in the restoration of degraded Coastal Sage Scrub in Southern California to meet conservation goals. Thus, understanding the resilience of these systems is of great importance given their high value intersection with human settlements. The presence of invasive annual species has been suggested to add complexity to ecological restoration efforts by inhibiting the growth of native species, changing fire regimes, and altering water balance. To further understand these ideas, I utilized a long-term experiment testing the effectiveness of “passive” restoration, the removal of non-native species without expensive site preparation or resource-intensive active planting / seeding of native species, which means that the approach could be designed to have widespread positive effects at potentially minimal costs. I found that passive restoration was successful at meeting restoration goals of increasing native shrub cover. Two ecological mechanisms – the establishment of new individuals on the landscape versus the expansion of plant size of existing shrubs – were likely responsible for the variation in patterns of recovery for localities with different initial native shrub cover. These patterns give insight into how to affect change in communities through management intervention. Better formulating a conceptual model of the contemporary dynamics of Coastal Sage Scrub informs decisions on expending limited resources to different intensities of restoration across a complex landscape to maximally impact conservation.

Introduction

The link between disturbed or degraded habitat and non-native species invasion is well established (Vitousek et al. 1997). Degraded areas are often at higher risk of invasion by non-native plant due to shifts in ecological filters facilitating their establishment, growth, and reproductive success (Hobbs and Huenneke 1992; D'Antonio, Dudley, and Mack 1999). Invasive species appear to successfully compete with native species for water and soil resources, and anthropogenically-altered landscapes allow invasive species to flourish to a greater degree as compared to natives in physical and biological settings sufficiently altered from that which these natives have evolved (Mack et al. 2000). Worldwide, human-caused habitat destruction threatens biodiversity and often operates synergistically with changes in non-native species invasion to cause further irreparable harm to already vulnerable systems (Simberloff et al. 2013; Gallardo et al. 2016).

The last five years of drought in Southern California highlight the unique challenge of addressing multiple sources of disturbance on already vulnerable habitats. Climate projections suggest that extreme climate years, such as the one in 2014, where low precipitation and high summer temperatures coincided, may occur more frequently in the future (AghaKouchak et al. 2014). The historical disturbance wrought by fire, grazing, and habitat fragmentation, and the ongoing disturbance by pollution and invasion by non-native species may interact with the additional stress of low precipitation and high temperatures in unpredictable ways, creating new challenges for land managers. As such, managers require a greater understanding of mechanisms underlying ecological dynamics in order to successfully develop interventions that will result in positive conservation outcomes for systems faced with novel combinations of system drivers (Beever and Belant 2016).

In efforts to conserve biological diversity, ecological restoration of degraded habitat is considered essential (Benayas et al. 2009), but is understandably challenging and potentially cost-intensive (Robbins and Daniels 2012). Abiotic and biotic feedbacks can act to retain landscapes in their degraded states (e.g., Suding, Gross, and Houseman 2004), which arise from features such as limited species-richness in the potential native species pool, shifts in trophic interactions and mutualisms from species mis-matches, alterations in biogeochemical cycling and resource-use, or continued species invasion and alteration of disturbance dynamics. A recent research push has been to understand how combinations of efforts across the stages of restoration maximize cost-effective strategies to best leverage limited funding for conservation (e.g., Kimball et al. 2015). However, what has been clear to practitioners and scholars is that the influence and continued invasion of non-native species during the restoration process proves a difficult dynamic that has lasting effects on systems as restoration efforts are carried out to support conservation goals (D’Antonio and Meyerson 2002).

Coastal Sage Scrub (CSS) in southern California is an ecologically important habitat crucial to the survival of numerous important species of birds, reptiles, amphibians, rare plants, and mammals, and also at significant risk to both future human and climate influences (Davis, Stine, and Stoms 1994; Riordan and Rundel 2014). Methods of restoring degraded areas are critical to land managers meeting conservation goals, which are often limited by funding and additionally challenged by disturbance in the form of grazing and fire. In this region, the difficulty of restoring this habitat is compounded by intermittent drought, which adversely affects investment in planting of native species in restoration efforts during unfavorable establishment periods (Kimball et al., 2015). CSS also shows a range of degradation, where some native perennials can remain present throughout the landscape, so as to potentate changes in existing native plant cover and potential establishment from natural seed rain. Previous studies on this habitat have shown that the distribution, performance, and abundance of native species are dependent on factors of environmental variation in space and time, including slope, mean high and low temperatures, precipitation, soil moisture, along with drought extent and duration (Franklin 1995; Franklin 1998; Kimball et al., 2017), making such dynamics vital to successful projects (Landres, Morgan, and Swanson 1999).

This study takes place across Orange County, CA in areas where native coastal sage scrub communities are impacted by a number of non-native, invasive species. Though fire is a historical disturbance, now several of the most serious threats to coastal sage scrub include habitat loss due to urbanization, pollution by nitrogen deposition, and invasion by exotic species. Each of these pressures operates to reduce the abundance of key native shrub species. In Southern California, the most common shrub species in coastal sage scrub are *Artemisia californica, Eriogonum fascisculatum,* and *Encelia californica*, all of which are critical to habitat that supports listed species of concern by U.S. and CA management agencies (Diffendorfer et al., 2007), dictating conservation goals. In this thesis, I investigate one critical management option, specifically the effectiveness of "passive restoration", the removal of non-native species from existing habitat without additional modification, over 7 years across a regional gradient in temperature. I further evaluate these sites and their variation in native perennial plant cover in the context of interannual variation in rainfall associated with historical low rainfall years in California between 2012 and 2016. Throughout, I ask the following question:

> Is ‘passive restoration’, the removal of non-native species without additional resource investment in treatments, effective at increasing native cover, and does the response depend on initial proportion of native species?

Ecological Setting

Coastal Sage Scrub (CSS) is an ecologically valuable habitat found generally along the coastal region of California and Baja California. It is characterized by the presence of several species of mesophyllous shrubs, including *Artemisia californica, Encelia californica,* and several species in the *Salvia* genus*,* as well as *Eriogonum fascilulatum* and several perennial grasses. CSS also has a rich understory of forbs, including species in the *Phacelia, Cryptantha, Chaenactis,* and *Lupinus* genera, as well as the perennials *Dicholostemma capitum* and *Mirabilis laevis.* CSS is currently one of the most threatened California habitats, facing disturbance from fire, agriculture, urbanization, nitrogen deposition, and invasion by non-native species (Riordan and Rundel 2014).

