

2016

Using Linear Mixed Models to Analyze Native and Non-Native Species Abundances in Coastal Sage Scrub

kaylee anderson
Scripps College

Recommended Citation

anderson, kaylee, "Using Linear Mixed Models to Analyze Native and Non-Native Species Abundances in Coastal Sage Scrub" (2016).
Scripps Senior Theses. Paper 807.
http://scholarship.claremont.edu/scripps_theses/807

This Open Access Senior Thesis is brought to you for free and open access by the Scripps Student Scholarship at Scholarship @ Claremont. It has been accepted for inclusion in Scripps Senior Theses by an authorized administrator of Scholarship @ Claremont. For more information, please contact scholarship@cuc.claremont.edu.

**USING LINEAR MIXED MODELS TO ANALYZE NATIVE AND NON-
NATIVE SPECIES ABUNDANCES IN COASTAL SAGE SCRUB**

A THESIS PRESENTED

by

KAYLEE MICHAEL ANDERSON

TO:
THE KECK SCIENCE DEPARTMENT
OF CLAREMONT MCKENNA, PITZER, AND SCRIPPS COLLEGES

IN PARTIAL FULFILLMENT OF
THE DEGREE OF BACHELOR OF ARTS

SENIOR THESIS IN BIOLOGY
APRIL 25, 2016

Table of Contents

Abstract	3
Introduction	4
Materials and Methods	9
Results	13
Discussion	19
Conclusion	23
Acknowledgements	24
Literature Cited	25

Abstract

Coastal Sage Scrub (CSS) is a low scrubland plant community native to the coasts of California, housing many threatened and endangered species. Due to the invasion of non-native plants, many areas of CSS have type converted to annual grasslands and the fire frequency has accelerated; fire in turn, may facilitate further invasion, leading to a loss of biodiversity. While many studies document post-fire succession in these communities, pre-fire data are rarely available for comparison, especially data on seedling emergence. I analyzed post-fire recovery of a type-converted grassland community, comparing seedling emergence data for the first and third year after fire to the three years preceding the fire. Non-native species abundances declined more after the fire than did native abundances. This pattern was still present in 2015, three years post-fire. Two native species, *Amsinckia menziesii* var. *intermedia* (*Amsinckia*) and *Phacelia distans* (*Phacelia*), were subjects of seed addition treatments pre-fire, but I found no evidence that past seeding increased their abundances post-fire. *Amsinckia* did recover to its pre-fire density three years after the fire, while the density of *Phacelia* declined over 75% in both the year immediately post-fire and three years after the fire. However, a third native species, *Lupinus bicolor* (*Lupinus*), was both much more abundant and also more spatially widespread both immediately after the fire and two years later. This supports the hypothesis that *Lupinus* is stored in the soil seed bank and the fire may have given this species the opportunity to recover by lowering abundances of non-native competitors. This analysis will inform future conservation efforts by improving our understanding of how seed banks impact the post-fire recovery of native species.

Introduction

The invasion of exotic annual plants of Mediterranean origin into semi-arid shrub ecosystems throughout the Western United States continues to cause the conversion of large areas into communities dominated by annual grasses (Vitousek 1990). It is commonly acknowledged the invasions present a major threat to the biodiversity of native communities. An estimated 400 of the 958 threatened and endangered species in the United States are listed as a result of competition with, or predation by invasive species (Wilcove et al., 1998, cited in Pimentel et al., 2005). The exotic species can affect the native plants by monopolizing limiting resources, altering soil stability, promoting erosion, and changing the fire regime (Vitousek 1990, Richardson et al. 2000). Invading species that alter the fire trends are recognized to be the most impactful invaders (Vitousek 1990). Due to an increase in natural litter from the invasive species, the fire frequency increases. After fires, native species often recover at a slower rate than non-native species. In turn, this can lead to more fires fueled by invasive species, creating a self-perpetuating feedback loop. This effect has the potential to cause a drastic shift towards an invasive species dominated ecosystem.

Coastal Sage Scrub

Coastal sage scrub (CSS), a native California plant community, experienced one of the most dramatic known ecological invasions by annual grasses and forbs native to Eurasia and the Mediterranean in the 1850's (Mooney et al. 1986). Historically, CSS was completely dominated by shrubs, however much has transformed into what is known as, type-converted grassland. This transition is due to grasses invading the land until the grasses exclude the shrubs.

Over three decades ago, it had already been estimated that 85-90% of CSS biodiversity had been lost (Westman 1981). In addition to the native grasses, the invasive species continue to present a great threat to the large number of endangered, threatened and “special concern” species (CNPS 2001). Due to the growing concern over CSS decline and loss of biodiversity, the preservation and restoration of CSS vegetation is a priority (Rubinoff 2001).

Historic grazing, habitat fragmentation due to urbanization, increased nitrogen deposition, and increased fire frequency facilitate the invasion of the Mediterranean annual grasses (Alberts et al. 1993, Zink et al. 1995, Allen et al. 2000). Because of the high level of disturbance to California land, the native species struggle to maintain a stable ecosystem, whereas the success of the invasion of CSS can be contributed to the exotic species’ tolerance for grazing, drought, and disturbance (D’Antonio *et al.* 2007). Interestingly, through seed-addition experiments, native species in CSS are perceived to be superior competitors, but they have low seed dispersal abilities, limiting their dominance in type-converted grasslands (Seabloom *et al.* 2003). The invasive species are known to quickly colonize these disturbed areas, followed by little to no natural re-colonization of CSS (Stylinski & Allen 1999). This is in part due to their characteristic high rates of propagation and germination, suppressing the rejuvenation of CSS (Eliason and Allen 1997). These traits also can suppress the germination and growth of native shrubs (Eliason and Allen 1997, Allen et al. 2000).

