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RESEARCH

Where Have the Native Grasses Gone?: What a Long-Term, Repeat Study Can Tell Us about California's Native Prairie Landscapes

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Much of the foothill and valley areas of coastal southern California are covered by stands of non-native grasses with occasional scattered patches of native bunch grasses. For decades, the dominant view held that these native bunchgrasses, particularly *Stipa pulchra,* once covered these lands and that grazing practices were a key cause of their decline. The so-called bunchgrass dominant paradigm (BDP) put forth by Clements influenced thinking on grassland ecology and biogeography for decades until it was discredited. Recent research suggests that grazing and related disturbances might have supported native bunchgrasses, but results are mixed and most studies cover only a short time frame. This research uses a long-term, repeat study design to analyze and compare data from three surveys of 15 permanent quadrats in La Jolla Valley, California, to determine changes in grassland cover over 34 years. A unique aspect of the study is that the site was selected by researchers precisely because it contained excellent 'relic' stands of *Stipa pulchra* (in accordance with the BDP) and the baseline study was conducted shortly after the area was released from grazing and placed under conservation management. We compared data on species frequency and percent cover collected using the same sampling routine for three periods: 1981, 1994, and 2015, to document the shifts in vegetation. We found that native grass cover decreased dramatically (especially on the valley floor), exotic grass cover fluctuated widely over time, while both native and exotic forb cover increased over time. The findings support the notion that prior grazing management practices may have supported the former stands of *Stipa pulchra*.

Keywords: *Stipa pulchra*; bunchgrass dominant paradigm; Santa Monica Mountains; restoration

1. Introduction

Stands of non-native grasses cover much of the foothills and valleys of southern California (Minnich, 2008). Indeed, native plants dominate few of California's grasslands today and even those locales with native grass species contain large amounts of non-native plants (D'Antonio et al., 2007). Researchers and practitioners have long questioned the original vegetation cover of these landscapes. For decades the dominant view held that the original vegetation was composed of native bunchgrasses, particularly the perennial *Stipa pulchra,* but also *Stipa lepida.* This view was supported by the so-called bunchgrass hypothesis or bunchgrass dominant paradigm (BDP) (Holstein, 2001). In recent decades, however, this paradigm has largely been discredited (Hamilton, 1997; Minnich, 2008; Schiffman, 2005) and replaced with the theory that bunchgrasses played a much smaller role on the landscape in California than was once thought and that forbs and, in some areas shrubs, were more dominant prior to European arrival (Engelberg et al., 2013; Minnich, 2008; Schiffman, 2005).

This shift in thinking about the ecology of native bunchgrasses raises questions about how bunchgrasses came to be common in certain areas of California and whether or not their prevalence is more a function of biogeography (environmental characteristics such as topography, soils, precipitation, etc.) or of disturbance history and ecology (grazing and other disturbance regimes). Although Clements (1934) considered bunchgrasses to represent the climax state in many parts of California—thus a function of biogeography—numerous other scholars have long attributed the presence of *Stipa* to disturbances. Bartolome and Gemmill (1981), for example, referred to *Stipa* as, 'opportunistic, with few of the characteristics of typical climax species' (182). Based on a 20-year study following the removal of grazing, these authors found a decline in *S. pulchra* cover along permanent transects at the Hopland reserve in northern California. They concluded that *S. pulchra* is the most common California native grass, not because the species dominated the original California grassland, but that 'it was a survivor because it is adapted to disturbance' (182).

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Their perspective epitomizes the disturbance hypothesis. They noted that disturbances that reduce associated annuals are important for colonization by *S. pulchra* because seedlings do not survive where there is dense annual cover and that once established, a *S. pulchra* plant can persist under moderately heavy grazing. It also has a long life expectancy of 20–200 years (Marty et al., 2000).

A recent meta-analysis of studies of grazing in California grasslands found that *S. pulchra* grass cover generally increased with grazing, although the high variation among studies was not predicted by the explanatory variables evaluated (Stahlheber and D'Antonio, 2013). The analysis yielded a picture of the complex response of *S. pulchra* to protection from livestock grazing. In particular, in some cases exclosures resulted in an increase in needle grass while in others they did not.

One explanation for the variability in the findings is that the effects of disturbances are not straightforward and depend upon their timing (seasonality) in addition to other factors, most notably weather (precipitation amounts and timing), which is difficult to control for in research experiments. For example, Schellenberg et al. (2020) recently concluded that it was not possible to separate the relative contribution of drought effects from those of the seasonality and intensity of disturbance on *Stipa*. They note that because most studies cover only short durations, the vagaries of weather often determine study results.

A second explanation for the variability in study findings has to do with disturbance histories that may have subtle long-term effects. Two theories useful for conceptualizing the long-term consequences of past events are landscape legacies and the extinction debt. The former takes the approach that ecosystem processes and patterns depend on both the contemporary environment and the persistent effects, or *legacies*, of past events. As such, disturbance regimes generate biological legacies that interact with environmental conditions to shape ecosystem recovery (Franklin et al., 2000). As Keeley et al. (2011) have argued, recurring disturbance patterns exert strong selective pressure on life-history strategies that affect population survival and spread. Consequently, species evolve survival and regeneration strategies that are tuned to particular disturbance regimes rather than individual events. As such, the cessation or dramatic altering of a disturbance regime may be detrimental to certain species. The latter theory involves *extinction debt*—the delayed extinction of species—which results because long-lived plants may respond slowly to events such as habitat destruction (Cousins, 2009; Loehle et al., 1996). Accordingly, local extinction of species can occur with a substantial delay following habitat degradation. Species with long generation times and populations near their extinction threshold are most likely to have an extinction debt. Cousins (2009) reported that extinction debt is more common in landscapes with more than 10% of the original grassland area remaining; in fragmented landscapes where the habitat loss started 70–200 years ago, most extinctions would already have occurred. As such, Hughes et al. (2013) argue that transitions between ecological regimes often unfold over decades or longer, with major consequences for our capacity to detect, avoid, or reverse them posing problems for biological conservation efforts.