Disturbance, whether natural (such as fire) or man-made (such as pollution or development), has a profound impact on the structure and function of CSS. Historically, fire occurred at most about every 20 years (Westman 1982), and some localities had figure frequencies extending to up to every 100 years (Minnich 1983). Establishment occurred following these disturbances by the resprouting of some species from perenniating tissues like crowns and germination of others from seeds queued by environmental features of fire. Many herbaceous species are only present during the first years following a fire, and diversity fluctuates over time between disturbance (Keeley and Keeley 1984; O'Leary and Westman 1988). Historical fires tended to be infrequent, due to lack of ignition sources (lightning is uncommon in Southern California), but intense, due to the buildup of fuels and the intensity of wind events. However, these patterns have changed with the increasing urban-wildland interface. Additionally, with increasing human population and needs over the last several centuries, activities such as grazing of domestic animals and building of cities and infrastructure have become some of the dominant sources of disturbance in coastal sage scrub. Less visible, but just as damaging are the effects of pollution, primarily nitrogen deposition, and extended drought associated with climate change (Kimball et al. 2014). Anthropomorphic disturbance has also led to invasion by non-native species, which can have lasting effects on the structure and function of coastal sage scrub (Talluto and Suding 2008). These sources of disturbance have profoundly altered fire regimes, with more frequent, but less severe burns (Keeley, Fotheringham, and Morais 1999), which have important consequences for native recovery patterns as well as invasion by non-native species (Keeley, Baer-Keeley, and Fotheringham 2005).

Though the goal of ecological restoration may be to return a system to its pre-disturbance state, it may not be possible, because of the abiotic and biotic interactions since the disturbance was initiated (Hobbs and Cramer 2008). In coastal sage scrub, many sources of disturbance, such as grazing, have decreased or altogether ceased, and the system is not guaranteed to recover to its previous state. Invasion by non-native species, often by the exploitation of gaps in the canopy left by disturbance, can profoundly alter the dynamics of the landscape and can persist even after the original source of disturbance is removed (Suding, Gross, and Houseman 2004). This presents a challenge for land managers.

Restoration of coastal sage scrub is both incredibly important in order to maintain biodiversity and preserve this threatened habitat, as well as potentially expensive and difficult. Most restoration efforts involve some combination of site preparation, including removal of non-native species (though the removal of their seeds is difficult), seeding or planting of natives, watering, and weeding, and feature a wide range of costs (Kimball et al. 2015). These interventions can be expensive and tax manager's limited funds for conservation. It is therefore vital to explore methods that are both efficient and cost-effective, and to ensure that we understand their applicability and limitations.

Passive restoration is one method to carry out cost-effective restoration of disturbed areas of native vegetation, relying on natural processes to facilitate recovery of ecosystem structure and function (e.g., Eliason and Allen 1997; Marushia and Allen 2011). Such restoration would depend on reducing invasive species to low levels, enabling the existing successional model of the restored system to lead to positive outcomes. The merits of passive restoration are that it is comparatively inexpensive, and if successful, could be widely implemented with little oversight, allowing agencies to direct limited resources to other important projects. However, it is unclear how site factors, such as initial native cover values promoting maximum impact, time since disturbance, or environmental context (temperature / precipitation) may influence the success of this approach (Holl and Aide 2011).

Introduction to Project

This project takes place in Orange County, CA, where average precipitation is around 34cm per hydrologic year, primarily occurring in the winter and spring. The project was set up in 2009 by the Irvine Ranch Conservancy, and continues through 2017. In this study, I investigate the effectiveness of a passive restoration project over seven years on coastal sage scrub distributed throughout Orange County, CA. Across a regional gradient, I evaluated sites with similar variation in initial native perennial plant cover (Fig. 1). I addressed the following questions:

1. Is passive restoration effective at increasing native cover?
2. Does initial native cover influence passive effectiveness? and,
3. How does environmental variation in space and time influence outcomes?

In this experiment, I tested the hypothesis that passive restoration increases the cover of native species because non-native removal reduces resource limitation from competition. I anticipated that a minimum threshold of initial native cover for where a benefit of this treatment may be expected is quite low given the persistence of some native species (and thus a seed bank) throughout the region, and that passive restoration may no longer be effective at relatively high initial native cover values, where competition between native species influences abundance to a greater extent than competition between natives and non-natives. Additionally, I hypothesized that in settings with more extreme temperature and precipitation fluctuations (inland sites), escape from competition would favor recruitment of native species, resulting in more dramatic treatment effects as compared to relatively temperate coastal sites.

Methods

Experimental Setup

Ten sites, located throughout Orange County, CA, were established in 2009 (Fig. 1). The sites were categorized as “inland” or “coastal”, in order to group them together by region, where differential management and past disturbance may have influenced the recovery of native shrubs. The sites were chosen to have at least 50m radius unbroken habitat of mixed shrubs and invasive grasses, and a maximum of ~55 % of the native perennial cover made up by early successional shrubs, and no more than 20 % of the native cover made up of native herbaceous cover. At the same time, the plots were chosen to limit the functional variation in non-native species to invasive grasses (primarily in the *Bromus* and *Avena* genera) and black mustard (*Brassica nigra*), with less than 20% of the non-native cover being comprised of something other than these common species.

At each site, eight 5-x-5 m^2 plots were established that included paired initial native shrub cover classes (20-30 %, 30-40 %. 40-50 %, 50-60 %). One of each paired plot was randomly assigned to non-native species removal, while the other is used as an un-manipulated control. Non-native species in treatment plots are treated with a low-dose glyphosate in the winter, and weeded in the spring. The herbicide used is a 0.5% concentration of Roundup PROMAX®, applied with a targeted backpack sprayer to the non-native seedlings within the plot and within a 1m buffer around the plot. The spring weeding is performed either with a weed whip, or hand-clipped, depending on the site and the accessibility and density of species. However, to simulate the limitations of such a management treatment on a large scale, the weeding is restricted to take out obvious patches of non-native species, and is deliberately time-restricted so as to not to eliminate every non-native individual from the plot, including from underneath shrubs. The spring weeding is intended to primarily prevent substantial seedset of non-native species in plots following the growing season.

Data Collection

The entirety of each 5x5 m plots were sampled. All species within plots were recorded to understand species composition (categorized as native and non-native) and I used visual estimates of cover in each plot recorded each year at the peak of the growing season in the spring. The focus is on determining cover of native perennial shrubs, native perennial grasses, native forbs, and any surviving non-native species. I evaluated the performance of the visual estimates of cover by additional methods, employing the point intercept method for plots in the spring of 2017. Six, five meter long transects were laid out across each of 16 plots from the entire experimental array and sampled by inserting a dowel vertically into the canopy at 0.5 m intervals. ‘Touches’ of any species in this sampling were recorded by species and evaluated from the entire plot to compare with the visual cover estimates for that specific plot.