Impact of Fire on CSS

While native CSS exhibits a fire return of approximately every 30 years, with the large and growing presence of exotic species, the average fire interval has shortened to

only 8 years (Keeley 1984, Minnich and Dezzani 1998). As the abundance of exotic annual species increases, the environment is altered (Wolkovich *et al.* 2009). Characteristic of the CSS invasion, exotic species are capable of shifting the environment, further facilitating the invasion, and through a mechanism of increasing litter quantities, the fire regime accelerates (D'Antonio and Vitousek, 1992). It is said that CSS benefits from their natural fire frequency because many native plants are adapted to fire and can resprout or germinate from the seed bank in response. Some CSS species are even stimulated to germinate by wood charate and heat (Keeley 1987). However, the accelerated fire regime is ultimately observed to only further non-native species domination (Keeley 1984, D'Antonio and Vitousek, 1992).

While research regarding the succession of CSS after a fire is available, the results of the studies are often contradictory. Some researchers have observed only sporadic resprouting of coastal sage scrub (Kirkpatrick and Hutchinson 1980, Zelder 1977), whereas others have found a widespread resprouting ability of native species (Westman 1981, Wells 1962). Aspects of variability in the methodology are likely the cause of the diverse results; for example, some study sites were highly invaded, while others were not. While these previous studies follow the succession for up to two years, many of the studies do not have a pre-fire reference point. This is problematic because there are no long-term observations of the effects of burns at these sites and no previously recorded species abundance trends.

Recent studies are limited, however, the accelerated fire regime has been observed to prevent the reestablishment of CSS, ultimately resulting in type-conversion (Davis *et al.* 2004; Talluto and Suding 2008). The focuses of these studies are

Riversidian and Venturan sites; however local ectopic variation exists within CSS. This means CSS is found around many areas of southern California, but there are local climate differences, and subsequently the patterns of recovery will vary. For example, a more arid climate would likely recover slower than a site with more precipitation. Research in more burn sites would be beneficial to understanding the recovery of specific CSS sites.

Further, Gressard (2012) found results suggesting that the presence of invaders reduces the native species abundance recovery post-fire, but given a long enough recovery period, native species are able to completely recuperate. Nevertheless, long-term research involving both pre- and post-fire records at an individual site is sparse.

Seed Banks

While the recovery and restoration of aboveground invaded CSS has been studied, the role of soil seed banks is less well understood due to challenges presented in studying them. Soil seed banks are defined as viable seeds stored in the soil (Roberts 1981). Studies on seed banks can provide insight to the future aboveground vegetation, species' seed production, and uncover the duration each seed persists in the soil (van der Valk and Pederson 1989). An important role of seed banks is they offer an effective means for plants to avoid temporally unfavorable habitats. For example, a species may not be able to survive a fire, but can have dormant seeds in the seed bank with the ability to germinate after the fire (Bond and Van Wilgen 1996).

Fire has an immense impact on soil seed banks. Soil heating, wood charate, and smoke can alter the density and composition of the seed bank (Hill and French 2003, Coates 2003). Since the composition and the number of residual seeds in a soil seed

bank will directly affect the future vegetation, damage to a seed bank can dramatically affect the recovery of the habitat after a disturbance. The timing and the frequency of the fire play critical roles in the survivorship of the seeds (Roche et al. 1998). Yearly fall fires were found to destroy nearly all CSS native species. Another study found that a late-season fire disproportionately reduced the number of exotic grass seeds, but did not significantly change the native seed density (Cione *et al.* 2002, Cox and Allen 2008).

One study suggests there is a small window of opportunity immediately post-fire to help manage invasive species and increase native diversity; however, exotic species were seen to recover within one season after the fire, so the time to act is minimal (Cox and Allen 2008). This previous research suggests some interesting patterns in post-fire recovery. After soil samples were collected, they germinated seeds in a lab, where the seeds received frequent watering. The patterns found by Cox and Allen (2008) are unlikely to be reproduced in the field, especially if some post-fire years receive unusually low rainfall. Therefore, the effects of natural environmental conditions on the germination after a fire are of particular interest. Furthermore, it's important to note native grasses often do not recover immediately after a fire, but the non-native forbs recover quickly after fires due to their competitive seedling stage behaviors, and especially in the absence of native species competition (Eliason and Allen, 1997, Cox and Allen, 2008).

Research Questions and Study Goals

This study utilizes three years of pre-fire and two years of post-fire data on seedling emergence to explore questions about the impact fire has on the native and exotic species germination in type-converted California grasslands.

With these data, I asked the questions: (1) how did the fire impact the abundances of native and non-native species? and (2) what were the spatial patterns of recovery after the fire, and do they seem most consistent with colonization by dispersal, or with emergence from the seed bank?

Materials and Methods

Study site

Data was drawn upon from past field experiments and studies carried out between 2009 and 2016 in the Robert J. Bernard Field Station (BFS) in Claremont, California (Fig. 1). The BFS, approximately 86 acres of land located within the properties of the Claremont College Consortium, contains coastal sage scrub, Riversidian alluvial fan scrub, live oak forest, and grassland. The climate is considered a “Mediterranean Climate,” characterized by sunny, warm, and rather

low precipitation, restricted to the cooler winter months. Due to this climate, the growing season for vegetation is limited to approximately October to April (<http://www.bfs.claremont.edu>). Historically in the BFS, rainfall averages 44.04 cm per year (1971-2000, Western Regional Climate Center for Claremont, CA). However, 2015

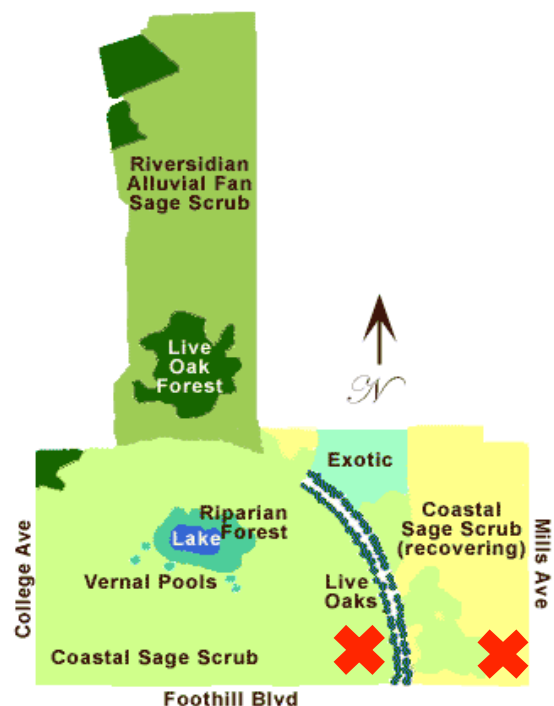


Fig 1. Map of the BFS. Retrieved from <http://www.bfs.claremont.edu/overview.html>. ✖ = locations of established blocks

ranked as the second most severe drought on record in California due to unusually high temperatures and low precipitation (NOAA 2016).