In summary, understanding the impacts of grazing (or release from grazing) on native California species is complicated by the fact that in such semi-arid rangelands it may take as long as 20 years for a site to receive a representative range of precipitation. In addition, altering of past disturbance regimes may change the competitive advantages of species triggering gradual declines, which are difficult to perceive especially when species are long lived, as is the case with *Stipa*. As such, long-term data are necessary to detect phenomena that would otherwise be beyond the scope of human observation. The use of permanent plots for long-term study is a valuable method for this type of analysis. In such cases where environmental changes occur over relatively long time periods, Diamond (1986) has argued that such natural experiments are especially useful because they may achieve a higher level of realism than short-term field or laboratory experiments. The downside of is that it is not possible to control for some variables. In addition, while historic data sets are clearly rare and valuable resources, Keeley (2004) cautions that if the original plots cannot be precisely located, major errors may ensue. Fortunately, in our case, the original plots were marked with angle irons and rebar, facilitating the resampling process.

In this case study, we resample a series of 15 formerly grazed plots originally selected for research because they were interpreted as some of the best pure and original stands of *Stipa* in one of the finest examples of native California grasslands, La Jolla Valley (LJV), California. We present findings from a restudy of this grassland and argue that precisely because the original research was established under the broad framing of the BDP, it offers a unique opportunity to study the effects of release from grazing on high quality stands of *Stipa*. This long-term study is useful because it increases our understanding of the biogeography and ecology of California native landscapes by tracking shifts in plant cover over a 34-year period following release from disturbance. The study seeks to increase understanding by examining whether native bunch grasses expanded or contracted in percent cover and frequency following release from grazing and related disturbances. We also seek to inform debate on two broader questions: (i) what are the preferred environmental or biogeographical conditions of *Stipa* in the region? And (ii) if bunchgrasses were not the dominant historical vegetation form, then why were there large patches of them at the time of an initial assessment of LJV in the early 1980s?

These questions are of utmost importance for restoration efforts, which seek to replace exotic grasses with native plants. In addition, while much has been written about the drier interior regions of southern California (Riverside County, for example) and the Central Valley (Minnich, 2008), less is known about the prevalence or lack of bunchgrasses in coastal mountain valleys where soil and precipitation conditions might favor them.[1] We use the emerging framework of *critical physical geography* (Lave, 2014) to help frame our explanation of the impacts of the BDP on research design as well as to interpret our findings.

2. Background

2.1 Critical Physical Geography

Critical physical geography (CPG) aims to scrutinize not only research findings, but equally importantly, the concepts and categories used in biophysical geographic research. As Sayre (2015) has argued, scientific ideas have histories; they should not be taken for granted as given, but understood as the result of actions taken by particular people in particular contexts. This is especially critical in cases where repeated use over time cemented concepts into the literature and occluded the assumptions that attended them at the outset, as was clearly the case with the BDP.

Fredric Clements, a powerful figure in American ecological science, popularized the BDP. Clements developed his theory based on his relic ecology methodology he pioneered in the 1920s (Clements, 1934). He came to California to study relic patches of vegetation in an effort to determine the lands' original plant cover. Based on his model, he inferred that the valleys in California were once dominated by perennial bunchgrasses that were converted to annuals by overgrazing. Critically, these ideas held sway for decades (in spite of often-contradictory research results) and they influenced thinking about native landscapes by many that followed (see below). The BDP influenced numerous assessments of grassland quality as well as scientific research (e.g., Heady, 1977) and later, many restoration projects, which focused on replacing exotic grasslands with bunchgrasses (many of which failed) (e.g., Lesage et al., 2018). Over time Clements' theory was gradually challenged through careful examination of historical records by the likes of Holstein (2001), Schiffman (2005), and Minnich (2008), through paleoecological research by Evett and Bartolome (2013), as well as experimental studies (Bartolome and Gemmil, 1981) and a serious critique of Clements' own theory and methods by Hamilton (1997).

Our purpose in addressing the influence of Clements' work here is not to drive an additional nail into Clements' paradigm—other scholars have done this—rather, following Sayre, it is to frame previous works in their proper context. It is important to understand how the BDP influenced the ways in which California grasslands were viewed, how this effected the kind of research that was undertaken in them, and how we should interpret the results of such research today.

We suggest that a CPG approach offers a perspective to frame an examination of the enduring impacts of the BDP on grassland research. While the origins of the paradigm have been more or less well documented by others (e.g., Hamilton, 1997; Holstein, 2001) the long-term impacts of the core ideas have been the focus of less research. Specifically, while Clements' BDP undoubtedly held sway over understanding California environments for decades (Minnich, 2008), much less is known about how Clements' ideas influenced particular research projects and thus knowledge development. We suggest that a close examination of one such project offers potential for interpretation of study results that might be useful for understanding the dynamics of some native Californian landscapes.

In this study, we resample a series of plots originally selected for research because they were interpreted to be some of the best pure and original stands of *Stipa* in one of the finest examples of native California grasslands, La Jolla Valley (LJV), California. We present findings from a restudy of this grassland and argue that precisely because the original research was established under the broad framing of the BDP, it offers a unique opportunity for study. Critically, the authors of the original study did not randomly select their plots; rather they carefully selected ones that they deemed the best stands of needle grasses in a site considered an exemplary example of original native grassland. Our objective is thus not only to repeat the experimental study, but also to place the work in its original context to aid in explaining the results.

Clements' idea that California valley grasslands were once covered by native purple needle grass (*Stipa spp)* was linked to LJV through the works of several scholars whose use of terminology clearly reflect Clements' influence. Barry described large stands of intact needle grass as worthy of preservation in his map from 1972 based on his own field surveys (**Figure 1**). Following Clements, Barry referred to these patches as 'relics' of a once larger prairie. Barry himself was building upon the work of Harold Heady, who felt that no other stands in the state were as vigorous or as dense as those found at LJV. After a survey to locate and evaluate 'remnants of the pre-Spanish Central Valley Prairie,' Barry wrote, 'Dr. Harold F. Heady says this is *the* finest stand of purple *needlegrass* he has ever seen. The author has come to the same conclusion; no other stands in the state are as *vigorous or* as dense' (Barry, 1972: vii). He continued, 'The object of this study is to establish the pristine state of the *California prairie* and to ecologically evaluate remaining *relic* examples of this prairie ecosystem' (ix, italics added). Indeed, both 'California prairie' and 'relic' are terms that hearken back to Clements. Barry himself was building upon the work of Heady, who felt that no other stands in the state were as vigorous or as dense as those at LJV (quoted in Barry 1972: 36).

