

## ABSTRACT

# ANTHROPOGENIC DISTURBANCE REGIMES AND COASTAL SAGE SCRUB RECOVERY: COMPARING THE LONG TERM IMPACTS OF GRAZING AND CULTIVATION IN SOUTHERN CALIFORNIA

By

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Coastal sage scrub (CSS) is a unique and highly threatened vegetation community in coastal Southern California and northern Mexico, with 90 percent lost to development, agriculture, and invasive species. Understanding CSS recovery is critical to its survival. This study looks at the long-term effects of grazing and cultivation in southern California by tracking the extent of exotic grassland in two valleys in the Santa Monica Mountains over sixty years. The rates of native shrub return in a grazed valley were compared to those in a cultivated valley. Transects compared physical differences of stable and recovering grassland-shrubland boundaries. Native shrubs returned to the grass valley that was grazed nearly one and one-half times faster than the valley that was cultivated. Cultivation may result in a type conversion of CSS to a new steady state of exotic annual grassland. The field transects showed that stable and recovering boundaries had different physical characteristics.



ANTHROPOGENIC DISTURBANCE REGIMES AND COASTAL SAGE SCRUB  
RECOVERY: COMPARING THE LONG TERM IMPACTS OF GRAZING  
AND CULTIVATION IN SOUTHERN CALIFORNIA

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## CHAPTER 1

### INTRODUCTION

Coastal sage scrub (CSS) is a unique and highly threatened vegetation community in coastal southern California and northern Mexico. Ninety percent of this native vegetation community has been lost to development, agriculture, and invasive species, so understanding the reasons and processes involved in CSS recovery is critical to its survival and restoration (Westman 1981). Significant research studies have explored the recovery of CSS, but they tend to focus on the dynamics of and factors influencing the recovery from an ecological perspective. Other studies examine historical land use in southern California, but these rich historical accounts often stand alone, without application to an evaluation of current conditions. Still other research looks at the impact of anthropogenic disturbance on CSS, but it fails to define the specific differences between land use regimes, the details of which have diverse effects on native shrubs. Because a large portion of CSS range overlaps with major population and agricultural centers, we must bring together ecological research, land use history, and anthropogenic disturbance studies to fully understand CSS recovery.

Over the past several decades the fields of ecology and biogeography have gone through a major transition that includes a shift in perspective from equilibrium and

steady-state-based models to those based on fluctuation, history, and disequilibrium. Along with this shift, disturbance has been recognized as an important and natural part of any ecosystem, and understanding the details of such disturbance regimes has become vital (Pickett and White 1986; Worster 1990; Zimmerer and Young 1998). Researchers have been working diligently to define natural disturbance regimes, including their type, frequency, intensity, and spatial extent. To date, the majority of this research has focused on natural disturbance regimes, with insufficient attention paid to human activity.

While the impacts of anthropogenic disturbance have long been appreciated in ecology, there has been a tendency to leave the specifics of human disturbance regimes unexamined (McDonnell and Pickett 1993). Although this practice is slowly changing, a common shortcoming of ecological research is that factors like the intensity of human activity, its frequency and duration, and its exact nature are often left understudied. Ecologists may simply note the activity —grazing, excavation, brush clearance— without scrutinizing the specifics of the regime itself. This omission points to a tendency in ecological research to ignore the subtle and sometimes long lasting impacts of different anthropogenic disturbance regimes on ecosystems and biogeography (McDonnell and Pickett 1993).

Delineating the diverse processes of human disturbance regimes is a key component of predicting and managing the long-term impact of human activity. It is quite apparent that an area excavated for quarry rock will experience different changes over time than one used for military drills, but much less is known about the differing long-term impact of more common anthropogenic disturbances such as grazing,

mechanical disturbance, and farming. There is also limited understanding of which disturbance regimes lead CSS to type convert.

Type conversion is the process by which one vegetation form replaces another, as when woodland replaces grassland. The phenomenon is well known in ecosystems with a mixture of woody and herbaceous vegetation forms such as savannas and other mixed shrub/grasslands. In these systems, type conversion involves the replacement of the dominant vegetation form by a minor form such as the replacement of grasses by shrubs in a grassland or vice-versa (Scholes and Archer 1997). Such type conversion often involves one native community replacing another, but it may also represent a shift from native dominance to dominance by non-native species, as is the case when CSS is replaced by exotic annual grasses native to the Mediterranean basin (Minnich and Dezzani 1998).

Although “type conversion” indicates a shift in land cover, it does not address the permanence of the new community, although permanence is often implied. A type conversion can be considered permanent if it results in a change in vegetation cover and the establishment of a new and stable steady state. This phenomenon has been documented in rangeland by Westoby, Walker, and Noy-Meir, who suggested that the dynamics they observed could be explained by a combination of stable vegetation communities they called “states,” and “transitions” between steady states that are caused by disturbance events or management decisions (Westoby, Walker, and Noy-Meir 1989). The trajectory of a vegetation community can be determined by this multiple steady-state model only if both biophysical and land use factors are considered. If we want to establish whether a permanent type conversion to a new steady state has taken place, we

have to measure the return of native vegetation many decades after release from anthropogenic activity. Native vegetation regrowth is often the single measure of how well a system is recovering, and it may also signal the improvement of other parts of the system like soil and hydrology.

The research presented in this paper explores two major human disturbance regimes in southern California—grazing and cultivation—and seeks to determine if either regime results in the replacement of CSS by a steady state of exotic annual grassland. The few studies that have examined these topics indicate that type conversion may or may not result in a new steady state and little research has explored the reasons for the differing outcomes. Research suggests that following release from grazing CSS tends to gradually recover, although in some cases the recovery may be very slow, and in others, CSS may not recover at all (Freudenberger, Fish, and Keeley 1987; Stylinski and Allen 1999; Eckardt 2006). Several studies find that cultivation can result in a permanent type conversion and the establishment of a new steady state, whereas mechanical disturbances such as shrub removal may or may not result in a permanent shift (Davis 1994; Stromberg and Griffin 1996; Stylinski and Allen 1999).