Statistical Analysis

All data were analyzed in R, a freely available, open source statistical programming language (version 3.0.0; 2013-04-3, R Foundation for Statistical computing). I used a repeated measures ANOVA to understand the impact of the passive restoration (Treatment), initial cover (Cover), year, and region (inland and coastal) on several dependent variables, including total native cover (perennial and annual species), and species richness. Follow-up tests were performed to tease out differences among interaction effects. Data are archived in the OC Data Portal (http://ecodataportal.org/), with appropriate metadata. Comparisons of the point-intercept method and visual cover estimates were made with simple regression, focusing on the cover of native perennial species (the target variable for restoration success).

Results

Overall, the estimates associated with the visual method of determining native shrub cover and the point-intercept method were adequately similar (visual estimate = 0.94*point-intercept + 0.91; $R^2 = 0.88$; $p<0.05$). The difference in estimated cover between these two methods varied slightly as a function of the different components of total plant cover – it was smallest for shrub cover (1.08 ± 4.13 %) and highest for non-native annual grass cover (8.30 ± 5.49 %), but these differences among estimates were not statistically significant. Generally, the point intercept method recorded higher cover values, most likely due to the probability of sampling sub-canopy individuals. The small deviation in estimates of cover provide a bounds to understand potential treatment effects through time as documented by the visual approach.

Across all treatments and years, I found that weeding plots resulted on average in a 6.7% increase in native perennial percent cover as compared to control plots (Table 1, $p<0.05$; Figure 2). However, there was significant variation around this mean depending on location. In addition, native perennial percent cover also varied by year, increasing the most in the early years of the study (essentially between the first and second year), and declining from 2013 onwards. In fact, the average cover of these categorized plots initially increased from ~40% to greater than 50%, then dramatically decreased to less than 30% by the sixth year of measurement. These differences in time likely reflect variation in annual rainfall across the years, where from 2009 to 2011 seasonal rainfall reached historic averages for the region, but from 2012 on, a protracted drought was entrenched in the region; 2014 recorded the lowest rainfall for many places in Southern

California in recorded history (Griffin and Anchukaitis 2014, Table 2). Though initial native perennial level did not have a significant interaction with treatment for native perennial cover, I found a significant interaction between initial cover level and year (Table 1, $p<0.05$), where the four initial cover levels remained parallel until the final year of the study, when the highest initial cover level dropped below the second and third highest.

Spatially divergent patterns in passive restoration emerged across the data set, where the treatment effect of non-native removal on perennial cover was slightly larger in the coastal than in the inland region (Table 1, $p<0.05$, Figure 3). In this case, much of the difference in treatment effect spatially appears to derive from a period of decreasing perennial cover that began between 2013 and 2014, where inland sites decreased at different rates (weeded-versus-control), thus altering the magnitude of the treatment effect. Plots in the coastal region maintained consistent differences between weeded conditions and controls throughout the duration of the experiment.

Across all treatments, I found that passive restoration by removing non-native species resulted in an average 13.9% increase in native species richness compared to control plots (Table 3, $p<0.05$; Figure 4). Native species richness also varied by year, with highest richness occurring in 2015, presumably reflecting performance of species in the previous, relatively wet years, where dispersal and establishment were likely occurring to a greater extent than in dry years. Richness decreased, across all treatment combinations in the final year of the study, likely related to the co-occurrence of one of the driest growing season yet expressed for the region in the rainfall record (NOAA – State of the Climate, Table 2). Additionally, while I found that species richness tended to be higher in the inland region, passive restoration resulted in a much greater effect on this parameter in the coastal region as compared to the Inland region (Table 3, $p<0.05$; Figure 5).

The year of peak effect of passive restoration on native perennial cover occurred in 2013. Following three years of consistent removal of non-native species, there was on average a difference of 11.2% in native perennial cover between the weeded and control plots (Table 4, $p<0.05$, Figures 2, 6). Evaluating this peak year alone, the initial cover level of plots receiving passive restoration was not a significant factor in predicting measures of success (cover, species richness). However, several interesting patterns emerged – I found that the highest initial cover level, 50-60%, has the second highest treatment effect – a 30% increase in the weeded plots over the control plots, following the second to lowest initial cover level, 30-40%, which had a 45.1% increase. The lowest initial cover level, 20-30% had only an 18.9% increase, while the second highest cover level, 40-50%, which had a 10.8% increase (Table 4, $p<0.05$, Figure 6). These patterns can be further explored by grouping by functional type, with weeded plots being a total average of 27.1% higher for native shrub cover and an average of 20.3% higher for native perennial forb cover (Figure 7). The non-native cover levels in these plots were also significantly affected by weeding, with the lowest cover level (20-30%) being the least affected by treatment, showing a decrease of 65.1% from the control plots to the weeded plots, and the largest effect, a 79.3% decrease, in the second to highest cover level (40-50%) (Table 5, $p<0.05$, Figure 6).

The peak year of weeding effect on native species richness occurred in 2015, where I found a 30.3% increase in weeded plots over control plots (Table 6, $p<0.05$, Figures 4). Native species richness, unlike native perennial cover, responded to the initial cover levels more in the way that I had hypothesized. Native species richness at the lowest initial cover level, 20-30%, was most affected by weeding, with a 39.6% increase in weeding over control plots (Figure 7). This is in contrast to the highest initial cover level, 50-60%, which was least affected by weeding, with just an 11.9% increase in weeded over control plots. Non-native species richness followed a similar pattern, with the largest effect, 36.4% increase in species richness, seen in the lowest initial cover level, 20-30%. It appears that weeding positively affects both native and non-native species richness most strongly in the lowest starting cover level, and least in the highest starting cover level. This pattern in native species richness is driven by both perennial and annual native species richness, where overall native richness is consistently higher in weeded plots, and that the difference between weeded and control plots is lower in the highest initial cover level than at the lowest initial cover level (Figure 7).

Discussion

Land managers spend significant energy and money on restoration, and it is unknown the degree to which the presence of non-native species hinders that effort. Discovering mechanisms that enhance the environment with favorable cost-effective approaches is a key challenge facing restoration ecology, land managers, and policy makers (Kimball et al., 2015). The ability to find simple interventions that re-direct the course of restoration projects would allow managers to spread the impact of potentially limited funds over larger spatial scales. In this thesis, I evaluated an approach at passive restoration, focused on the removal of non-natives species in a water-limited coastal sage scrub, with the goal of interrupting the influence of these species on the composition and growth of the native flora. I evaluated this treatment in the context of such issues as site initial condition and a sharp temperature cline across an environmental gradient. I found that passive restoration is effective at promoting native perennial species recovery in Coastal Sage Scrub rather rapidly (one-to-two years), and positively influenced native species richness on a longer time-scale (five-to-seven years). However, the benefits on native cover associated with passive restoration are significantly influenced by patterns of precipitation, where early gains in native cover associated with relatively wet years are diminished by a protracted drought. It is difficult to speculate on the ecological outcomes if the pattern of rainfall had occurred as an opposite trend (drought first, followed by significant rainfall). Equally as important, it is unknown the degree to which the changes in ecosystem structure and function from passive restoration over this multi-year period may predispose coastal sage scrub to resilient drought responses, allowing more rapid recovery of favorable native plant performance as compared to sites not receiving invasive control upon some future return of relatively high rainfall years. As such, long-term evaluation of restoration success is an important area of research broadly required by many design and implementation questions (Wortley, Hero, and Howes 2013).