2.2 The La Jolla Valley Restudy

Our case study begins with the work of Suzanne Goode who conducted an inventory in 1979 on the species composition of the grassland in LJV. Goode collaborated with Carole Gale in 1981 to produce a survey of the LJV grassland (**Figure 1**). These two studies, conducted only about a decade after LJV had become part of a State Park eliminating grazing and mechanical disturbance, established a solid baseline for monitoring the stands of *Stipa* over time. As Gale wrote, 'The purpose of this study was to locate the best surviving stands of *Stipa pulchra* (and any other native grasses) in the valley, establish permanent quadrats, sample, and create a baseline of data for use in an ecological monitoring program.'

It is not surprising that the permanent plots selected by Gale and Goode for their baseline study closely fit the area described by Heady and Barry as the ideal relic stands of *Stipa*; indeed, Barry served on Gale's thesis committee. In essence, the ideas of Clements, which trickled down through the works of Heady, Barry, and others, influenced

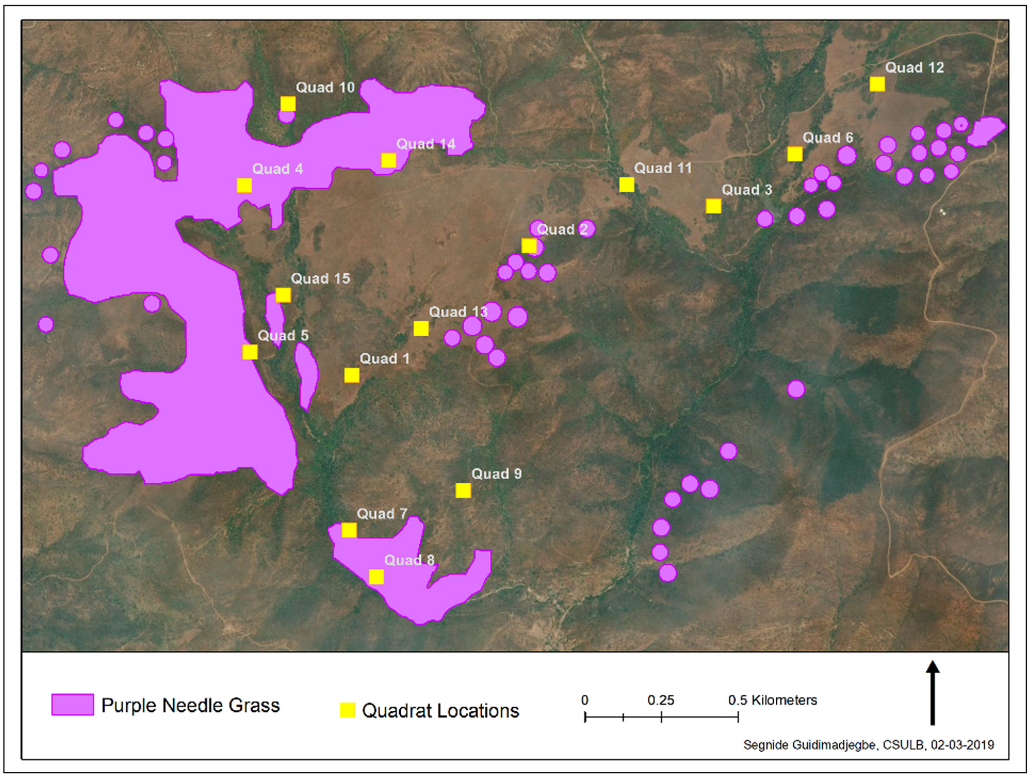

Figure 1: Quad locations from the original LJV study by Gale (1983) and Goode (1981) overlaid on historic stands and point locations of *relic* native bunchgrasses recreated from Barry (1972).[2]

the establishment of the locations of the study plots in LJV. As Gale (1983: 5) wrote in her thesis: 'This study may also contribute to filling a gap in the research on native California grasses since "quantitative descriptions based on plot sampling of the relic perennial grasslands have not appeared" (Heady, 1977).' In addition, Berry had assumed that overgrazing caused the demise of the perennials and that ceasing grazing would result in restoration of the bunchgrass habitat and this idea formed part of rational for the baseline study in LJV.

It is important to note, however, that grazing was not the only disturbance in La Jolla and other valleys in California during much of the twentieth century. In fact, 'grazing' as it is commonly used in the literature, is somewhat of a misnomer in that the practice of cattle 'ranching' very often included other disturbances such as mechanical disking, plowing, clearing, and burning of shrubs to promote grasses. Efforts to improve pasture through mechanical means to remove shrubs was a key part of widespread programs of the University of California Agriculture extension services (Laris et al., 2016). Hobbs (1983) documented areas of brush clearance or mechanical disturbance beginning as early as 1938 in LJV and continuing for decades. Although we do not know how often and when, these disked lands were also periodically set on fire to burn shrubs. As the historical record indicates, rancher actions on rangelands such as LJV were complex involving multiple and various disturbance regimes, which undoubtedly had long lasting impacts on native plant cover (Brennan et al., 2018; Engelberg et al., 2013). It is often assumed that these impacts were largely negative for the native species. If true, however, how did the relic patches of *Stipa* persist in LJV through a long period of ranching?

The goal of our research was to resample the plots and to compare these with results from the baseline studies as well as data from a restudy conducted in the early 1990s by Strassforth (1996). We sought to test the hypothesis that needle grasses would increase in cover and frequency following release from intensive anthropogenic disturbances. An increase would suggest that such disturbances had had negative impacts on these grasses, whereas a decline would suggest the opposite. We examine the shift in cover of *Stipa* on multiple plots situated differently in the LJV and draw conclusions about where it performs best and in cases where it performed poorly, we document what replaced it.

3. Methods

La Jolla Valley is located approximately 1.3 km inland from the Pacific coast in Point Mugu State Park, approximately 20 kilometers northwest of Malibu, California (**Figure 2**). The climate is Mediterranean with cool, wet winters and hot, dry summers. From 1998 to 2008 the average summer daily maximum temperature was approximately 22 degrees C, and the average daily minimum temperature in the winter was 8 degrees C. Average annual precipitation is 26.4 cm (Western Regional Climate Center, 2009). The land encompassing the valley and surrounding hillsides was purchased and used for grazing cattle from at least 1873 until the ranching period ended in 1965 (Hobbs, 1983). The valley has experienced periodic fires about every 20 years and was last burned by the Spring fire in 2013 and prior to that in 1993.