In order to explore the long-term impacts of livestock grazing and cultivation, this study tracks the grassland/shrub dynamics over a thirty-year period for two valleys with distinct anthropogenic disturbance regimes. It compares two time periods, one of mostly heavy anthropogenic disturbance and one of almost no disturbance for two exotic grass valleys, one mostly grazed and one mostly cultivated. This study revisits La Jolla Valley and Serrano Valley of southern California, whose grassland changes and boundary characteristics were investigated in Hobbs's 1983 dissertation. Hobbs's work combined

extensive interviews with former landowners and workers with archival photo and record analysis to piece together a rich and detailed land use history for both valleys. When supplemented by additional research for the current project, Hobbs's land use history paints a clear picture of the differences between the two valleys: Extensive grazing over more than a century in La Jolla Valley and nearly eight decades of cultivation, including frequent soil tilling, Serrano Valley. The vegetation in both valleys now consists of large swaths of exotic grassland, surrounded by native shrubs. Because the two valleys are environmentally similar and have experienced almost identical fire regimes, they offer a straightforward opportunity for comparing the long-term impacts of grazing and cultivation on the return of native shrubs. The hypotheses of this study are as follows:

1. Grazing and cultivation have different long-term impacts on native shrub return.
2. Cultivation may cause CSS to type convert to a new steady state of exotic grassland.
3. Areas that experience significant native shrub return have different biophysical and environmental characteristics than areas that experience little or no native shrub return.

Exploring these hypotheses is especially important in a state that has experienced human disturbance regimes for hundreds, if not thousands of years. The introduction of agriculture in the early nineteenth century signaled the beginning of an era of extensive grazing and farming throughout most of California, much of which continues today. With development and urbanization, however, a great deal of former pasture and cropland has been ceded to state and local parks departments, who are tasked with

management and in certain cases restoration. Given the complex land use history in the state, combined with environmental factors, it is difficult for new land managers to determine the area's former natural state, or what the benefits of restoration efforts might be. Establishing the real and varied impacts of different human disturbance regimes, and defining those regimes in detail, will help California land managers better understand the areas that they protect and illuminate the changing face of California as former pasture and cropland are left untended into the future.



## CHAPTER 2

### EXISTING RESEARCH AND THEORETICAL CONTEXT

Environmental factors are a key determinant in the distribution of vegetation across a landscape. Topography, climate, and edaphic characteristics, however, do not always provide complete explanations; environmentally identical places may have very different vegetation communities. Disturbance, whether of natural or human origin, is often responsible for these differences (MacDonald 2003). When natural disturbance regimes do not explain the variation, one must then turn to human disturbance regimes for answers. Human interactions with the natural world can have significant and often unexpected effects on the physical environment. This is especially true in places where urban areas and wildland meet (e.g., Beckman and Berger 2003; Liu and Koptur 2003). Wildland that is close to densely populated regions and that is controlled or managed by human beings is neither completely natural nor solely a product of society. Rather, it represents a fusion of human activity and the natural environment, partly natural, partly anthropogenic.

Vale argued that it is the degree of humanization that matters and that we should abandon attempts to draw a line between “pristine” and “humanized” landscapes (Vale 2002). In evaluating the state of a particular landscape, Vale encourages researchers to

ask the question, “Did (and do) the fundamental characteristics of vegetation, wildlife, landform, soil, hydrology, and climate result from natural, nonhuman processes, and would these characteristics exist whether or not humans were (and are) present?” (Vale 2002, 5). Asking this question forces one to discard generalities about the human impact and begin to examine the specific interactions between humans and their natural environment.

Despite the deep connections between nature and society, until recently the canon was dominated by research that focused mainly on ecological accounts of landscape and vegetation changes. This tendency toward biophysical explanations may be due to the Western tradition of separating human society from the natural environment, both physically in the ways we partition the landscape and ontologically in the ways we think and talk about the natural world (Neumann 2003). As Duvall has argued, most studies of vegetation have adopted reductionist approaches to research, primarily by looking at only natural or only anthropogenic spaces in landscapes (Duvall forthcoming). Few have considered how social and biophysical factors interact to create vegetation patterns across landscapes.

Although Duvall was writing about the African savannas, his general argument holds true for most environments. Historically, the debate over the origin of the composition of vegetated landscapes has been framed as an either/or argument: A given landscape has either human or natural origins but not both (Duvall forthcoming; Laris forthcoming). This so-called nature-society dichotomy continues to influence biogeographical and ecological research efforts, even as the underlying models in ecology have shifted to focus more on the role of disturbance and change (Laris

forthcoming). This dualistic point of view is problematic because it impedes integrated approaches that consider the ecological consequences of human attitudes and practices toward nature. Further, it leaves no place for objects or species that are neither completely natural nor completely a product of human society, such as rangeland and cropland (Laris forthcoming). In order to fully understand a process that includes both ecological and anthropogenic factors, we must discard the nature-society division and consider human beings and the natural environment as two parts of a single system (McDonnell and Pickett 1993; Kotchen and Young 2007; Duvall forthcoming; Laris forthcoming).

Bringing biophysical and societal explanations together requires us to recognize that the human role in environmental change is specific, patterned, and meaningful and that these patterns and meanings directly affect vegetation dynamics (Robbins 2004). Blaikie and Brookfield suggest that the best way to explore the context of human-environment interactions is by forming a “chain of explanation” (Blaikie and Brookfield 1987, 27). In doing so, one looks to progressively larger scales to explain change. In the case of vegetation dynamics, biophysical factors may explain why a community flourishes in a certain place, but they provide only proximate answers. It is the immediate interactions between people and the natural environment, and the specific societal context in which those interactions occur that drive changing plant dynamics in the urban-wildland interface (Robbins 2004). This direct interaction and its context offer the clearest link between social processes and vegetation community changes.