In September 2013, approximately 17 acres of the BFS along the Foothill Blvd frontage were charred in a brush fire caused by sparks from a power tool used by Golden State Water Company (<http://www.bfs.claremont.edu>).

Like many coastal sage scrub habitats, the BFS is type-converted, likely a result of past disturbances, such as farming (Thomson et al. 2016). The native species this study focuses on are *Amsinckia menziesii* var. *intermedia* (*Amsinckia*), *Phacelia distans* (*Phacelia*), and *Lupinus bicolor* (*Lupinus*). These three species are all annual plants. The common exotic species include *Bromus diandrus*, *B. madritensis*, *B. hordeaceus*, and *Erodium botrys*.

Block Establishment

Over the course of 3 years, 26 blocks were established in random locations in the fields of the BFS. Eight blocks were established in 2009, ten blocks in 2010, and eight blocks in 2012 (Thomson *et al.* 2016). Each block measures 2.5 m x 2.5 m, with four 0.75 m x 0.75 m plots, one in each corner, and a 1 m buffer zone between the plots. The data were collected by subsampling a total of nine 0.1 m x 0.1 m subplots evenly spaced throughout the plot.

These blocks were originally used for an experiment to cross two factors— native seed addition and invasive competitor removal. The four plots in each block were assigned one of the following treatments: control, native seed addition, exotic species removal, and both native seed addition and exotic species removal. Thatch was removed from competitor reduction plots, followed by clipping the grasses every 4-5

weeks thereafter. The native species that were subject to seed addition were *Amsinckia*, *Phacelia*, and *Clarkia purpurea* var. *quadrivulnera*. The native seed addition treatments were only applied once in any given block, in November of the year the block was first established.

Data Collection

The week following a significant rainstorm (>0.1 cm), plant surveys were used to determine the number of individuals for each species present in each plot (Table 1). If a seedling was unidentifiable, the species was recorded as “unknown.”

Table 1. The dates of the censuses recorded for each year.

	2009-2010	2010-2011	2011-2012	2013-2014	2015-2016
1	Oct. 27-Nov. 3	Oct. 18-22	Oct. 12-14	Oct. 17-20	Oct. 14-20
2	Dec. 17-19	Nov. 4-9	Dec. 1-3	Nov. 8-13	Nov. 14-22
3	N/A	Dec. 9-13	Dec. 21-22	Dec. 3-18	Jan. 23-Feb. 22

For each species found, abundance was estimated and classified into the following categories: (a) 1, (b) >1 but ≤ 5, (c) > 5 and ≤ 10, (d) > 10 but ≤ 25, (e) > 25 and ≤ 50, (f) > 50. If a native species was found in less than three subplots, a “whole” plot density was recorded. The subplot data were used to estimate the whole plot abundances, when whole plot counts were not taken.

Data Analysis

The data were organized into three groups: pre-fire (years 2010, 2011, and 2012), immediate post-fire (year 2013) and 3 years post-fire (year 2015). *Amsinckia* and *Phacelia* were included in this study because they were part of the original seeding experiment and were found in a reasonable number of plots, before and after the fire. Although *Clarkia* was in the seeding experiment, it was not present in any plots, pre- or

post-fire. *Lupinus* was chosen as another native species for analysis because it was found in at least some plots before and after the fire.

Since *Amsinckia* and *Phacelia* were both subject to seed addition experiments, the same analyses were carried out for both species. Multiple data points were recorded each year to represent the different censuses. Overtime, the densities tended to increase as more individuals germinated, therefore, a maximum value was used as a representative of each year, instead of a mean or sum value. Due to normality problems of the data, a square root transformation was applied to the densities for *Amsinckia* and *Phacelia*.

The design of this study incorporated both fixed and random effects. The random effects were the blocks and the plots. The plots were a random effect because species densities were measured repeatedly in each plot over multiple years. The fixed effects included the seed addition treatment (past seeding or no seeding), and timing with respect to fire (pre-fire, immediate post-fire, or three years post-fire). A linear mixed model was used to analyze the impact of the fire on seedling densities of *Amsinckia* and *Phacelia*.

To test for the significance of the two fixed effects, a full model was fit to the data, including both fixed and random effects, using the lme4 package 1.1-7 (Bates *et al.* 2014) in R. A manual step-wise analysis was then carried out, removing one factor at a time. At each step, the fixed factor with the weakest evidence for an effect, as reported by the t statistic, was removed. A Likelihood Ratio Test was conducted comparing the reduced model with the model from the previous step. The test revealed if removing the

factor significantly reduced the ability of the model to predict density. This process was repeated until all fixed effects had been removed, and their significance assessed.

For the *Lupinus* abundances, no past seed addition experiments had been conducted. Because the species densities of *Lupinus* in plots were either low or not present, the data were converted to a categorical variable, measuring presence and absence of the species in a plot. Chi-square contingency tables in R were utilized to determine whether the probability of finding plots where *Lupinus* was present before the fire differed from the probability of finding *Lupinus* either a) in 2013 (immediate post-fire) or b) in 2015 (3 years post-fire).

Results

Species Abundance

Both non-native and native species experienced the highest abundances in 2010 (Fig. 2 & 3). The non-native species were greatly more abundant overall than the native species (Mean \pm SE: max: 339.8 ± 20.8 non-native vs. max: 22.4 ± 3.4 native). A smaller range of densities was observed between all five years for the native species (Min: 9.3 ± 0.9 in 2013 and max: 22.4 ± 3.4 in 2010), than the difference between non-native species (Min: 85.4 ± 7.1 in 2015 and max: 339.8 ± 20.8 in 2010). Interestingly, the non-native species abundance dropped quite significantly in the post-fire years (93.3 ± 5.2 in 2013, 85.4 ± 7.1 in 2015). The native species declined in abundance in the immediate post-fire year, 2013, although the abundance recovered by 2015.