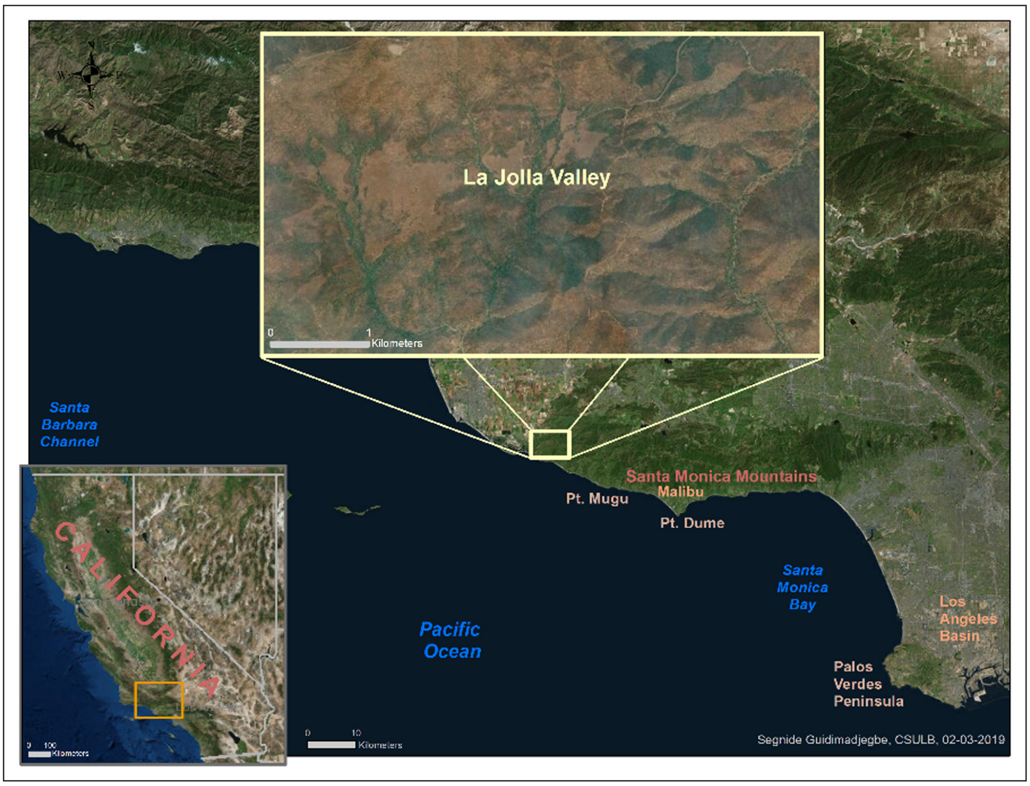

Figure 2: Location of La Jolla Valley in the Santa Monica Mountains.

Gale and Goode chose fifteen locations across the valley for their study quadrats (**Figure 1**). These locations were carefully chosen because they represented the 'best surviving stands of *Stipa pulchra*' with the exception of two plots (Gale, 1983). Two quadrats (XIII and XV) were selected because they contained introduced grasses or forbs. Quadrat XIII represented the most dominant introduced grass in the valley at the time, *Festuca perennis* and Quadrat XV was established in the 'worst weedy' forb site in the valley (Goode, 1981). According to Gale (1983), most of the plots were located on the valley floor, but six plots were established in 'ecotones' composed of oak-woodland located in riparian corridors and coastal sage shrublands located on the uplands adjacent to the valley. Strassforth (1996) restudied each plot for three consecutive years after the 1993 Green Meadow wildfire. We relocated each of the 15 original 24 m × 16 m quads, which had been marked with rebar and angle irons, and conducted a restudy in spring of 2015.

Following the original methods, a grid was established to divide each quadrat into sixteenths, each measuring 4 m × 6.25 m. The frequencies of forb, shrub, and grass species were sampled using a 25 cm × 25 cm quadrat by counting each species observed. Following Gale's original method, we began sampling at a location one meter below and one meter to the right of the quadrat's upper-left corner, the quadrat was dropped, and all species within it recorded in a simple frequency count. As the researcher walked backwards to avoid bias within the quadrat in a spiral pattern the quadrat was dropped in a random location every fifth step. This procedure was repeated for fifty samples.

To determine percent cover, we employed the Daubenmire (1968) method. Following Gale (1983), a stratified random sample of four sixteenths in each quadrat was used to lay out two transects running the 6.25 m length of the plot. Beginning 25 centimeters in, and every 25 centimeters thereafter, a metal wire was placed and plants touching the wire were recorded producing 25 readings per transect and 200 per quadrat. To measure the density of the various species of shrubs within the quadrats, counts of each species were taken by plot. All dead shrubs (post 2013 fire) were also recorded to provide an estimate of the number of shrubs in the quadrats pre-fire.

Data were entered into a spreadsheet and combined with values from Strassforth (1996) and Gale (1981) for comparison. For each quadrat, cover data was divided into the following categories: native grasses, exotic grasses, native forbs, exotic forbs, shrubs, and bare ground. We performed Fisher's Exact tests to test the relationship between the changes in relative cover of forbs and grasses and native and exotic grasses between 1981 and 2015. We created contingency tables with counts of the number of quadrats with increases in relative cover and the number of quadrats with decreases. One table was created for forbs and grasses and another for native and exotic grasses. We chose Fisher's Exact tests due to their accuracy with small sample sizes.

4. Results

4.1 Floristics

Pooling data from all of the collection methods, 54 species of grasses, shrubs, and forbs were identified, 42 of which are native to the region (~78%). All 15 of the shrub species are native. Two out of the five perennial grass species were native, *S. pulchra* and *S. lepida* (40%). Lastly, 25 of the 34 forb species were native (~74%). It should be noted that the record of forbs present might be incomplete as the flowering periods are brief and the timing varies by species; therefore, they may be misidentified or missed.