## Disturbance

Where once it was thought that ecosystems marched toward a climax of stability and homeostasis, it is now recognized that the natural environment does not progress in the direction of equilibrium and that disturbance is an important part of the functioning of most ecosystems (Pickett and White 1986). Fire, flood, and other interruptions to the status quo can germinate seeds, fertilize soils, and create new ecological niches (e.g., Baskin and Baskin 1997; Carlton and Bazzaz 1998). In their discussions of this shift to non-equilibrium ecology, Worster and Zimmerer and Young note the effect such a change in thinking may have on conservation and preservation efforts (Worster 1990; Zimmerer and Young 1998). Worster specifically worries that some people may make the argument that if change is natural, then human-induced change is acceptable. Both Worster and Zimmerer and Young, however, point out that natural and human disturbance are not one and the same: “It is the frequency, rate, kind, and degree of change that must matter” (Zimmerer and Young 1998, 7). That is, it is the human disturbance regime—its intensity, frequency, duration, and spatial extent—that matters, not just the type of disturbance.

This idea is in line with Connell’s intermediate disturbance hypothesis, which states that diversity is highest when disturbance is intermediate in terms of frequency and intensity (Connell 1978). Thus, humans can disrupt ecosystem functioning and threaten native biodiversity either by increasing or decreasing the frequency and intensity of disturbance or by introducing a new disturbance (Zimmerer and Young 1998). Whether or not an ecosystem is accustomed to a disturbance is important; disturbance with which species have evolved will have very different effects than entirely new disturbance

regimes. Stylinksi and Allen refer to this latter type of disturbance as exotic disturbance, a disturbance that is introduced to an ecosystem by humans and to which the native ecosystem is not accustomed (Stylinksi and Allen 1999). Fire and native animal grazing are examples of natural disturbance; major soil excavation would be an exotic disturbance in most places.

Disturbance also plays a major role in two aforementioned key concepts of modern ecology, multiple steady states and type conversion. Multiple steady-state ecology asserts that a particular ecosystem may have multiple steady states that can persist over long periods of time, depending on environmental factors and disturbance regimes (Pickett and White 1986; Laycock 1991). Such a steady state may appear to be what ecologists once referred to as a climax state (Pickett and White 1986), only to shift to a different steady state when an environmental change occurs or a new disturbance regime begins. Such shifts may also be called type conversions, as noted earlier, meaning that one vegetation community has converted into a different vegetation community (MacDonald 2003). Type conversions happen naturally, but they are often associated with anthropogenic disturbance regimes.

This shift to non-equilibrium ecology has another very different impact on conservation and preservation efforts. Environmental management projects, including restoration, are often based on the maintenance of, or return to, the natural environment as it was before human impact. However, the condition land managers attempt to preserve may be but a snapshot in a changing landscape, a state that may persist only through the active suppression of natural disturbance (Sprugel 1991; Behnke and Scoones 1993). Still, such uncertainty does not have to preclude conservation efforts. Rather,

Walker suggests that we combine “the strengths of social and biophysical ecological theory” so that we might better manage landscapes and address environmental degradation (Walker 2005, 79). Rather than attempt to separate people and nature in order to preserve some singular ideal, natural state, we should minimize our “destructively chaotic” disturbance and permit the landscape the flexibility to change naturally (Worster 1990, 16). Unfortunately, this approach can be difficult when people live within the area that requires disturbance.

Aside from modern disturbance, researchers have begun to acknowledge over the last few decades that humans have been modifying their natural environment for far longer than previously recognized. Pre-Columbian North America was not “pristine” as many had thought, but instead was subject to significant anthropogenic influence, albeit not on the scale it is today. Denevan notes, “The Indian impact was neither benign nor localized and ephemeral, nor were resources always used in a sound ecological way” (Denevan 1992, 370). That is, Native Americans manipulated the natural environment to satisfy their needs just as post-Columbian Americans have since their arrival (Anderson 1990).

The effects of Native Americans on the landscape have been documented in various studies. For example, it is well known that the use of fire by Native Americans shifted the extent of the North American plains eastward (Sauer 1950). More recently, scientists have found that parts of the Amazon rainforest contain relics of past human settlements and that subtle practices enriched the soil with carbon, resulting in long-lasting impacts on vegetation cover (Erickson 2006). Therefore, the truly pre-human state of many ecosystems cannot be known.

Vale cautions against the two extreme visions of pre-Columbian North America, the earlier romantic vision of a pristine and untouched continent and the more recent vision of an entirely inhabited and altered Native American landscape (Vale 2002). Rather, he advocates a more tempered picture of historical anthropogenic disturbance in North America, one that recognizes the impact of Native Americans as significant but does not overstate their influence spatially or temporally. Such an approach mirrors the previously discussed balancing of human and natural influences on the landscape; we must consider both when researching the pre-Columbian era, as well as the modern era.

In examining a particular disturbance regime, it is important to distinguish between native disturbances, natural events to which the vegetation community has adapted such as fire and native animal grazing, and exotic disturbance, introduced activities to which native species have no adaptation such as farming and urban development (Stylinski and Allen 1999). While humans have no doubt modified the natural disturbance regimes of fire and native animal grazing through fire suppression and introduction of livestock, native California plant communities at least have mechanisms for dealing with some level of these disturbances (Hayes and Holla 2003; Bartolome et al. 2004; Keeley, Fotheringham, and Baer-Keeley 2005).

Such resilience may not extend to wholly new and introduced disturbances, like tilling, soil excavation, and construction, however. Stylinski and Allen found that sites subject to these exotic disturbances were dominated by exotic annual species, a state that persisted for the entire seventy-one years of study (Stylinski and Allen 1999). The exotic annual plant communities appeared to persist permanently. Grasses of the Mediterranean basin, which make up a huge portion of exotic California grasslands, evolved over

thousands of years to cope with and even thrive under agricultural conditions, which have been present in the Mediterranean basin for millennia (Stylinski and Allen 1999). Native California plant communities, including CSS, have had only a few hundred years to adapt to agriculture, the blink of an eye in evolutionary time scales.