The results of my analysis provide a number of interesting outcomes and points of departure for further research. First, I showed that initial native perennial cover level did not influence the recovery of natives undergoing passive restoration, which was unanticipated. Of course, the response variable of interest is native plant cover, which can be influenced by a number of different processes. Removal of non-native species may allow individual shrubs access to more soil resources through release from competition and thus promote the growth of existing stands of native species. It is also possible that removal of non-native species germinating and competing with native germinants for space alters the environment surrounding plant establishment and thus plant density, which can also influence total cover. Finally, non-native species removal may influence the ability of native species to persist through drought (Eilts and Huxman 2013), which acts to maintain cover during periods of resource limitation. As such, the mechanisms underlying this passive restoration approach deserve attention in order to understand its impact on a diversity of localized ecological condition and the spatial and temporal applicability to other restoration contexts.

Though the interaction of initial cover level and treatment on native annual cover and richness are not significant in my analysis, the higher initial cover plots have less annual cover in general, both native as well as non-native, so the effect of treatment could be more noticeable at the lower initial perennial cover levels. Native annual diversity on a small scale has been shown increase resistance to invasion (Kennedy et al. 2002), and it is possible that annual cover and richness are linked, and affected by both initial cover and treatment at the plot scale. Whether the treatment affects native annual diversity, which in turn affects native annual cover, or whether the two properties simply share common factors, requires further study. Since richness in coastal sage scrub is primarily driven by annual species (Westman 1981), further exploration of the impact of non-native species presence and removal on native annual richness is important for restoration.

Secondly, passive restoration is differentially impactful across the environmental cline evaluated in this study. It appears that the coastal sites in my study area experienced a greater response to non-native removal as compared to the inland locations. This pattern appears to be most related to the changes in native perennial cover occurring upon the onset of the regional drought, where all inland treatment combinations and the control treatment for coastal locations demonstrated more significant declines in native perennial cover. It appears that the overall response is in contrast to my initial hypothesis and suggests that other factors than precipitation and temperature may be influencing the response to weeding, including initial species composition within the plots, historical disturbance, or some other unknown variables, all which warrants further exploration.

Finally, though the passive restoration treatment is “effective” in that the weeded plots consistently have higher native cover, the question of whether this is an effective restoration technique may require a more specific analysis and an understanding of the other structural changes in these systems and their long-term implications. Generally, areas to be restored are larger than the experimental plots, and have other considerations, such as a much shorter timeline to “succeed”. Though many restoration projects end after

5 years (Bowler, 2000) and I started seeing effects of treatment in the first year of the treatment, it is unknown whether the treated plots will continue to have higher cover compared to control plots even after the treatment ends, and how long such an advantage may last. Further appropriate scaling of costs through careful analysis would be needed. While this technique is relatively cost- and labor- effective as compared to seeding and planting, it is not applicable to areas with little or no native perennials. The general application of this restoration technique would be to large-scale sites with some level of remaining coastal sage scrub shrubs, although further analysis is needed to assess the level of perennial cover and composition of native species needed to achieve efficacy. Furthermore, spatial variation and history of disturbance can compound the effectiveness of different restoration treatments (eg., Kimball et al., 2015), and understanding how these spatial dynamics influence both the invasion of a site and its potential to be restored is vital to efficient land management.

Evaluating how the treatment and initial cover levels influence recovery from the recent drought will be necessary to further explore the patterns I have documented so far. I anticipate that some sites will recover more readily than others, based on factors such as native perennial species composition and resource availability. The species composition of non-natives is likely to change as well, perhaps away from *Salsola tragus*, which has been abundant at several sites in recent years, and back towards *Brassica nigra* and other non-native grasses.

Taken together, my findings suggest that passive restoration is effective at increasing native cover and richness. Cover increases are achieved primarily through perennial species, and richness from both native perennial and native annual species.

Though initial native cover level did not have an obvious influence on recovery, it may be important to the patterns of cover and richness in perennial versus annual species, which are vital features of this system with implications for higher trophic levels. Spatial variation interacted with treatment, though not the way I expected, and the drought added an extra dimension to this study that suggests long-term approaches to understanding this question are warranted. Other factors, such as species composition and history of disturbance, undoubtedly contribute to the patterns of cover and richness that I have seen over the course of the study. Overall, this study highlights the effect of the removal of non-native species on stands of existing coastal sage scrub.

Figures

Map produced Feb 2011 IRC
Aeiral source: © Eagle Aerial, Flown April 2008

Figure 1. Location of the 10 sites selected for experimental manipulation, indicated by gold stars and location names. At each site, four different perennial plant cover classes were manipulated through non-native species removal to evaluate the effects of passive restoration. Southern, "Coastal" sites include Strawberry Farms, West Canyon, Cattle Crest, Veeh Creek, and Laguna Laurel, where all other sites are categorized as northern or "Inland".