4.2 Percent Relative Cover

The results of this study and those from prior ones for relative cover of all grasses are shown in **Figure 3** where it can be seen that while the percent cover of needle grasses has declined, that for exotic annuals, especially *Avena*, has increased over the study period. The grasses with the greatest current species cover were the *Avena* species—*Avena barbata* and *Avena fatua.* The *Avena* species were present in nine out of fifteen quadrats with an average relative cover of 29%. Cover per quadrat ranged from 1% to 78%. The grass with the next highest cover was *S. pulchra.* It was present in 11 of the quadrats, averaging just under 6% and ranging from 1% to just below 27%. Following *S. pulchra* were *F. perennis*, *P. aquatica*, and *S. lepida.*

The percent relative cover for each category (native and exotic grasses, forbs, shrubs, or bare ground) over time is shown in **Figure 4**. It is clear that the percent cover of grasses in general declined from the 1990s to 2015, while forbs increased substantially. It is also apparent that native grasses have declined significantly while exotic ones have fluctuated and forbs have increased through time. Shrubs declined slightly during the early period, while there was an increase in bare ground.

4.3 Species Frequency

As with the cover data, the exotic *Avena* species had the greatest average percent frequency, 42.4%. Its frequencies ranged from 0% to 96%. The second most frequent grass species was *S. pulchra.* It had an average frequency of 15.6% and ranged from 0% to 42%. Next was the exotic species *F. perennis,* with 13.7% average frequency. Second to last was the exotic species *P. aquatica,* at 7.3% average frequency. Lastly, *S. lepida* had the lowest average frequency, at 2.5%.

The forb with the greatest average frequency was *Deinandra fasciculata,* with 33.9%. It was also the forb with the greatest percent relative cover. *D. fasciculata* was equal in frequency with *Dichelostemma capitatum* and the exotic *Sonchus asper*. The exotic *Erodium cicutarium* had the next highest average frequency, 24.1%. *Calystegia macrostegia*, *D. capitatum*, and *So. Asper*, with average frequencies of 22.4%, 19.6%, and 16.7%, follow it respectively. Four of the five most frequent forbs were native species. The fifth forb species, *So. asper*, ranged from 0.1% to 14.5% average frequency.

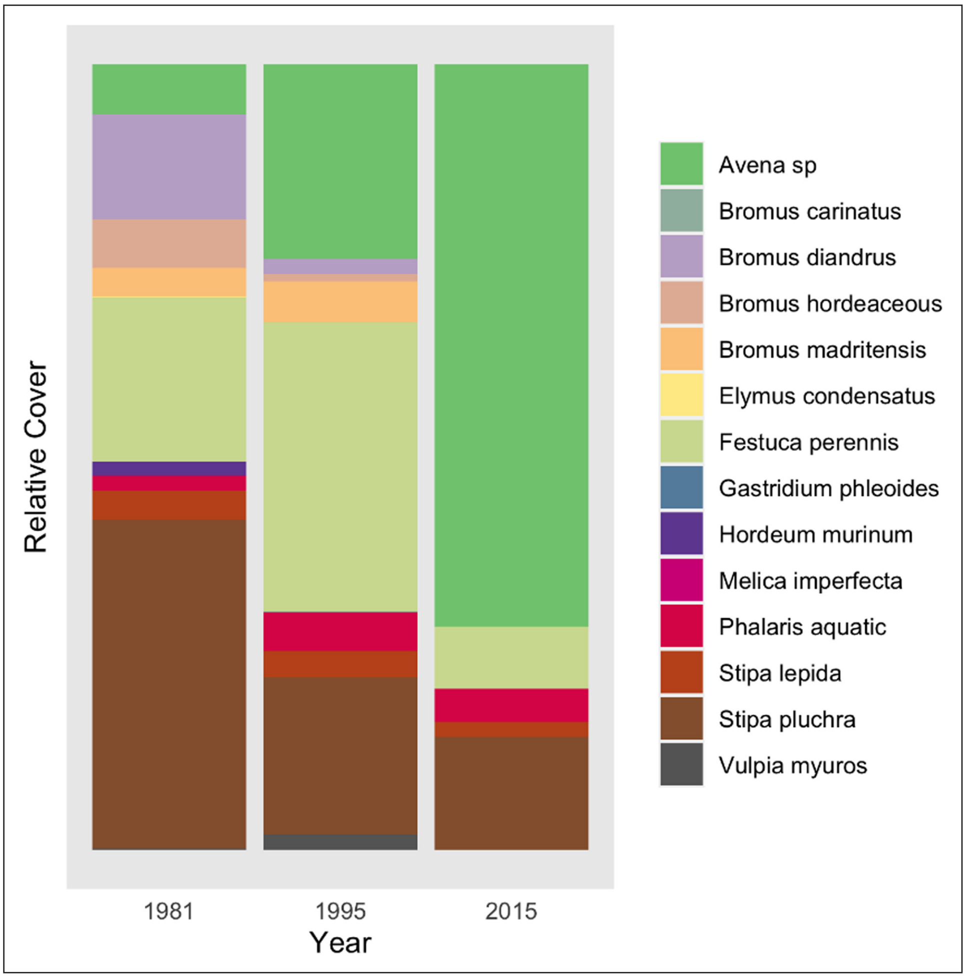

Figure 3: Percent relative cover of grasses over time in LJV.