Disturbance, both human and natural, also plays a role in vegetation dynamics, as certain disturbance regimes may favor one species or vegetation community over another (Woinarski and Ash 2002). Factors such as disturbance frequency and intensity may influence how each species responds and interacts, and therefore affect the composition of the vegetation community in which the species reside (O'Leary and Westman 2008). Foster, for example, documented how the land use practices of the colonists in New England more than 200 years ago continues to influence the occurrence of tree species today; areas that were farmed have distinct species cover when compared to areas used for wood lots (Foster 1992). Similarly, several researchers have documented how hoe farming and changes in fire regime in African savannas can transform woody vegetation cover (Fairhead and Leach 1996; Laris 2008). Some communities, like CSS, the focus of this study, have come to be defined by their disturbance regimes, with fire regime often thought to shape the species composition, diversity, and level of invasive species seen in CSS (Keeley, Fotheringham, and Baer-Keeley 2005). Most vegetation communities experience multiple disturbance regimes simultaneously, at different spatial and temporal scales, further highlighting the need to thoroughly understand each individual disturbance, as well as how disturbance regimes interact with each other (Stromberg and Griffin 1996).



## Grassland-CSS Relationships

The dynamics of CSS and grassland depend both on the physical environment and the natural and anthropogenic disturbance regimes that impact coastal southern California.

### Coastal Sage Scrub

CSS is one of three sage scrub communities in California and Baja, Mexico, extending from the central California coast through northwestern Baja. CSS experiences mean annual rainfall between roughly 25 cm and 45 cm, with average rainfall decreasing from the northern to the southern limits of its range, but it often receives significant moisture from coastal fog as well. CSS is dominated by semi-woody shrub species, and most of the flora are drought-deciduous, with a smaller portion represented by evergreens and succulents. Common shrub species include a number of members of *Salvia* (i.e., *Salvia mellifera*, *S. leucophylla*, and *S. apiana*), two species of the sunflower (Asteraceae) family (*Artemisia californica* and *Encelia californica*), and two buckwheat species (*Eriogonum fasciculatum* and *E. cinereum*). The evergreen *Rhus integrifolia*, *Malosma laurina* (formerly *R. laurina*), and *Heteromeles arbutifolia* are also present, with the former being most abundant. CSS also supports the succulents *Opuntia littoralis*, *O. oricola*, and *O. prolifera*. Unlike chaparral, the average height of the shrubs is about 0.5 to 1.5 m, and the cover is open and flexible enough that one can walk through it. CSS tends to be a floristically diverse combination of annuals, perennials, and geophytes, although some of the aforementioned species can dominate large areas (Rundel and Gustafson 2005; Rundel 2007).

CSS is one of the most threatened plant community types due to the dense population and high urbanization of its range, with habitat loss to development or type conversion ongoing (Minnich and Dezzani 1998). Westman estimated that only 10 percent of CSS's original extent remains today (Westman 1981). This is of special concern because CSS is home to several endangered animal species, including the California gnatcatcher, whose habitat must consist of dense, diverse CSS (Atwood 1994; Underwood, Ustin, and Ramirez 2006).

Fire is a natural part of the CSS system. Unlike other ecosystems that experience minimal diversity post-disturbance, CSS diversity often peaks shortly after fire; many CSS species thrive free from the closed canopy and limited resources found in unburned CSS (Carrington and Keeley 1999). Fire helps maintain the diversity that is characteristic of CSS, as a significant portion of CSS plants have seedlings that establish post-fire, many of which are actually fire-dependent (Vogl and Schorr 1972). Thus, it is this disequilibrium that helps to maintain the structure and diversity most associated with CSS.

There is, of course, a natural limit to the benefits of fire to diversity in CSS; too frequent fires (three to five year fire return interval) may lead to type conversion of CSS to something closer to grassland (Minnich and Dezzani 1998), and a highly frequent fire regime may be associated with higher levels of exotic invasive species (Keeley, Fotheringham, and Baer-Keeley 2005). The effects of an intense or frequent fire regime on CSS are still being debated. Depending on intensity, fires generally kill all above-ground biomass, while, for some species, below-ground biomass survives (Keeley 1987). CSS species can be broken down into categories corresponding to their response to fire:

Sprouters are those species that resprout from surviving biomass (e.g., root crowns or tubers) after a fire, while obligate seeders are those species that are completely killed by fire and therefore depend on germination of the existing seed bank in order to maintain their populations (Zedler, Gautier, and McMaster 1983). The seed banks of some CSS species can remain dormant in the soil for decades, only to spring forth post-fire (Keeley, Fotheringham, and Baer-Keeley 2005). Even hot, intense fires tend to leave some below-ground biomass intact enough to resprout. It should be noted, however, that the post-fire response of an individual species also depends on fire intensity (Rundel and Gustafson 2005).

While some CSS species require fire (or its heat or resulting charred wood and increased light exposure) to germinate their seeds, others require extended periods of time with no fire in order to expand their populations (Keeley 1987). Zedler, Gautier, and McMaster found that an extremely short period between fires (three years) severely limited the ability of some CSS species to recover post-fire (Zedler, Gautier, and McMaster 1983). Thus, it is an intermediate fire return interval, one that both periodically germinates fire-dependent species and also allows for seed dispersal and germination without fire, that benefits most CSS species (Minnich and Dezzani 1998).

Some researchers claim that CSS persists only with disturbance, and that without fire, grazing, or other anthropogenic influence, CSS would convert to other types of vegetation communities, such as oak woodland or native grassland (Vogl 1976).

Research has shown that the vegetation mosaic of CSS, chaparral, oak woodland, and annual grassland in coastal California cannot be explained by substrate, slope, aspect, or

soil depth alone (Callaway and Davis 1991). This conclusion implies that other factors, such as disturbance, including human activity, play a role.

### California Grasslands

Where once were hillsides and valleys of native perennial shrubs, forbs, and bunch grasses, much of California is now covered in exotic grasses. California annual grasslands are an introduced ecosystem, representing one of the few instances of an exotic vegetation community establishing itself so widely and lastingly (Mack 1989). The combination of the introduction of Mediterranean basin annual grasses, such as wild oat and rye, and anthropogenic disturbance, including fire management, grazing, farming, and development, have allowed the grassland community to persist and spread throughout a huge portion of the state, often replacing CSS and chaparral (Coleman and Levine 2005). California grasslands are generally less diverse than the native shrub communities and are often dominated by a few widespread exotic grasses, most of them annual species (HilleRisLambers et al. 2010). This pattern leads to greater season-to-season and year-to-year fluctuation in biomass, which puts animal species unaccustomed to such variation at a disadvantage (Cione, Padgett, and Allen 2002). Further, the abundance of dry fuel in the summer in an exotic grassland can lead to more frequent fires, which in extreme cases can cause even more CSS to convert to grassland (Minnich and Dezzani 1998).