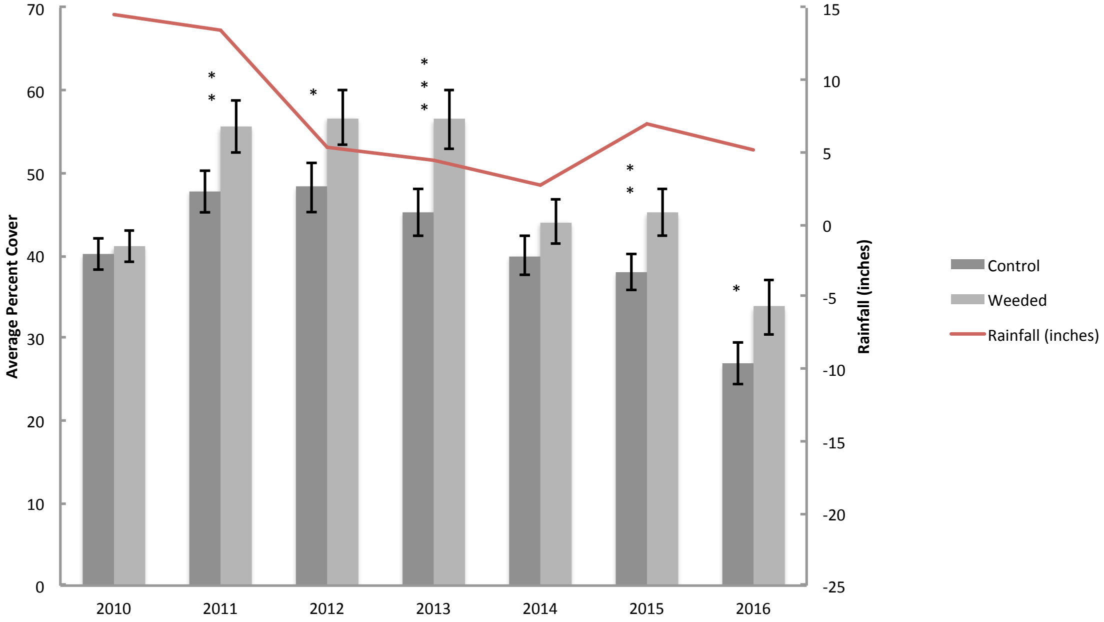

Figure 2. Native perennial species cover in plots receiving passive restoration ('weeded') versus controls through the seven years of the study. The cover of both weeded and control plots increases for several years before a decline after 2013. 2013 was the year with the greatest treatment effect, followed by 2014 that illustrated no significant treatment effect. (* Indicates pairwise significant differences within years between treatments. '***' $p<0.001$; '**' $p<0.01$; '*' $p<0.05$)

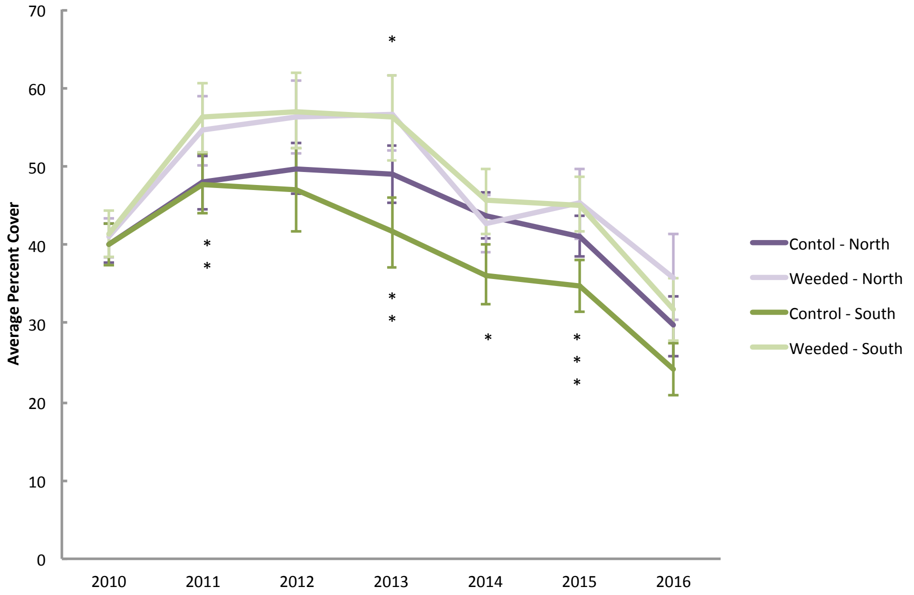

Figure 3. Native perennial species cover in plots receiving passive restoration ('weeded') versus controls, comparing northern and southern regions over the seven years of the study. Overall, the coastal sites were generally more affected by treatment, starting in 2012 and continuing through 2016. However, in 2014 there was a significant treatment by cover interaction, when the inland sites treatment effect decreased dramatically and the coastal sites continued to show a strong treatment effect. (* Indicates pairwise significant differences within years between treatments. '***' $p<0.001$; '**' $p<0.01$; '*' $p<0.05$)

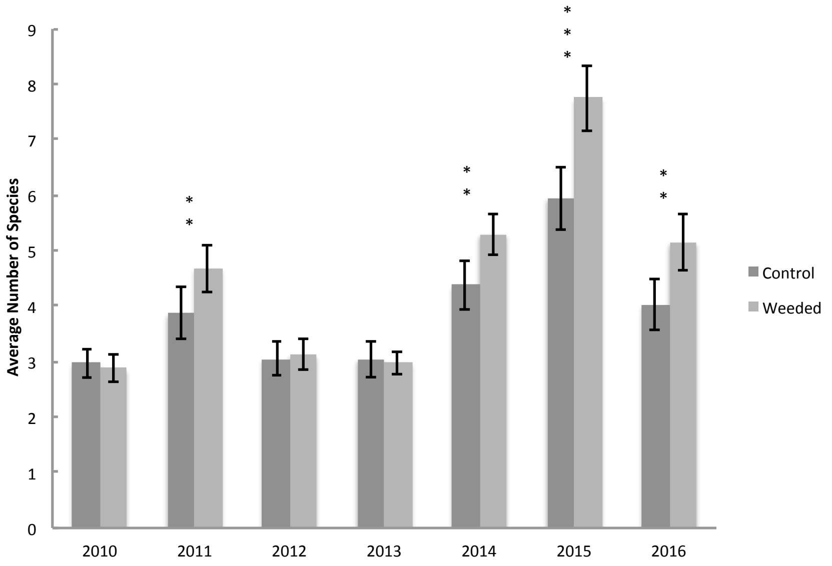

Figure 4. Native species richness in plots receiving passive restoration (‘weeded’) versus controls through the seven years of the study. The richness in of both weeded and control plots increased in 2014 and 2015, with 2015 having the highest species richness so far in the study, followed by a drop in 2016. (* Indicates pairwise significant differences within years between treatments. ‘***’ p<0.001; ‘**’ p<0.01; ‘*’ p<0.05)

Figure 5. Native species richness in plots receiving passive restoration ('weeded') versus controls through the seven years of the study for northern and southern regions. In 2015, the year with the highest native species richness, the inland sites experienced no treatment effect, while the coastal sites continued to have higher native species richness in weeded plots. (* Indicates pairwise significant differences within years between treatments. '***' $p<0.001$; '**' $p<0.01$; '*' $p<0.05$)