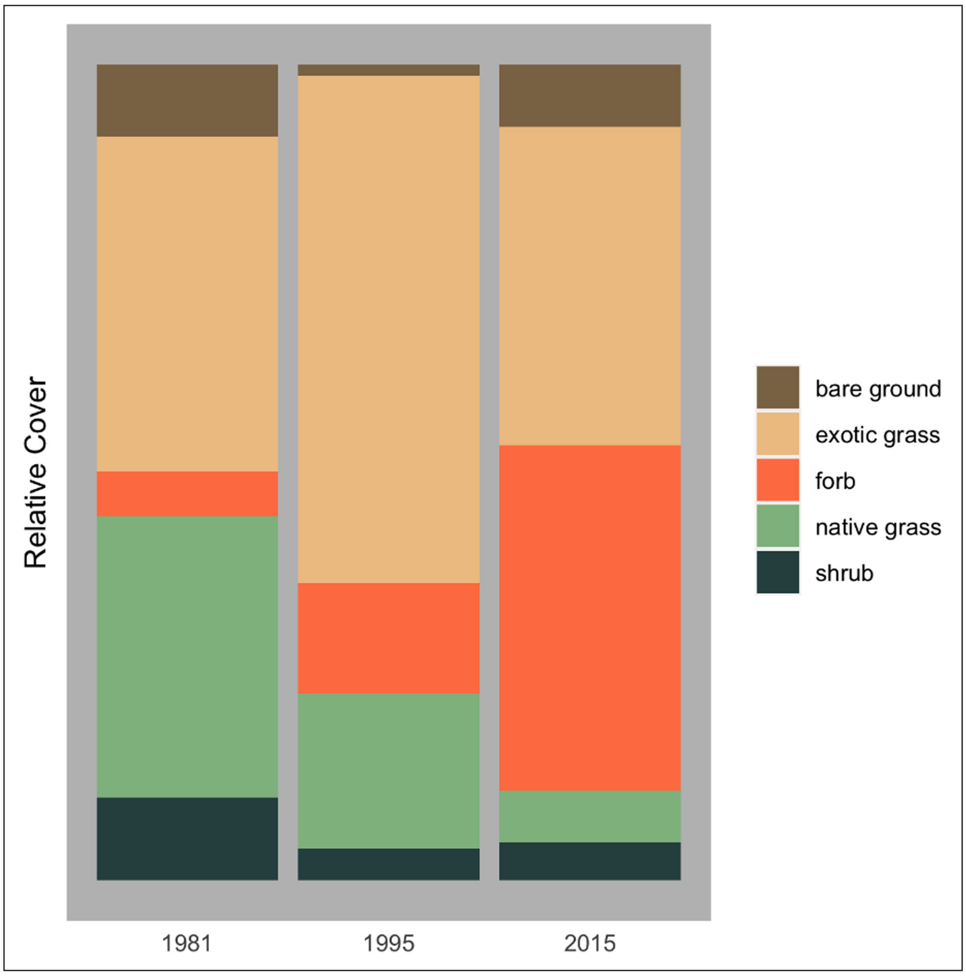

Figure 4: Changes in relative cover of native and exotic grasses, forbs, shrubs, and bare ground.

The shrub species with the greatest frequency was *Eriogonum cinereum*. Out of the fifteen quadrats its average frequency was 6.9%. The next most frequent shrub species were *Artemisia californica*, *Salvia leucophylla*, and *M. laurina* with 2.3%, 2.1%, and 2.0% average frequencies respectively. The six other shrub species had average frequencies of less than 1%.

Several trends became apparent when the data from the three periods are viewed together. Both native and exotic forbs increased between each data collection. There were consistently more native forbs than exotic ones and native grasses decreased in cover. Though exotic grasses fluctuated, they always made up a greater amount of cover than their native counterparts. Lastly, cover of bare ground fluctuated and shrubs declined. The Fisher's Exact test of the increases and decreases of forb and grass cover across quadrats from 1981 to 2015 had a p-value of 0.00012 indicating that we can reject the null hypothesis of independence (**Table 1**).

In 1981 grasses averaged 75% relative cover, with 34% natives and 41% exotics. The cover of grasses remained close, 76% in 1995, but native grasses decreased to 17% and exotics increased to 59%. By 2015, average grass cover had decreased to 43%, 7% native and 36% exotic. The results of the Fisher's Exact test of increases and decreases of native and exotic grasses across quadrats from 1981 to 2015 (**Table 2**). The low power of our study suggests that p-values higher than the conventional 0.05 can be interpreted as indicating a true pattern and thus that

Table 1: Fisher's Exact Test for Count Data for increase/decrease in cover of grasses and forbs by quadrat from 1981 to 2015.

Vegetation Form	Increase	Decrease
Grass	1	14
Forbs	14	1

Fisher's Exact Test.
P-value = 0.08008.
95% CI: 0.002183889 1.190995284.
odds ratio: 1151766.

Table 2: Fisher's Exact Test for Count Data for increase/decrease in cover of grasses by quadrat from 1981 to 2015.

Vegetation Form	Increase	Decrease
Native Grass	1	14
Non-Native Grass	6	9

Fisher's Exact Test.
P-value = 0.0001157.
95% CI: 4.268043 2505.233273.
odds ratio: 45.18712.

there has been a decrease in native grasses since 1981. Forbs, on the other hand, had increased in average cover between each data collection period. In 1981 forb cover was only 6% (3% native and 3% exotic) but increased to 19% in 1995 (15% native and 4% exotic). By 2015 forbs made up 44% of cover (31% native and 14% exotic), thus surpassing grasses. Shrubs decreased from 10% in 1981 to 4% in 1995 and in 2015.

From 1981 to 1995, the 13 quadrats with *S. pulchra* decreased in percent cover of this species, and did so by an average of 52.3%. From 1995 to 2015, 12 quadrats contained *S. pulchra*, and 10 showed a decrease in cover (76.9% on average). Quadrats 4 and 11 showed an increase in *S. pulchra* cover from 1995 to 2015, 65% and 73%, respectively. In 1981 Carole Gale found only exotic grasses in quadrat 15, it was not resampled in the 1990s, and in 2015 no grasses were found in this quadrat.

To see if percent relative cover results differed based on location within the valley, we categorized quadrats into one of two categories: [valley] floor or [valley] edge. Quadrats 7, 8, 9, and 10 made up the latter category, with the remaining (1–6 and 11–15) making up the former (see **Figure 1**). Percent relative cover for native and exotic grasses and forbs, shrubs, and bare ground were averaged among the quadrats of each category. These values were the basis for comparison, and depicted in **Figure 5**.