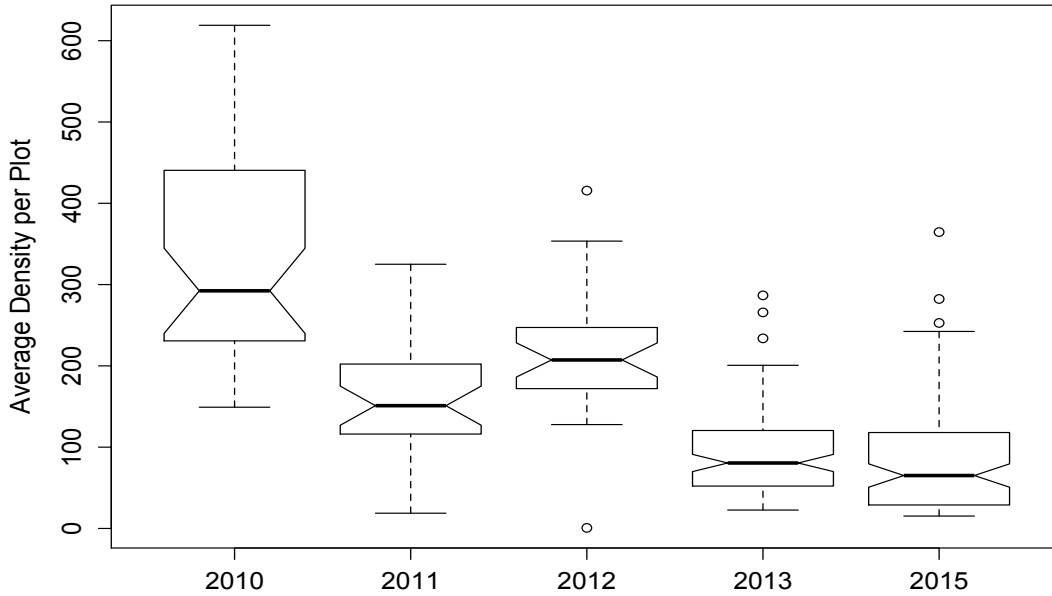


Figure 2. The average plot density of non-native species during the 2010 to 2015 growing season. Solid bars represent the median, notches the standard error, boxes the first and third quartile, whiskered bars the 95th percentile, circles outliers.

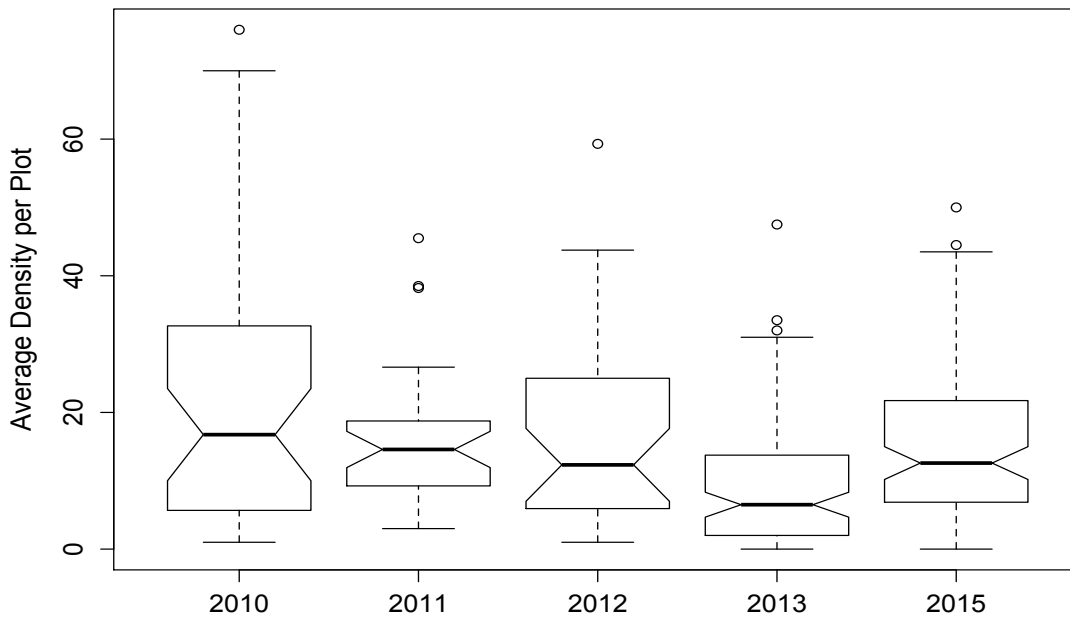


Figure 3. The average plot density of native species during the 2010 to 2015 growing season. Solid bars represent the median, notches the standard error, boxes the first and third quartile, whiskered bars the 95th percentile, circles outliers.

Mixed Models

Different times with respect to fire showed significant differences in *Amsinckia* density (Fig. 4, LRT, $df = 2$, $X^2 = 49.5$, $p < 0.0001$). Specifically, the first year post-fire revealed reduced *Amsinckia* abundances relative to pre-fire conditions (estimate of difference with SE: -1.02 ± 0.17), but the third year post-fire was no different than pre-fire (0.03 ± 0.18).