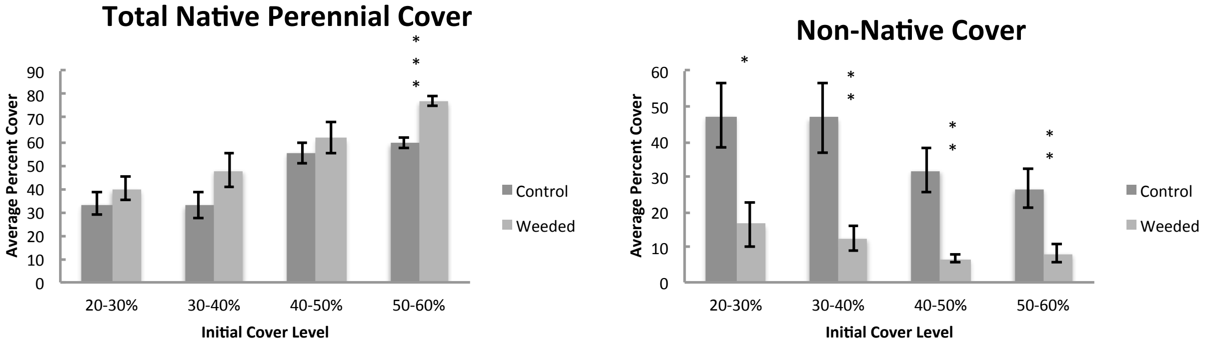

Figure 6. Native perennial species and non-native species area cover in plots receiving passive restoration ('weeded') versus controls across four initial cover levels, in 2013, the year with the highest treatment effect. Contrary to my expectations, native perennial cover level did not have the most drastic treatment effect at lowest initial cover levels. Non-native cover followed a similar, though reversed, pattern with a treatment effect throughout the four cover levels being highest at the second highest cover level, and lowest at the lowest cover level. (* Indicates pairwise significant differences within years between treatments. '***' $p<0.001$; '**' $p<0.01$; '*' $p<0.05$)

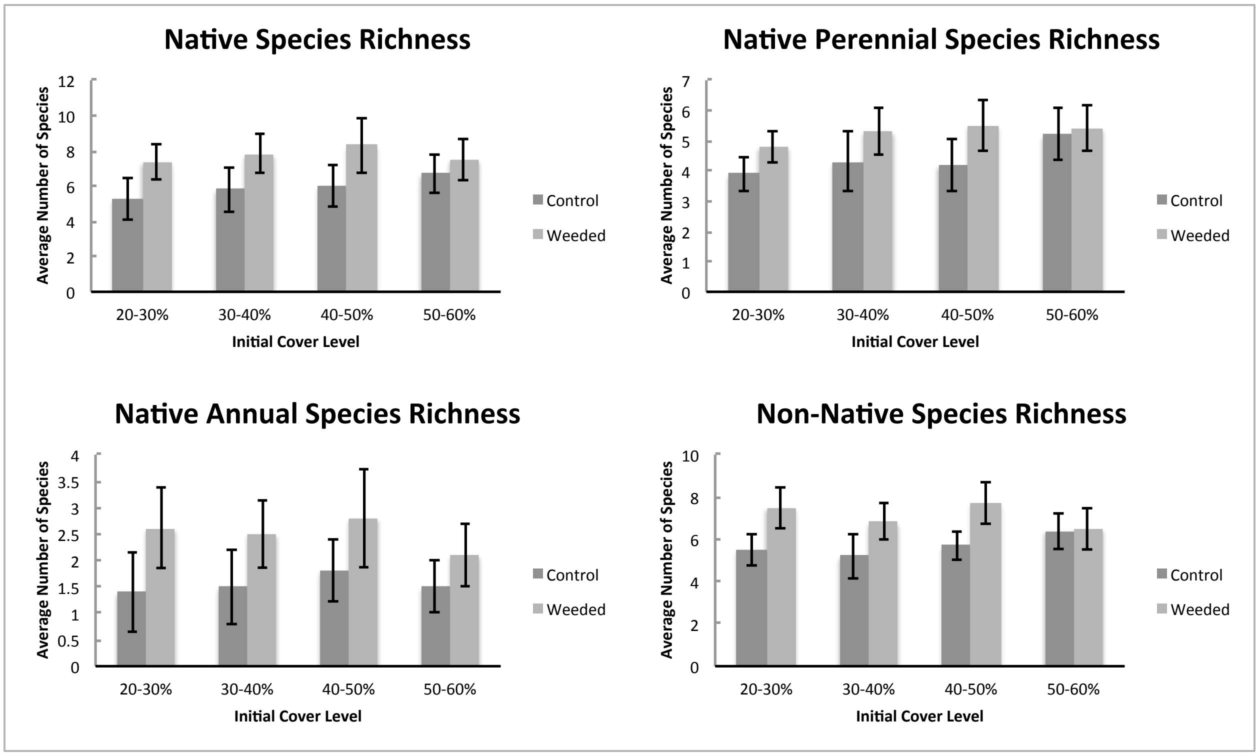

Figure 7. Species richness of functional groups in plots receiving passive restoration ('weeded') versus controls across four initial cover levels, in 2015, the year with the highest treatment effect on native species richness. Native species richness was most affected by treatment at the lowest initial cover level, and least affected at the highest initial cover level. This patterns holds when broken down to native annual and perennial species richness. Interestingly, non-native species richness follows the same pattern, with highest treatment effect at the lowest cover level. (* Indicates pairwise significant differences within years between treatments. '***' $p<0.001$; '**' $p<0.01$; '*' $p<0.05$)

Tables

Table 1. Analysis of variance (ANOVA) with Native Perennial Species Cover as a dependent variable (%) including treatment (weeded versus control), cover (initial cover class), year (of the study), region (Inland/Northern versus Coastal/Southern), and their interactions.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Treatment	1	6048	6048	37.402	2.19E-09	***
Cover	3	54774	18258	112.914	<2e-16	***
Year	6	29475	4912	30.381	<2e-16	***
Treatment:Cover	3	559	186	1.153	0.32728	
Treatment:Year	6	1295	216	1.335	0.24011	
Cover:Year	18	6984	388	2.399	0.00114	**
Treatment:Region	1	716	716	4.43	0.0359	*
Cover:Region	3	3724	1241	7.676	5.26e-05	***
Year:Region	6	557	93	0.574	0.75099	
Treatment:Cover:Year	18	1662	92	0.571	0.9201	
Treatment:Cover:Region	3	425	142	0.876	0.45354	
Treatment:Year:Region	6	362	60	0.373	0.89626	
Cover:Year:Region	18	2446	136	0.84	0.65225	
Treatment:Cover:Year:Region	18	777	43	0.267	0.99905	
Residuals	423	68398	162			

Treatment is ‘weeded’ / ‘control’, while Cover is the initial cover-class categorizations associated with plot layout, and Region is ‘Inland’ versus ‘Coastal’ within the landscape. Significant effects are documented with an ‘*’.