When divided into edge and floor categories, many trends remain the same. Exotic grasses increased then decreased in cover over time and native grasses decreased. On the valley floor exotic grasses made up a greater percentage of cover than natives while on the valley edge there were more native than exotic grasses cover in 1981 and 2015. Native and exotic forbs increased in each data collection interval, from 1981 to 2015, with the exception of exotic forbs on the valley floor from 1981 to 1995 (4% to 3%). Looking at shrub cover for all three categories of quadrats (floor, edge, and overall) they all showed a decrease from 1981 to 1995. From 1995 to 2015 the floor

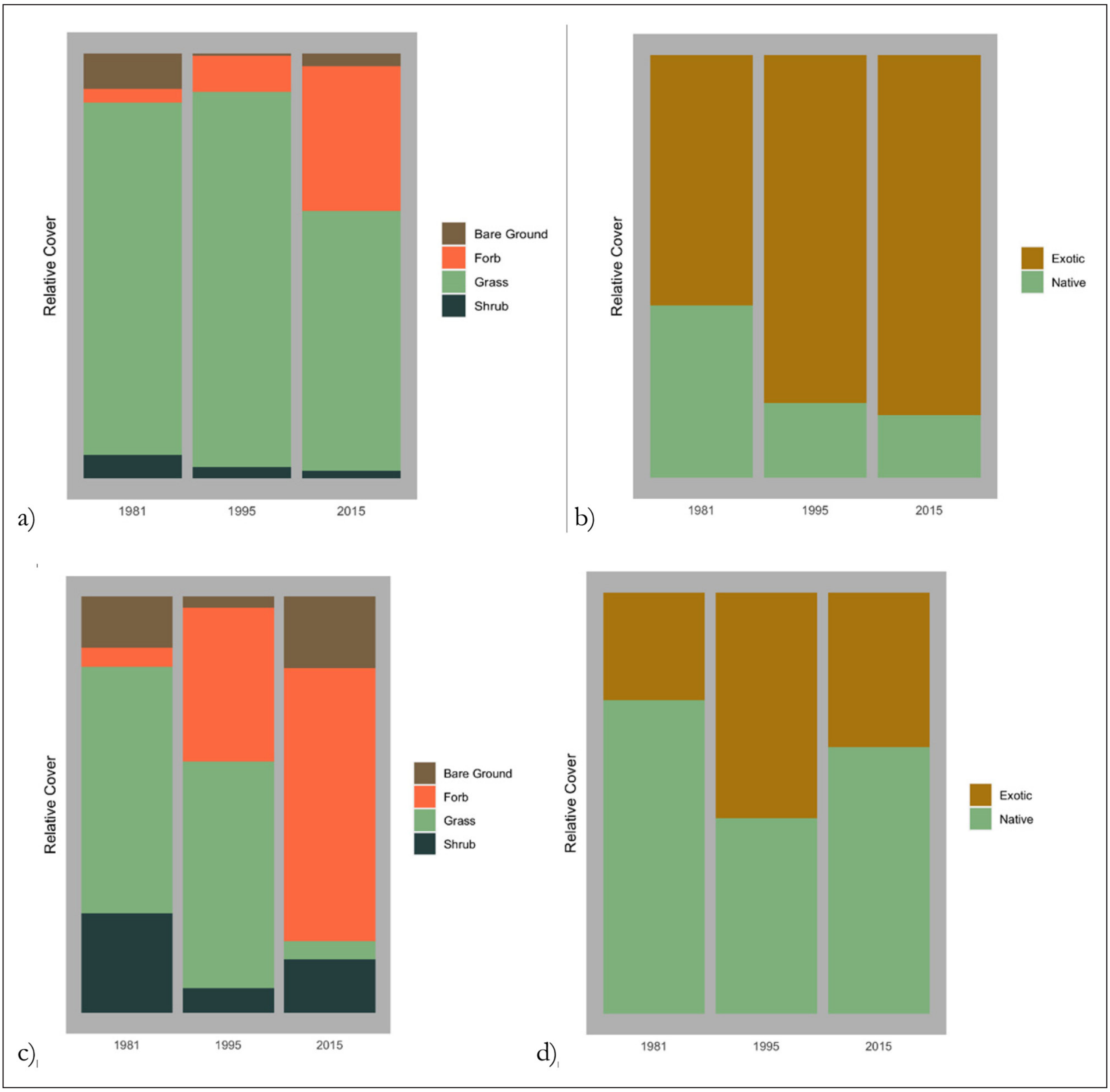

Figure 5: Percent average cover by category for floor **(a, b)** and edge **(c, d)** quadrats 1981–2015.

quadrats showed further decrease and edge quadrats increased, but overall shrub cover remained the same.

The most notable difference between floor and edge was in terms of native versus exotic grasses. In 1981, quadrats on the valley edge showed greater cover by native than by exotic grasses (41% versus 21%) By 1995, native grass cover decreased (to 22%), and exotic grass cover increased (to 29%) on the valley edge. Native grasses continued to decrease by 2015 (to 3%), but this time exotic grasses decreased as well (to 2%). On the valley floor, exotic grass cover averaged for the 11 quadrats was always dramatically higher than native grass cover.

5. Discussion

This study finds that since the period of grazing and mechanical disturbance ended in LJV, native California bunchgrasses have declined dramatically. Between the first study in 1981 and the second from 1994 to 1996, *S. pulchra* declined by 57%. Native grasses further declined by 61% from the 1990s to 2015. Somewhat surprisingly, the results indicate that exotic grasses have also declined, although slightly, over time while native forbs show an increase (although this could reflect annual fluctuations in precipitation rather than a trend). Shrub cover fluctuated during the study period, as did bare ground (likely a function of the two fires that occurred during the period). The study also finds that vegetation cover varies somewhat between valley floor and the edge or slope locations. Overall, the findings document a dramatic decrease in native grass cover since the end of the ranching era and the establishment of the grassland reserve.

The findings compare favorably with those of Bartolome and Gemmill (1981) who found a similar decline in *S. Pulchra* for their 20-year post-grazing study at the northern California site of Hopland.[3] In particular, on a slope in the absence of sheep grazing, the formerly abundant *S. pulchra* plants dramatically declined between 1959 and 1979 from 2.18 to 0.05 plants/m (177). In a restudy by Merenlender (2001) found that *S. pulchra* density increased between 1979 and 1991 only to decline again from 1991–2000).