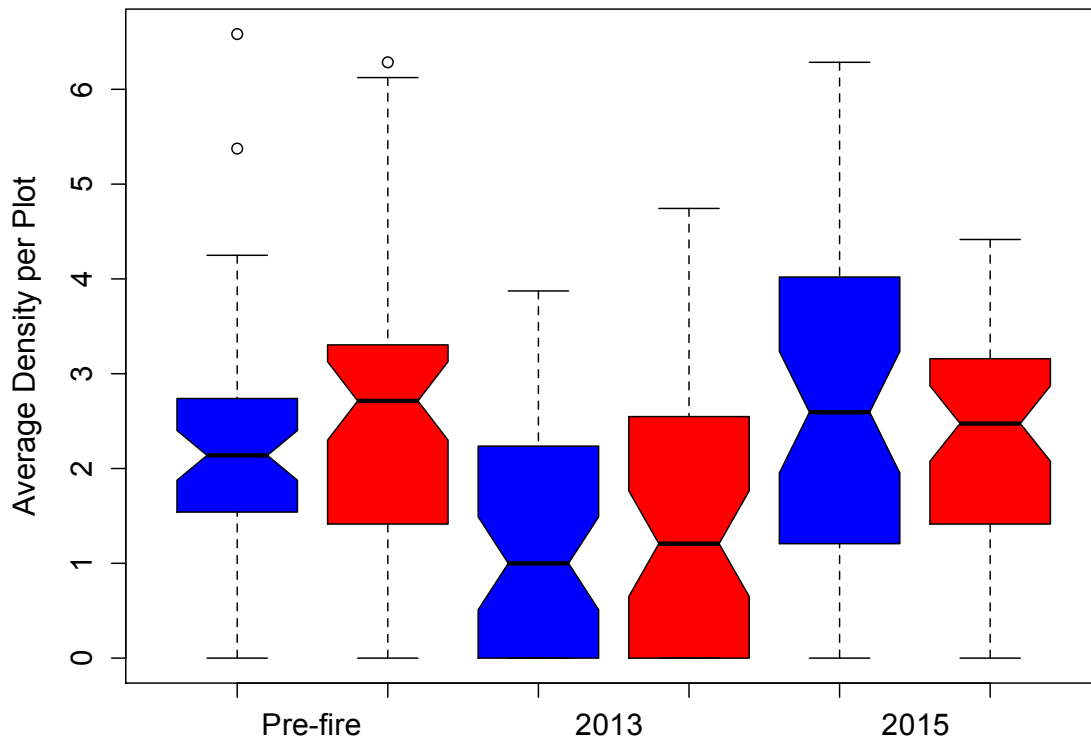


Figure 4. The effects of seed addition and timing with respect to fire on the average germination of *Amsinckia* per plot in pre-fire growing seasons, immediate post-fire growing season, and two years post-fire. Solid bars represent the median, notches the standard error, boxes the first and third quartile, whiskered bars the 95th percentile, circles outliers. ■ = Not Seeded, ■ = Seeded

The species density recovered to about 2.42 ± 0.18 germinants/plot in 2015, a similar to pre-fire density (2.39 ± 0.22). While the pre-fire abundances show some evidence of effect due to past seeding (Fig. 4), the seeding treatments did not have any statistically significant effect on the densities of *Amsinckia* (LRT, $df = 1$, $X^2 = 0.5$, $p =$

0.48). For *Amsinckia*, there was no significant interaction between seeding treatments and time with respect to fire (LRT, $df = 2$, $X^2 = 2.4$, $p = 0.3$).

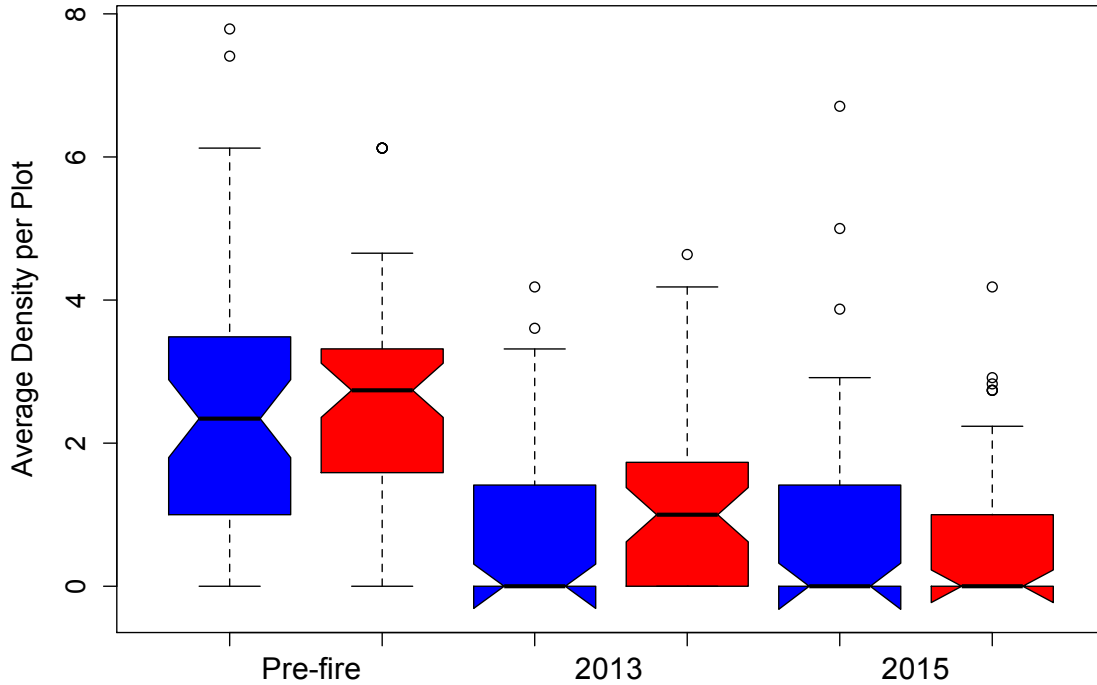


Figure 5. The effects of seed addition and fire occurrence on the average germination of *Phacelia* per plot in pre-fire growing seasons, immediate post-fire growing season, and three years post-fire. Solid bars represent the median, notches the standard error, boxes the first and third quartile, whiskered bars the 95th percentile, circles outliers. ■ = Not Seeded, ■ = Seeded

The densities for *Phacelia* differed among different times with respect to fire (Fig 5; LRT, $df = 2$, $X^2 = 82.9$, $p < 0.0001$). Similar to *Amsinckia*, *Phacelia* also exhibited the highest abundance in the pre-fire years. *Phacelia* declined in the first year post-fire (estimated difference with SE: -1.57 ± 0.19), and even more so, three years post-fire (-1.78 ± 0.20). These declines were even stronger than observed for *Amsinckia*: 75.2% decline in 2013 and 77.5% in 2015, both relative to pre-fire densities. While *Amsinckia* abundances recovered by 2015, there was no noticeable recovery of *Phacelia* three

years after the fire. Interestingly, the graphs show a potential seeding effect in 2013, but the seeding effect and the interaction between seeding treatment and time were both not significant (LRT, $df_{\text{seeding}} = 1, X^2 = 0.7, p = 0.79$; $df_{\text{interaction}} = 2, X^2 = 1.72, p = 0.42$).