### Grassland-CSS Interactions

Grassland and CSS are often found adjacent to each other in southern California. Depending on myriad processes, CSS may advance into grassland over time, or vice versa. However, several factors have been found to favor grassland over CSS under

certain circumstances. Cox and Allen found that grassland and neighboring CSS had up to 400 times the number of exotic grass seeds per square meter as native shrub seeds (Cox and Allen 2008). This difference in seed bank may be a primary reason for the dominance of exotic annual grasses (Seabloom et al. 2003). Exotic grasses and their resulting accumulation of litter can also block much-needed sunlight from native forbs, preventing their establishment in areas dominated by grasses (Coleman and Levine 2005). Nitrogen deposition from air pollution has also been shown to promote grasses, but only in areas of low fire frequency (Talluto and Suding 2007), and grasses themselves have been shown to increase soil nitrogen levels, further inhibiting shrubs (Wolkovich et al. 2010).

An important factor in grassland-CSS interactions is their relationship to people. Human practice may favor exotic grassland over native shrubs, due to the value of grassland as pasture and cropland (Mack et al. 2000). In a highly populated state like California, where a significant portion of land is either inhabited by people or supports people through agriculture, it is not uncommon for native vegetation to give way to commercial uses like grazing and cultivation (Macfadyen 2009). It was not until recently that native shrub vegetation and the habitat it supports have been recognized as having their own inherent value.

California Exotic Grasses as Invasive Species. It is often unclear which grassland-CSS processes are due to disturbance regimes, environmental factors, or competitive exclusion. Minnich and Dezzani claimed that, although anthropogenic activity may in some part lead to the conversion of CSS to grassland, it is the competitive advantage of the grasses that is truly responsible for type conversion (Minnich and

Dezzani 1998). These exotic grasses are considered invasive species, the presence of which can alter ecosystem properties, functioning, and disturbance regimes themselves (Wilson 1992; D'Antonio 2000). Invasive species can affect native species directly as predators, disease vectors, and competitors (D'Antonio et al. 2001). Specifically, they can wipe out native prey populations that have no natural defenses (e.g., Dowding and Murphy 2001), introduce diseases against which native species have no immunity (e.g., Siemann and Rogers 2003), and out-compete native species for resources (e.g., Harms and Hiebert 2006).

Beyond these direct effects, invasive species can have significant indirect effects. The direct effects noted above may indirectly impact other species that depend upon the reduced or extinct native species through species cascades (Wilson 1992). Invasive species may modify ecosystem functioning, thereby threatening the majority of species inhabiting that ecosystem (Vitousek 1990). The ultimate effect of these invasive species is often lower biodiversity, which in turn leads to increasing homogenization; while the same total number of individuals may exist, the vast majority may be represented by a single or small group of dominant species (Gaston 2005), as in the case of the few Mediterranean basin grass species spread throughout California.

Invasive species are more prone to causing homogenization than native species because in order to successfully invade, a species is likely to be dominant and have a wide ecological niche, leading to functional and spatial homogenization (e.g., Mckinney and La Sorte 2007). As processes that facilitate invasions such as secondary releases continue, initially isolated invasive populations will begin to fill in the gaps, "leading to a greater degree of biotic homogenization at a continental scale" (Qian and Ricklefs 2006,

1296). This homogeneity makes ecosystems more vulnerable to many threats, including stochastic events, climate change, and anthropogenic influence (Gaston 2005).

### CSS Boundaries and Type Conversion

Since many studies have found that physical factors like substrate, topography, and climate cannot fully explain the distribution of CSS vegetation (Wells 1962; Riordan and Rundel 2009), research has focused on several other possible explanatory factors, including fire, grazing, and mechanical disturbance, often associated with cultivation. The distribution of vegetation in most CSS habitat is the result of a complex web of interactions between these and biophysical factors (Wells 1962). That is, much CSS is influenced by some or all three of these elements, which in turn interact with the biophysical properties of the landscape. The important question is, Which of these factors or combination of factors leads CSS to type convert to grassland, or vice versa?

Although there is a growing body of research on the impacts of anthropogenic disturbances on CSS, much of it has focused on fire regime (Keeley and Keeley 1984; Keeley, Fotheringham, and Morais 1999; Keeley 2005; Keeley, Fotheringham, and Keeley 2005). Less research has examined the effects of land uses such as grazing and mechanical disturbance associated with cultivation (e.g., plowing and disking), and this body of work often fails to distinguish between disturbance regime types and subtle differences that can have very long lasting impacts on vegetation cover. This unexplored variation may be one reason that studies seeking to explain the underlying reasons for vegetation cover in coastal California are often inconclusive. Further, much research to date examines the long-term impacts of various disturbance regimes, but does not discuss the possible permanence of these impacts. That is, the research does not fully address

whether a type conversion has taken place that results in a new steady state of exotic grassland.

Fire, the most extensively researched factor in CSS distribution, has been shown to both benefit and suppress CSS, as previously discussed. Fire cannot be studied in isolation, however. Anthropogenic factors like grazing and air pollution change the way that CSS recovers after fire (O’Leary and Westman 1988; Callaway and Davis 1993); environmental processes like precipitation events can alter the rate and manner of recovery (Keeley and Keeley 1984); and depth of seeds in the soil can determine whether they can germinate with precipitation or require fire to do so (Keeley 1987). Very frequent fires can lead to type conversion of CSS to grassland (Callaway and Davis 1993; Minnich and DeZanni 1998), but too infrequent fire may lead to a decrease in the species diversity for which CSS is known (Carrington and Keeley 1999). Research in similar mixed grass-woody communities in Europe indicates that infrequent fire may even lead to type conversion to oak woodland or forest (Rodrigue 2004). The current study controls for fire by studying two sites that have a similar, intermediate fire return interval, allowing for the study of other factors influencing the distribution of CSS.