Table 2. Precipitation data from John Wayne Airport, Santa Ana, California, USA for the seven years of the study, compared to the 30 year average (from 1981 to 2010). Hydrologic year is the cumulative precipitation between October and the following September. Data from NOAA and Weather Underground.

Hydrologic Year	Precipitation (in)	% of Average
2009	7.71	57.84
2010	14.61	109.60
2011	13.44	100.83
2012	5.41	40.59
2013	4.52	33.91
2014	2.73	20.48
2015	7.04	52.81
2016	5.25	39.38

Table 3. Analysis of variance (ANOVA) with Native Species Richness as a dependent variable (number of species), including treatment (weeded versus control), cover (initial cover class), year (of the study), region (Inland/Northern versus Coastal/Southern), and their interactions.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Treatment	1	4.07	4.073	28.28	1.70E-07	***
Cover	3	0.71	0.235	1.632	0.1812	
Year	6	46.7	7.783	54.041	<2e-16	***
Treatment:Cover	3	0.26	0.086	0.598	0.61629	
Treatment:Year	6	2.9	0.484	3.358	0.00304	**
Cover:Year	18	1.48	0.082	0.571	0.91994	
Treatment:Region	1	4.52	4.518	31.373	3.84E-08	***
Cover:Region	3	1.07	0.356	2.471	0.06133	.
Year:Region	6	2.88	0.48	3.333	0.00322	**
Treatment:Cover:Year	18	0.83	0.046	0.319	0.99691	
Treatment:Cover:Region	3	1.16	0.387	2.69	0.04591	*
Treatment:Year:Region	6	0.58	0.096	0.667	0.67634	
Cover:Year:Region	18	2.18	0.121	0.842	0.65021	
Treatment:Cover:Year:Region	18	1.12	0.062	0.43	0.98116	
Residuals	423	60.92	0.144			

Treatment is ‘weeded’ / ‘control’, while Cover is the initial cover-class categorizations associated with plot layout, and Region is ‘Inland’ versus ‘Coastal’ within the landscape. Significant effects are documented with an ‘*’.

Table 4. Analysis of variance (ANOVA) with Native Perennial Species Cover in 2013 as a dependent variable (%) including treatment (weeded versus control), cover (initial cover class), region (Inland/Northern versus Coastal/Southern), and their interactions.

Source	Df	SumSq	MeanSq	Fvalue	Pr(>F)	
Treatment	1	2526	2526	13.585	0.000516	***
Cover	3	13484	4495	24.177	3.63E-10	***
Treatment:Cover	3	540	180	0.968	0.414539	
Treatment:Region	1	226	226	1.216	0.274799	
Cover:Region	3	1144	381	2.051	0.117185	
Treatment:Cover:Region	3	55	18	0.099	0.96048	
Residuals	56	10411	186			

Treatment is ‘weeded’ / ‘control’, while Cover is the initial cover-class categorizations associated with plot layout, and Region is ‘Inland’ versus ‘Coastal’ within the landscape. Significant effects are documented with an ‘*’.

Table 5. Analysis of variance (ANOVA) with Non-Native Species Cover in 2013 as a dependent variable (%) including treatment (weeded versus control), cover (initial cover class), region (Inland versus Coastal), and their interactions.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Treatment	1	14770	14770	71.577	1.36E-11	***
Cover	3	3183	1061	5.142	0.00328	**
Treatment:Cover	3	723	241	1.168	0.33017	
Treatment:Region	1	1110	1110	5.38	0.02405	*
Cover:Region	3	1214	405	1.962	0.13022	
Treatment:Cover:Region	3	233	78	0.376	0.77079	
Residuals	56	11555	206			

Treatment is ‘weeded’ / ‘control’, while Cover is the initial cover-class categorizations associated with plot layout, and Region is ‘Inland’ versus ‘Coastal’ within the landscape. Significant effects are documented with an ‘*’.

Table 6. Analysis of variance (ANOVA) with Native Species Richness in 2015 as a dependent variable (number of species) including treatment (weeded versus control), cover (initial cover class), region (Inland versus Coastal), and their interactions.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Treatment	1	3.166	3.166	15.155	0.000266	***
Cover	3	0.337	0.112	0.538	0.658104	
Treatment:Cover	3	0.395	0.132	0.63	0.598694	
Treatment:Region	1	1.779	1.779	8.516	0.005059	**
Cover:Region	3	0.919	0.306	1.466	0.233723	
Treatment:Cover:Region	3	0.298	0.099	0.476	0.700404	
Residuals	56	11.699	0.209			

Treatment is ‘weeded’ / ‘control’, while Cover is the initial cover-class categorizations associated with plot layout, and Region is ‘Inland’ versus ‘Coastal’ within the landscape. Significant effects are documented with an ‘*’

LITERATURE CITED

AghaKouchak, Amir, Linyin Cheng, Omid Mazdiyasni, and Alireza Farahmand. 2014. “Global Warming and Changes in Risk of Concurrent Climate Extremes: Insights from the 2014 California Drought.” *Geophysical Research Letters* 41 (24): 8847–52.

Beever, EA, and JL Belant. "Ecological consequences of climate change: synthesis and research needs." Pp 285-297, in EA Beever, JL Belant (eds) *Ecological Consequences of Climate Change: Mechanisms, Conservation, and Management.* CRC Press, 342 pages.

Benayas, José M. Rey, Adrian C. Newton, Anita Diaz, and James M. Bullock. 2009. “Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis.” *Science* 325 (5944): 1121–24.

Bowler, P.A. 2000. “Ecological Restoration of Coastal Sage Scrub and Its Potential Role in Habitat Conservation Plans.” *Environmental Management* 26 (S1): S85–96.

D’Antonio, C.M., T.L. Dudley, and M. Mack. 1999. “Disturbance and Biological Invasions: Direct Effects and Feedbacks.” In *Ecosystems of Disturbed Ground. Vol.16*, 413–52.

D’Antonio, Carla M, and Laura A Meyerson. 2002. “Exotic Plant Species as Problems and Solutions in Ecological Restoration.” *Restoration Ecology* 10 (4): 703–13.

Davis, Frank W., Peter A. Stine, and David M. Stoms. 1994. “Distribution and Conservation Status of Coastal Sage Scrub in Southwestern California.” *Journal of Vegetation Science* 5 (5): 743–56.

Diffendorfer, James E, Robert E Chapman, Jennifer M Duggan, Genie M Fleming, Milan Mitrovitch, Matthew E. Rahn, and Rosalie del Rosario. 2002. “Coastal Sage Scrub Response to Disturbance . A Literature Review and Annotated Bibliography.” *California Department of Fish and Game*, 1–87.