Pre-fire vs. Post-fire

In 2013, the growing season immediately after the fire, 29.1% of the plots that did not contain *Lupinus* prior to the fire contained *Lupinus* (Fig. 6). About 2/3 of the

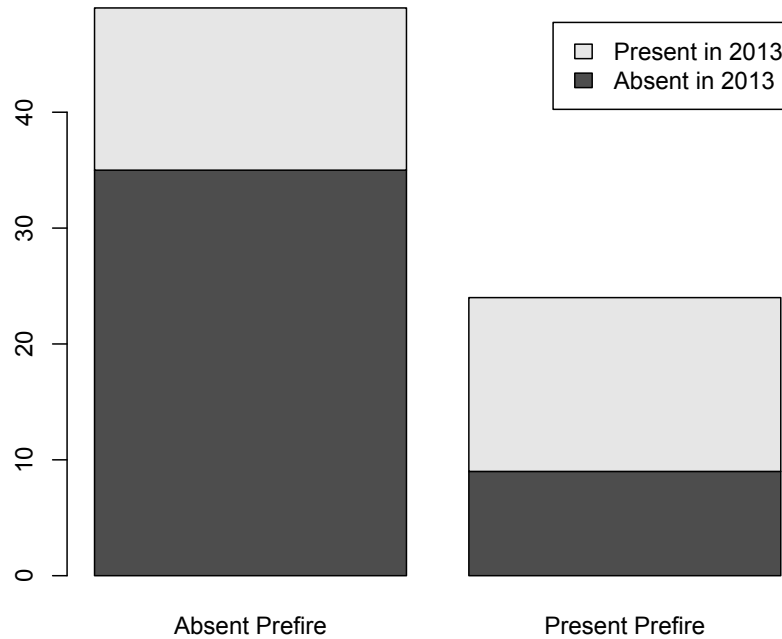


Figure 6. The correlation between pre-fire and post-fire occurrence with *Lupinus* in plots in the immediate season after the fire.

plots that had *Lupinus* before the fire also germinated *Lupinus* in 2013. Plots containing *Lupinus* before the fire have a significantly higher probability of containing *Lupinus* after the fire (Chi-Square, $X^2 = 7.68, df = 2, p\text{-value} = 0.02$).

The presence and absence trends of *Lupinus* in 2015 mirror the results from 2013. Of the plots that did not contain any germinated *Lupinus* before the fire, 34.8% of the plots contained germinated *Lupinus* three years post-fire (Fig. 7). Additionally, of the plots that showed *Lupinus* in years prior to the fire, 72.2% presented *Lupinus* in 2015. The plots that contained *Lupinus* before the fire had a significantly higher probability of *Lupinus* presence in 2015 (Chi-square: $X^2 = 8.27$, $df = 2$, $p\text{-value} = 0.02$).

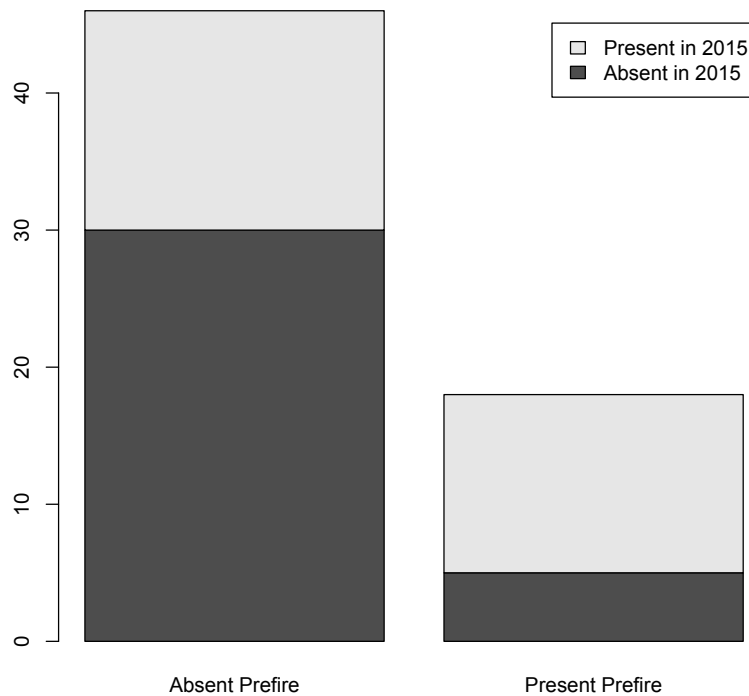


Figure 7. The correlation between pre-fire and post-fire occurrence with *Lupinus* in plots in the two years after the fire.

Discussion

Species Abundance

Both native and non-native species experienced lower abundance in the first and third year after the fire compared to pre-fire conditions. However, there was slight recovery of the native species abundances in the 2015 census, whereas the non-native species abundance did not exhibit recovery by 2015. Likewise, the decline in species abundance was far smaller in scale for native species compared to the exotic species. This suggests that the CSS native vegetation is more adapted to withstand the repercussions of a fire. It has been found that the dormancy of native seeds in CSS can be broken by exposure to fire, therefore causing the exhibited increase of aboveground native vegetation (Keeley 1987, Auld and Denham 2006). Additionally, seeds closer to the surface experience a much higher mortality rate than seeds farther from the surface (Auld and Denham 2006). Because exotic species have greater seed production and dispersal, the exotic seeds may be present closer to the surface and experience greater mortality from the fire, than dormant native seeds, which would be deeper in the soil.