Grazing has also been shown to have varying effects on CSS depending on intensity and timing, with some grazing at certain times of year benefiting native vegetation and heavy overgrazing at other times of year promoting exotic grasses (Stromberg, Corbin, and D’Antonio 2007). Grazing in the early spring, for example, may keep exotic grasses at bay and reduce their ability to compete with natives later in the year, as exotic grasses germinate earlier in the season and are thus targeted by early grazing (Dyer et al. 1996). Grazing also affects the amount of litter and live biomass



present, can modify edaphic characteristics, and may influence species composition (McNaughton 1968; Facelli and Pickett 1991; Hobbs 1996; Augustine and McNaughton 1998), thereby altering ecosystem functioning. Such effects may lead to changes in processes such as nutrient cycles and hydrology, which in turn can have significant impacts on many species across the ecosystem (Vitousek 1990).

Studies show differing long-term impacts of grazing, which may be due to both regional effects and the fact that areas of study may have experienced other anthropogenic disturbance like brush clearance and changes to the fire regime (Stromberg, Corbin, and D'Antonio 2007). Stromberg and Griffin found that native grasses were able to persist at many different levels of grazing and that grazing impacts like changes in soil chemistry and species composition were much stronger for recently grazed sites than sites that were grazed many decades ago (Stromberg and Griffin 1996). This effect may illustrate the ability of CSS to slowly recover from grazing and begin to return to its pre-grazing state.

Many studies on grazing, especially studies using experimental plots to exclude grazing, conclude that native plants do not return to dominance over a long period of time (White 1967; Micallef 1998). However, the effects of grazing are often conflated with other kinds of land use as well as climatic and environmental factors (Stromberg, Corbin, and D'Antonio 2007). Stromberg and Griffin's study found that cultivation and soil properties had a greater influence on the distribution of native grasses than did grazing, and Harrison also noted the significant effect of soil type (Stromberg and Griffin 1996; Harrison 1999). Stromberg, Corbin, and D'Antonio go so far as to conclude that a well managed grazing regime will benefit native species (Stromberg, Corbin, and D'Antonio

2007). Thus, the research to date has failed to show that grazing alone results in type conversion of CSS to a new steady state of exotic grassland.

Fewer studies explored the long-term effects of mechanical disturbance on the distribution and possible type conversion of CSS. Mechanical disturbance associated with cultivation may be the most intense of these disturbances, as tilling completely disrupts and turns over soil, altering soil compaction, chemistry, and nutrients and destroying seed banks and below-ground biomass (Davis 1994). White found that a former agricultural field continued to be dominated by exotic annual grasses several decades after cessation of farming, while Stromberg and Griffin extended this finding to a half century after cultivation had ceased (White 1966; Stromberg and Griffin 1996).

Davis attempted to fill the gap in this research with her Master's thesis, which showed that two cultivated sites did not return to their pre-cultivation state after more than seventy years, representing a true type conversion from the former steady state of CSS to a new steady state of exotic grassland (Davis 1994). Davis and other researchers concluded that, while natural disturbance may benefit native species diversity, anthropogenic disturbance regimes as intense as mechanical disturbance have the opposite effect (Denslow 1985; Laycock 1991). It may be that only intense anthropogenic disturbances have the ability to push an ecosystem past its natural threshold of resilience, beyond which it cannot return to its pre-disturbance state (Davis 1994).

Beyond anthropogenic disturbance, some research points to soil as the key factor explaining CSS distribution. It is clear that certain soil types favor one vegetation form over another, but this relationship does not always hold true. For example, while CSS is

most often found on upland slopes that tend to have coarser soils, CSS species are also found on the heavy clay soils that tend to dominate valley bottoms (Hobbs 1983). Moreover, it is quite apparent from the review of the literature that the same soils that are most often found under annual grasslands today—clay soils on flatlands—are also the soils preferred for cultivation and its associated mechanical disturbance (Davis 1994). As such, due to the widespread impact of mechanical disturbances on areas with gentle topography, it is not possible to determine the effect of soil texture on vegetation cover without reference to the history of disturbances.

One critical problem has been the tendency in the literature to conflate the terms farming and cultivation with agriculture and/or mechanical disturbance. Another is the tendency to ignore the fact that many grazing areas were also mechanically disturbed. Of the very few studies that examine the long-term impacts of cultivation, the majority find that lands that were regularly cultivated have the highest levels of non-native grasses and the lowest levels of CSS (White 1966; Davis 1994; Stromberg and Griffin 1996). Moreover, these studies find that the impacts of plowing and cultivation last for very long time periods, up to one-hundred years in some cases. Some studies note that an area is “cultivated” without documenting whether the cultivation involved clearing shrubs, mechanical disking or annual planting and harvesting of crops. The effects of mechanical disturbances such as disking and mechanical shrub removal without agriculture are much less explored, although one study finds that a single intense mechanical disturbance may result in the long-term elimination of CSS and its replacement by exotic annual grasses (Dean et al. 2009). Finally, few studies have examined the effects of mechanical disturbances in conjunction with grazing and fire. This study defines cultivation as the

combination of soil tilling and repeated crop planting and harvesting that Hobbs describes as taking place in one of the two valleys of study (Hobbs 1983).

The majority of studies on CSS/grassland boundaries have focused on the periods during which the lands were subject to frequent disturbances such as grazing, fire, or mechanical disturbance (e.g., Hatch et al. 1999; Hayes and Hall 2003; Kimball and Schiffman 2003; Keeley 2006). Far fewer studies have examined how shrublands recover and how CSS/grassland boundaries shift over time. In one of the few studies to examine recovering boundaries following the release from grazing, Eckardt documented changes in CSS and annual grassland areas for the Cheseboro Canyon area in the Santa Monica Mountains that was originally studied by Freudenberger, Fish, and Keeley (Freudenberger, Fish, and Keeley 1987; Eckardt 2006). Freudenberger, Fish, and Keeley had determined that the grassland/shrubland cover was not a function of topography alone, and they attributed the difference in cover to grazing and/or fire regime over the study period (1920-1980). At the time of their study, there was no accurate database on the fire regime. Eckardt reproduced their study and extended it another twenty years to include the period when grazing ended. His study found that fire regime did not determine the changes in vegetation cover during the study period, and he concluded that an additional factor such as grazing intensity or mechanical disturbance might explain the shifts in vegetation cover.