Our results found that the decline of native bunchgrasses was more pronounced on the valley floor than on the slopes. Indeed, after a decline during the first period, native grass cover on valley slope plots increased from the 1990s to 2015 while cover on the valley floor decreased for each period studied. This finding suggests that *Stipa* may have a competitive advantage on the slopes where soils tend to be shallower and coarser.[4] We speculate that these grasses have been more common on valley slopes or edges than on the floor, a finding supported by Holstein (2001). The steep decline in *Stipa* cover on the valley floor during the study period also supports Richard Minnich's (2008) theory that forbs, and not bunchgrasses, were once the dominant cover in California's valleys. It should be noted, however, that forb cover is often a function of annual precipitation events (unlike perennial grasses) (Minnich, 2008) and, as such, it is possible that our research simply captured an incidence of a forb bloom.[5]

Our findings also raise the question as to why there were such 'fine' stands of bunchgrasses found at the end of the ranching era in LJV. We consider two explanations. The first is that *Stipa* dominated the valley since Native American times and was perhaps facilitated by frequent fires set by the Chumash (Keeley, 2002). Well-timed (spring) fires support *Stipa* cover and the Chumash set regular fires (Anderson and Rosenthal, 2015). The onset of intensive grazing over 100 years ago in LJV fragmented and damaged the grassland ecosystem creating an extinction debt. As such, the fine stands of *Stipa* observed by the likes of Heady, Berry, and Gale and Goode were associated with that debt. Accordingly, our study may have documented the 'paying' of the extinction debt as observed in the steep decline in bunchgrass cover in the valley.

An alternative, and more probable explanation, is that the high presence of native bunchgrasses was in part a function of the disturbance regimes associated with ranching. In accordance with the legacy effect (Franklin et al., 2000), the removal of the regular regime of disturbances touched off the decline of native grass cover we observed. Johnstone et al. (2016) referred to this phenomenon as a 'resilience debt' that arises due to a change in disturbance regime, which affects information legacies (the adaptive traits of species to a particular disturbance regime) ultimately resulting in species decline. Although the precise mechanisms or disturbances that facilitated bunch grass maintenance in LJV cannot be determined, it is well known that *Stipa* does not reproduce well under intense competition from annuals and that timely removal of competition from annuals by grazing or burning benefits *Stipa* (Bartolome and Gemmille, 1981; Berry, 2003).[6]

Finally, this case study has also illustrated the usefulness of a critical, long-term, repeat study approach in two ways. First, the LJV case demonstrates the power Clements' narrative held over researchers working in California's grasslands and how this has had an impact on landscapes. Indeed, Holstein (2001) attributes the end of grazing and the decline of needle grasses at the Jepson Prairie to Clements' paradigm and 'BDP myths' (262). He concluded that *Stipa* grasses now face the threat of overprotection with the elimination of even 'light' grazing. As Sayre (2017) reminds us, 'overgrazing' was an inevitable part of how cattle ranching was historically viewed and these ideas may have had negative impacts on native bunchgrass cover in parts of California including places such as LJV and Jepson Prairie, where grazing was removed. Secondly, because the original baseline work of Gale and Goode was conducted within the context of the BDP, we know with certainty that they established their plots on what were deemed excellent stands of native *Stipa*. That these stands have nearly disappeared over the past few decades is evidence that grazing practices can maintain or perhaps facilitate *Stipa* in areas where forbs or annual grasses might otherwise have advantages.

As is the case with all long-term studies, our results are limited by the fact that many variables could not be isolated or manipulated. This is especially true for weather fluctuations and fire, which especially in tandem, can effect *Stipa* survival and regeneration rates (Schellenberg et al., 2020). *Stipa pilchra* is a long-lived species, however, and the decline documented by our 34-year analysis suggests that the process was not triggered by an individual event, but rather, was gradual.

6. Conclusion

The long-term LJV study finds that California's native bunchgrasses have declined dramatically since the end of the ranching era. Simultaneously, native forbs have increased (at least temporarily), especially on the valley floor. Our findings also suggest that the historical ranching practices in LJV likely supported the excellent stands of *Stipa* observed in the valley prior to release from grazing. These findings are in agreement with those of previous long-term studies in other parts of California that also found a decline in *Stipa* cover on lands released from grazing (Bartolome et al., 2004; Bartolome and Gemmill, 1981; Stahlheber and D'Antonio, 2013). Finally, our results suggest that *Stipa* grasses were likely more common on the valley slopes and edges, where their presence has not declined dramatically post-grazing, unlike on the valley floor.

Lastly, it is important to reiterate that results of research linking disturbance regimes to the presence and density of *Stipa* stands remains inconclusive (George et al., 2013; Hatch et al., 1999). Evidence suggests that the timing of disturbances are critical and that compound effects of grazing and burning must be considered (Stahlheber and D'Antonio, 2013). Missing from this body of recent work; however, is the role of mechanical disturbance, which was common practice on most California ranchlands. Recent studies indicate that these disturbances have longer-lasting impacts on native cover than does fire or grazing (Engelberg et al., 2013; Potts and Stephens, 2010). As such, a more complete model of needle grass ecology may need to include multiple and diverse disturbance regimes.

Data Accessibility Statement

Supplementary data for this project are stored on the Savanna LABO website: http://www.cla.csulb.edu/departments/geography/savannalabo/ under the subheading of La Jolla Valley.

Notes

[1] Jackson and Bartolome (2002) consider Coast Range Grassland as a third type of sub-community of native grasslands following coastal bluffs and the Central Valley.

[2] Note that the locations of Barry's stand and point locations are approximate and shown here to indicate the know presence of *Stipa* stands, not to delimit the extent of these native grasses, which likely covered a more contiguous area.

[3] Interestingly, Heady established the permanent transects at Hopland as well (Merenlender, 2001).

[4] Slopes tend to have coarser and shallower soils which are thought to support bunch grasses as well as shrubs when compared to valley floors; however, as Laris et al. (2016) noted, valley floors were also more frequently and intensively mechanically disturbed that slopes.

[5] Interestingly, Stassforth's (1993) restudy (carried out over three consecutive years 1994–1996) did not find great variation in the frequency of forbs nor grasses. Two clear exceptions were the forbs *Erodium cicutarium* and *Hemizonia fasciculate,* which declined in year three. *Avena* also declined slightly in year three while *Lolium perenne* increased.

[6] Hobbs (1983) interviewed the land owner and ranch managers for her dissertation. They indicated that between 1946 and 1952 the valley was heavily overgrazed by cattle. After 1952, grazing pressure was reduced, although cattle remained in the valley until 1965.

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Competing Interests

The authors have no competing interests to declare.

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