Although exotic seeds are less fire resistant and experience higher mortality rates, the fast seed dispersion and germination facilitate the rapid return of non-native species to burned areas. This process can lead to type-conversion after a fire in CSS (Zedler 1984). For this reason, I expected to find non-native abundances recovering in 2015 compared to 2013, but interestingly the data did not support this prediction. One possible reason is the very dry conditions during 2014-15. Non-native grass seeds tend to germinate in response to any early fall rainstorms, whereas native seeds require both colder conditions and higher precipitation to break dormancy (Thomson et al. 2016). It

is possible that in 2014 many grass seeds germinated, but then died due to the hot and dry conditions, while native seeds remained dormant. This idea is supported by the fact that native species abundances increased in 2015, but non-native abundances remained the same.

Non-native species exhibit a significant decline in abundance after the 2009-2010 growing season (labeled "2010"). Since rainfall was much higher for 2009-2010 than 2010-2011, there may have been less germination in 2011 in response to less rainfall. However, less precipitation did not noticeably impact the abundances of native species. This gives insight to the resilience of native species to temporary droughts. Further research of the resilience of native and non-native species to drought can provide information on the role drought may play in determining CSS response to fire.

Mixed Models

Both native species, *Amsinckia* and *Phacelia* showed a significant difference in their densities between pre-fire, the year immediately post-fire, and three years post-fire. This drop between pre-fire and the post-fire years can be explained by both seed mortality and the changes to soil caused by smoke, soil heating, and wood charate.

Both *Amsinckia* and *Phacelia* experienced a large drop in species abundance the year immediately after the fire, regardless of past seeding treatments. This was to be expected as the fire took place before the growing season, negatively impacting both the germination and the survival of established plants (O'Leary 1988). As mentioned previously, the shallower seeds that would have germinated were likely burned and therefore, did not germinate. Another likely cause of the density decline was the impact the fire had on how the water penetrated the soil. The observed increase in density in

2015 reveals there were seeds present in the seed bank, but the fire may have caused lower water penetration to the seeds, impacting the germination rates for 2013.

There was no statistical significance between the pre-fire and 2015, indicating the recovery of *Amsinckia* densities to pre-fire densities. The recovery of *Amsinckia* may be due to several factors. Because the fire had a large negative impact on the abundance of exotic species, *Amsinckia* may have had a window of opportunity with fewer competitors, similar to the conclusions made by Cox and Allen (2008). The native species' seeds would not have had to compete with the more dominant exotic species' seeds, allowing for more germination and survival.

Furthermore, no significant effect of the past seed addition treatments was observed in either pre- or post-fire abundances. Because seeds had been added 2-5 years prior to the fire, they were unlikely to still be in the seed bank after the fire. Also, the number of seeds initially planted was small (18-27 per plot). Seeding would only have been expected to influence recovery after fire if the treatment had led to the establishment of adult plants in the plots, which then could contribute a larger number of seeds into the seed bank. With over 5 years of recording seedling emergence, this gives evidence that the seed addition treatments did not have a strong, lasting effect on the restoration of CSS.

Phacelia showed one important difference in trends compared to *Amsinckia*; *Phacelia* was observed to have a near zero average density per plot in both post-fire records. Although *Phacelia* and *Amsinckia* had similar pre-fire densities, *Phacelia* was impacted more negatively than *Amsinckia*. One hypothesis is that the dry season of 2015 was more damaging to *Phacelia* than *Amsinckia*. Previous work observed the

mortality rates of *Phacelia* in dry years are higher than for *Amsinckia* (Thomson *et al.* 2016). The low pre-fire abundance may reflect fewer *Phacelia* seeds were present in the seed bank, therefore leading to little possibility for recovery of the species post-fire.

Pre-fire vs. Post-fire

The third native species I analyzed, *Lupinus*, exhibited significant differences between the probability of finding *Lupinus* pre-fire and finding it post-fire in both 2013 and 2015. The number of plots containing *Lupinus* in both 2013 and 2015 was significantly higher than the number of plots that contained *Lupinus* prior to the fire. This reveals the seed bank in the BFS likely contained dormant *Lupinus* seeds, since approximately 30% of the plots that did not have *Lupinus* before the fire were observed to have germinated *Lupinus*, immediately post-fire and three years post-fire. The increase in *Lupinus* abundance is consistent with predictions that native species would increase if they experienced lower competition from non-natives.

It cannot be ruled out the possibility that *Lupinus* was not in the seed bank, and instead, was dispersed to the plots right after the fire. This seems unlikely, though. Initially, a big increase in *Lupinus* was detected in 2013, even though the fire happened right before the first rainstorms. It also seems unlikely the seeds could have been dispersed into plots so quickly. Additionally, no substantial increase in *Lupinus* distribution has been observed in the plots since; these data show no increase in occurrence of *Lupinus* between 2013 and 2015. If the seed dispersal caused the initial increase, it would be expected there would have been a continued trend of increased spatial distribution.

Conclusions

These results suggest although the fire gives rise to an opportunity for recovery of native species in CSS, not all species react positively in the time frame immediately after the fire. *Amsinckia* recovers to near pre-fire density, whereas *Phacelia* does not. No abundances of native species were observed to be higher post-fire than pre-fire. In fact, abundances either recovered to only pre-fire levels or they decreased after the fire. This indicates the use of controlled fires in the BFS is not an effective method of restoration.

Moreover, *Lupinus* exhibited greater abundance and wider spatial distribution in both 2013 and 2015, suggesting a positive initial impact of the fire on this native species' restoration. Further research is necessary to determine which effect of the fire caused the increase in *Lupinus*—the decrease in invasive species density or the potential breakage of seed dormancy.

While previous research suggests positive initial results of fire on native species, these results show some interesting potential interactions with drought effects. Given the likelihood of hotter and drier future climate conditions, which will also promote greater fire, further work on how drought influences fire recovery is important.

Acknowledgments

I would like to thank Doctor Diane Thomson for her strong guidance and assistance throughout the semester. I would also like to thank Professor Emil Morhardt for his support and feedback. Additionally, I give many thanks to my family and friends who continued to push me throughout this process. Lastly I would like to thank Scripps College and the W.M. Keck Science Center for providing me with the tools necessary to complete this analysis.