Eckardt's study was one of the first to track the recovery of CSS in an area where grazing and mechanical disturbance had ended decades earlier (at least twenty years) (Eckardt 2006). His findings that CSS was expanding in some areas while contracting in others, and that these shifts were not dictated by fire regime brings to the forefront the

issue of long-term impacts of anthropogenic disturbances on CSS. The rapid decline of CSS documented by Freudenberger, Fish, and Keeley and confirmed by Eckardt during the first half of the twentieth century was not the outcome of fire but rather a function of intensive grazing and/or mechanical clearing of shrubs. The fact that large areas formerly covered in CSS remain in grassland today suggests that these impacts have long-term consequences. Other studies, however, including Hobbs's original work on my study areas, show that CSS does recover from disturbance over time to a certain extent (Hobbs 1983).

The results of these studies and others suggest a need to explore the long-term impacts of different mechanical disturbance regimes on CSS. Two approaches hold promise. The first involves tracking the recovery of CSS in areas with similar environmental characteristics but different known disturbance histories. The second involves exploring the differences between recovering and stable CSS/grassland boundaries to determine the factors that contribute to, or prohibit, CSS recovery. Both approaches are used in this study.

## CHAPTER 3

### STUDY AREAS

#### Description of Study Sites

This study returns to two of the three sites in Hobbs's study, La Jolla and Serrano Valleys in Mugu State Park at the western end of the Santa Monica Mountains in southern California (Hobbs 1983). The sites were chosen because they offer a straightforward opportunity to compare two different land uses, as they are otherwise quite similar: They are environmentally comparable, share the same fire regime, and were released from anthropogenic activity at about the same time. Hobbs's Santa Cruz Island site was excluded because it has a more varied land use history and a different fire regime than the mainland sites.

La Jolla and Serrano Valleys are located about 20 km north of Malibu, CA (Figure 1) and managed by the California Department of Parks and Recreation. Both experience the mild Mediterranean climate characterized by cool, wet winters and hot, dry summers. Annual precipitation recorded at Point Mugu Naval Weather Station is 268 mm (Hobbs 1983). The average summer daily maximum temperature is 21°C, and the average winter daily minimum temperature is 8°C. Humidity has a mean daily maximum value of 91 percent and a mean daily minimum value of 48 percent (Western Regional Climate Center 2010). It is important to note, however, that these data do not precisely reflect the weather in the two valleys, due to Point Mugu's location directly on the coast

and elevation of only 4 m. The valleys probably experience more variation in temperature (higher daily maximum means and lower daily minimum means) because of their greater distance from the ocean, higher rainfall due to orographic precipitation, and lower humidity. Fog is also a factor in the valleys, appearing nearly daily on summer nights and mornings, but usually clearing in the afternoons.

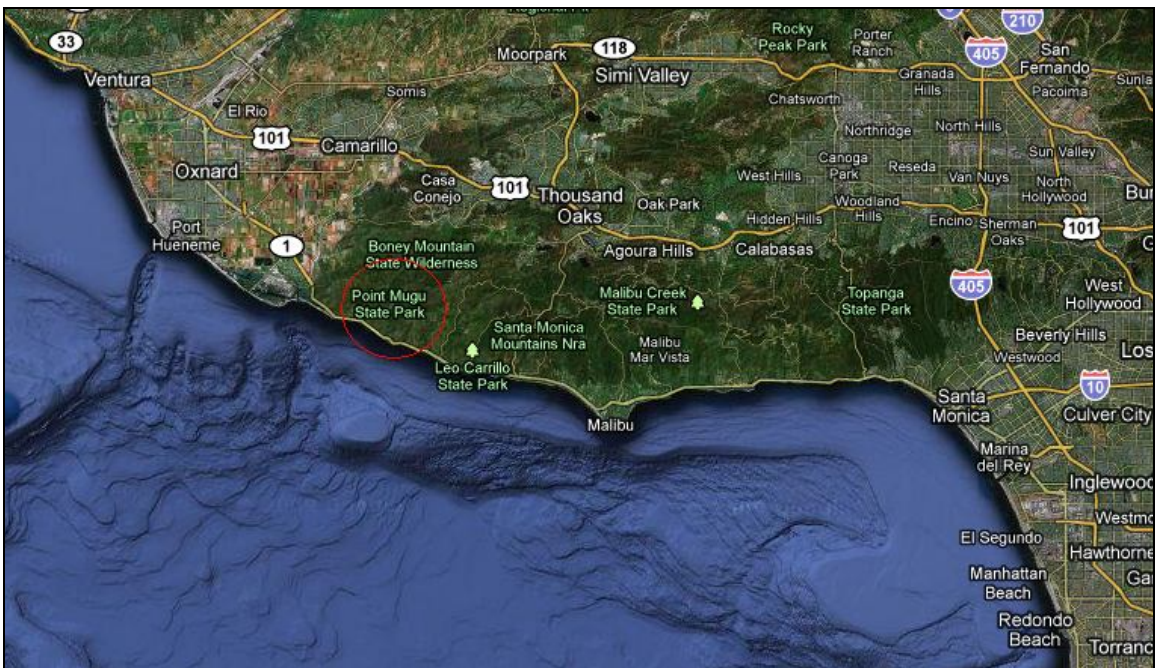


FIGURE 1. Location of Point Mugu State Park in Southern California (Google Earth).

### La Jolla Valley

La Jolla Valley is located west of Sycamore Canyon Road, about 1.3 km inland at its closest point to the sea and extending about 2.5 km northeast away from the coast.

The southwestern end is broad and expansive, with the valley narrowing to only about 0.5 km wide at its northeastern end. The topography is undulating, with hills and small ravines interrupting the valley floor and the surrounding mountains rising above the valley at varying slopes. La Jolla is a high valley for the Santa Monica Mountains, at about 250 m in elevation. It contains two stream networks that converge and drain through La Jolla Canyon to the Pacific Ocean. These streams are usually extremely low or dry within the valley, but the steeper and shadier canyon can maintain its flow in the winter. Despite the lack of year-round running water, the streams support riparian habitats along much of their length. The valley's substrate is composed of sandstone and shale, with different combinations of the two found in various parts of the valley (Hobbs 1983). Several soil types are present, including loam, clay loam, and clay. Soil compaction and rockiness fluctuate widely across the valley.