Diffendorfer JE, Fleming GM, Duggan JM, Chapman RE, Rahn ME, Mitrovich MJ, Fisher RN. 2007. "Developing terrestrial, multi-taxon indicies of biological integrity: an example from coastal sage scrub." *Biological Conservation* 140:130-141

Eilts, J.A., and T. E. Huxman. 2013. “Invasion by an Exotic, Perennial Grass Alters Responses of a Native Woody Species in an Arid System.” *Journal of Arid Environments* 88. Elsevier Ltd: 206–12

Eliason, Scott A., and Edith B. Allen. 1997. “Exotic Grass Competition in Suppressing Native Shrubland.” *Restoration Ecology* 5 (3): 245–55.

Franklin, Janet. 1995. “Predictive Vegetation Mapping: Geographic Modelling of Biospatial Patterns in Relation to Environmental Gradients.” *Progress in Physical Geography* 19 (4): 474–99.

Franklin, and Janet. 1998. “Predicting the Distribution of Shrub Species in Southern California from Climate and Terrain-Derived Variables.” *Journal of Vegetation Science* 9 (1993): 733–48.

Gallardo, Belinda, Miguel Clavero, Marta I. Sánchez, and Montserrat Vilà. 2016. “Global Ecological Impacts of Invasive Species in Aquatic Ecosystems.” *Global Change Biology* 22 (1): 151–63.

Griffin, Daniel, and Kevin J Anchukaitis. 2014. “How Unusual Is the 2012 – 2014

California Drought ?” *Geophysical Research Letters* 41: 9017–23.

Hobbs, Richard J., and Viki A. Cramer. 2008. “Restoration Ecology: Interventionist Approaches for Restoring and Maintaining Ecosystem Function in the Face of Rapid Environmental Change.” *Annual Review of Environment and Resources* 33 (1): 39–61.

Hobbs, Richard J, and Laura F Huenneke. 1992. “Disturbance , Diversity , and Invasion : Implications for Conservation” *Conservation Biology* 6 (3): 324–37.

Holl, K. D., and T. M. Aide. 2011. “When and Where to Actively Restore Ecosystems?” *Forest Ecology and Management* 261 (10). Elsevier B.V.: 1558–63.

Keeley, Jon E., Melanie Baer-Keeley, and C.J. Fotheringham. 2005. “Alien Plant Dynamics Following Fire in Mediterranean-Climate California Shrublands.” *Ecological Applications* 15 (6): 2109–25.

Keeley, Jon E., C.J. Fotheringham, and Marco Morais. 1999. “Reexamining Fire Suppression Impacts on Brushland Fire Regimes.” *Science* 284 (5421): 1829–32.

Keeley, Jon E., and Sterling C. Keeley. 1984. “Postfire Recovery of California Coastal Sage Scrub.” *American Midland Naturalist* 111 (1): 105–17.

Kennedy, Theodore a, Shahid Naeem, Katherine M Howe, Johannes M H Knops, David Tilman, and Peter Reich. 2002. “Biodiversity as a Barrier to Ecological Invasion.” *Nature* 417 (6889): 636–38.

Kimball, Sarah, Michael L. Goulden, Katharine N. Suding, and Scot Parker. 2014. “Altered Water and Nitrogen Input Shifts Succession in a Southern California Coastal Sage Community.” *Ecological Applications* 24 (6). Ecological Society of America: 1390–1404.

Kimball, Sarah, Megan Lulow, Quinn Sorenson, Kathleen Balazs, Yi Chin Fang, Steven J. Davis, Michael O’Connell, and Travis E. Huxman. 2015. “Cost-Effective Ecological Restoration.” *Restoration Ecology* 23 (6): 800–810.

Kimball S, Lulow ME, Balazs KR, Huxman TE. 2017. "Predicting drought tolerance from slope aspect preference in restored plant communities." *Ecology and Evolution* 7:3123-3131

Landres, Peter B, Penelope Morgan, and Frederick J Swanson. 1999. “Overview of the Use of Natural Variability Concepts in Managing Ecological Systems.” *Ecological Applications* 9 (4): 1179–88.

Mack, Richard N., Daniel Simberloff, W. Mark Lonsdale, Harry Evans, Michael Clout, and Fakhri A. Bazza. 2000. “Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control.” *Ecological Applications* 10 (3): 689–710.

Marushia, Robin G., and Edith B. Allen. 2011. “Control of Exotic Annual Grasses to Restore Native Forbs in Abandoned Agricultural Land.” *Restoration Ecology* 19 (1): 45–54.

Minnich, Richard. A. 1983. “Fire Mosaics in Southern California and Northern Baja California.” *Science*.

O’Leary, John F., and Walter E. Westman. 1988. “Regional Disturbance Effects on Herb Succession Patterns in Coastal Sage Scrub.” *Journal of Biogeography* 15 (5): 775–86.

Riordan, Erin Coulter, and Philip W Rundel. 2014. “Land Use Compounds Habitat Losses under Projected Climate Change in a Threatened California Ecosystem.” Edited by Ben Bond-Lamberty. *PloS One* 9 (1). Public Library of Science: e86487.

Robbins, Alicia S. T., and Jean M. Daniels. 2012. “Restoration and Economics: A Union Waiting to Happen?” *Restoration Ecology* 20 (1): 10–17.

Simberloff, Daniel, Jean Louis Martin, Piero Genovesi, Virginie Maris, David A. Wardle, James Aronson, Franck Courchamp, et al. 2013. “Impacts of Biological Invasions: What’s What and the Way Forward.” *Trends in Ecology and Evolution* 28 (1): 58–66.

Suding, Katharine N., Katherine L. Gross, and Gregory R. Houseman. 2004. “Alternative States and Positive Feedbacks in Restoration Ecology.” *Trends in Ecology and Evolution* 19 (1): 46–53.

Talluto, Matt V., and Katharine N. Suding. 2008. “Historical Change in Coastal Sage Scrub in Southern California, USA in Relation to Fire Frequency and Air Pollution.” *Landscape Ecology* 23 (7): 803–15.

Vitousek, Peter M., Carla M. D’Antonio, Lloyd L. Loope, Marcel Rejm??nek, and Randy Westbrooks. 1997. “Introduced Species: A Significant Component of Human-Caused Global Change.” *New Zealand Journal of Ecology* 21 (1): 1–16.

Westman, Walter E. 1981. “Diversity Relations and Succession in Californian Coastal Sage Scrub.” *Ecology* 62 (1): 170–84.

Westman, WE. 1982. “Coastal Sage Scrub Succession.” *USDA Forest Service, Pacific Southwest Forest and*, no. 1978: 91–99.

Wortley, Liana, Jean-Marc Hero, and Michael Howes. 2013. “Evaluating Ecological Restoration Success: A Review of the Literature.” *Restoration Ecology* 21 (5): 537–43.