Literature Cited

1. Alberts, A. C., A. D. Richman, D. Tran, R. Sauvajot, C. McCalvin, D. T. Bolger, 1993. Effects of habitat fragmentation on populations of native and exotic plants in Southern California coastal sage scrub. *So. Cal. Acad. Scien.* Los Angeles, California. pp 103-110.
2. Allen, E. B., S. A. Eliason, V. J. Marquez, G. P. Schultz, N. K. Storms, C. D. Stylinski, T. A. Zink, M. F. Allen, 2000. What are the limits to restoration of coastal sage scrub in southern California? USGS Open-File Report 00-62, Sacramento, California. pp. 253-262.
3. Auld T.D., A.J. Denham, 2006. How much seed remains in the soil after a fire? *Plant Ecol.* 187:15–24
4. Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. In: *R package version 1.1-7*.
5. California Native Plant Society (CNPS) (2001) Inventory of rare and endangered plants of California (6 edn). California Native Plant Society, Sacramento.
6. Cione, N.K., P.E. Padgett, E.B. Allen, 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restor Ecol* 10:376–384.
7. Coates, T.D., 2003. The effect of concentrated smoke products on the restoration of highly disturbed mineral sands in southeast Victoria. *Ecol. Manage Restor.* 4:133-139.
8. Cox, R.D, E.B. Allen, 2008. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecology* 198: 37-46.
9. D’Antonio, C.M., C. Malmstrom, S.A. Reynolds, J. Gerlach, 2007. “Ecology of invasive non-native species in California grassland.” *California Grassland: Ecology and Management*. University of California Press, Berkeley, California. pp.67-83.
10. Eliason, S.A, E.B. Allen, 1997. Exotic grass competition in suppressing native shrubland reestablishment. *Restoration Ecology* 5:245-255.
11. Gressard, S. C., 2012. Dynamics of invasion and native species recovery following fire in coastal sage scrub. UC San Diego: Retrieved from <http://escholarship.org/uc/item/4m399060>.
12. Hill, S.J., K. French, 2003. Response of the soil seed-bank of Cumberland Plain woodland to heating. *Austral. Ecol.* 28:14-22.

13. Keeley, J.E., 1984. Factors affecting germination of chaparral seeds. *Bull. South. Calif. Acad. Sci.*, 83:113-120.
14. Keeley, J.E., 1986. Resilience of Mediterranean shrub communities to fires. *Resilience in Mediterranean-type ecosystems*. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 95-112.
15. Keeley, J.E., 1987. Role of Fire in Seed Germination of Woody Taxa in California Chaparral. *Ecology*. Ecological Society of America: 434-43.
16. Keeley, J.E., S.C. Keeley, 1984. Postfire recovery of Californian coastal sage scrub. *Am. Midl. Nat.*, 111:105-117.
17. Kirkpatrick J.B., C.F. Hutchinson, 1980. The environmental relationships of Californian coastal sage scrub and some of its component communities and species. *J Biogeogr* 7:23-39.
18. Lentile, L.B., P. Morgan, A.T. Hudak, M.J. Bobbitt, S.A. Lewis, A.M.S. Smith, P.R. Robichaud, 2007. Burn severity and vegetation response following eight large wildfires across the Western United States. *Fire Ecology* 3(1):91-108.
19. Minnich, R. A., R. J. Dezzani, 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* 29:366-391.
20. Mooney, H. A., S. P. Hamburg, J. A. Drake, 1986. The invasions of plants and animals into California. *Ecology of biological invasion of North America and Hawaii*. *Ecol. Studies* 58:250-272.
21. O'Leary, J. F. 1988. Habitat differentiation among herbs in postburn Californian chaparral and coastal sage scrub. *American Midland Naturalist* 120:41-49.
22. Pimental D., R. Zuniga, D. Morrison, 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52:273-288.
23. Richardson D.M., P. Pysek, M. Rejmánek, M.G. Barbour, F.D. Panetta, C.J. West, 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6:93-107.
24. Roberts, H.A., 1981. Seed banks in soils. *Adv. Appl. Biol.* 6:1-55.
25. Roche S., K.W. Dixon, J.S. Pate, 1998. For everything a season: smoke-induced seed germination and seedling recruitment in a Western Australian Banksia woodland. *Aust J Ecol* 23:111-120.

26. Runbinoff, D., 2001. Evaluating the California gnatcatcher as an umbrella species for conservation of Southern California coastal sage scrub. *Conserv. Biology* 15:1374-1783.
27. Seabloom E.W., W.S. Harpole, O.J. Reichman, D. Tilman, 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc Natl. Acad. Sci.* 100:13384–13389.
28. Stylinski, C.D., E.B. Allen, 1999. Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. *Journal of App. Ecol.* 36:544-555.
29. Suding, K.K., G. Houseman, 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46-53.
30. Thomson, D.M., R. Cruz-de Hoyos, K. Cummings, E.L. Schultz, 2016. Why are native annual abundances low in invaded grasslands? Testing the effects of competition and seed limitation. *Plant Ecology*. 1-12.
31. van der Valk, A.G., R.L. Pederson, 1989. Seed banks and the management and restoration of natural vegetation. Academic Press, San Diego. pp. 329-346.
32. Vitousek P.M., 1990. Biological invasions and ecosystem processes: Toward an integration of population biology and ecosystem studies. *Oikos*. 57: 7-13.
33. Wells, P.V., 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo Quadrangle, California. *Ecol. Monogr* 32: 79-103
34. Westman, W.E., 1981. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62:170-184.
35. Wolkovich, E.M., D.T. Bolger, K.L. Cottingham, 2009. Invasive grass litter facilitates native shrubs through abiotic effect. *Journal of Vegetation Science* 20:1121-1132.
36. Zink, T. A., M. F. Allen, B. I. Heindl-Tenhunen, E. B. Allen, 1995. The effect of a disturbance corridor on an ecological reserve. *Restoration Ecology* 3:304–311.
37. Zedler, P.H., 1977. Life history attributes of plants and the fire cycle: a case study in chaparral dominated by *Cupressus forbesii*. Forest Service General Technical Report WO-3, Washington. pp. 451-458.

Citations of Web Documents

1. www.bfs.claremont.edu, 2016. Bernard Field Station. Bernald Field Station Faculty Advisory Committee, reviewed by Nancy Hamlett.
2. www.ncdc.noaa.gov, 2016. Annual Drought Report 2015. National Center for Environmental Information.