The vegetation in La Jolla Valley includes grassland, CSS, chaparral, and riparian woodland dominated by oak along the streams. Barry surveyed vegetation in the valley after its release from anthropogenic disturbance in 1965, finding that the dominant CSS species in the valley were *Salvia leucophylla*, *Artemisia californica*, and *Malosma laurina* and that exotic species like *Phalaris aquatica*, *Lolium perenne*, and *Avena fatua* dominated the grasslands (Barry 1972; Barry 1976). These species remain widespread. Goode's survey found similar dominance of exotic species in the grassland: Only two of the twelve grass species she found were native, *Nassella pulchra* and *N. lepida* (Goode 1981).

The entire valley has burned three times in the last century, in 1951, 1973, and 1993, translating to a fire return interval of about thirty years. (Fire return interval is



calculated by dividing the entire period of record by the number of fires.) Because the fire history for the valley is not extraordinary, and because it is uniform across the entire valley (i.e., the whole valley burned each time), the study naturally controls for fire regime as a factor influencing grassland-CSS dynamics in the analysis.

### Serrano Valley

Serrano Valley is located east of Sycamore Canyon Road, about 3.5 km from the coast, running east-west for a length of roughly 2.7 km. Like La Jolla, it is broadest at its western end, narrowing steadily to the eastern end, and it has similarly undulating topography. It is at a lower elevation, about 150 m, and further inland than La Jolla, which means that Serrano likely experiences slightly more rain, less fog, and more variation in temperature. The valley contains two streams and a small human-made pond that may dry completely in the late summer of dry years and is mostly brackish the rest of the year. The streams are frequently dry but support riparian oak woodland along their paths within the valley. They drain through Serrano Canyon to Sycamore Canyon and then to the Pacific Ocean. Most of the substrate is made of basalt, with a pocket of intrusive igneous rock (Hobbs 1983). Soils vary throughout the valley, with very rocky loam, clay loam, and clay found in various areas. Like La Jolla, soil compaction and rockiness also vary widely.

The vegetation in Serrano is similar to that in La Jolla, except for the extent of native bunch grasses. While at least some of the vegetation in La Jolla was known to have been native bunch grassland prior to the introduction of exotic grasses, Serrano has less native bunch grass and is thought to have once been mostly shrubland (Hobbs 1983). Early aerial photos reflect the prevalence of shrubland in Serrano Valley. The valley now

supports exotic grassland, CSS, chaparral, and riparian oak woodland, as previously described. Less has been written about the vegetation in Serrano than that in La Jolla, most likely due to inaccessibility and lack of use. Personal observations indicate a higher diversity in the types of exotic grasses.

Serrano's fire history is almost identical to La Jolla's, with the entire valley burning in 1955, 1973, and 1993. The same massive fires that burned La Jolla in 1973 and 1993 burned Serrano as well. As indicated for La Jolla, because of the relatively long fire return interval and the fact that the entire valley was covered by each burn, fire was controlled for as a factor in the vegetation changes.

#### Land Use and Grassland Changes in La Jolla and Serrano Valleys to 1983

The land use history discussed below is drawn directly from Hobbs's work (Hobbs 1983). Following the summary of Hobbs's research are clarifications based on this project's more recent research.

#### La Jolla Valley

Prior to the arrival of Mexicans in southern California, Chumash Indians resided in the valley, with a trail to the coast connecting La Jolla Valley to the large Chumash town of Xucu. The Mexican government granted the land to one of its citizens in 1836, thereby creating Rancho Guadaluca. Local landowner Richard Broome bought up the valley piece by piece between 1888 and 1891 and ran a cattle ranch with his sons for several decades. In 1921, Broome began leasing parts of his 25,000 acres for sharecropping. Broome maintained a portion of the valley for the breeding of draft horses. The 1934 Wieslander survey shows the valley as grassland, meaning that it was

not under cultivation at that time. (The Wieslander survey had a separate classification for cultivated land, reserved for areas with active crop cultivation.)

By 1938, land management had been transferred from Richard Broome to his son John, who oversaw some disking and brush clearance between then and 1946. Hobbs claims that aerial photography from 1938 shows evidence of these land activities over much of the valley. From 1946 to 1952, there was significant overgrazing of the valley by cattle. During this time, two exotic grass species, *Lolium perenne* and *Phalaris aquatica*, were introduced into a small part of the valley with prepared soils and sequestered from grazing. These two grass species persist in the valley today, dominating large portions of the grassland, often in concert with *Avena fatua*. Broome reduced the grazing pressure after 1952, but cattle were not removed until 1965, just before the land was acquired by the California Department of Parks and Recreation in 1966. Since acquiring the land, the state has installed a walk-in campground and maintains a fire road, but provides little other maintenance.

Hobbs examined aerial photos dating from 1938 to 1980 and found that CSS advanced and retracted throughout the time period, with various land uses having immediate impact on the CSS. She made the following determinations regarding grassland changes: During so-called cultivation and brush clearance prior to 1938, grassland expanded into sparse CSS, while some dense CSS became sparse. Between 1938 and 1946, CSS invaded grassland (about 8 ha) and sparse CSS became dense (about 13 ha). During the period of overgrazing, from 1946 to 1952, grassland again expanded into sparse CSS. Once the grazing pressure was reduced, CSS regained 5-10 ha of

grassland. Between the removal of cattle in 1965 and Hobbs's study in 1980, 30 ha of grassland became CSS, and an additional 24 ha of sparse CSS became dense.

Comments on Hobbs's La Jolla Valley Land Use History. Hobbs discussed the presence of Chumash in La Jolla Valley, but not the implications of their presence. Coastal California is thought to have had some of the highest densities of Indians in the American West, with an average of one to three (and sometimes as high as eight) people per square kilometer (Keeley 2002). Therefore, it is likely that the valley was experiencing some degree of human disturbance during this time. Native Americans were known to ignite fires for brush clearance and hunting purposes, so at the very least the Chumash likely altered the fire regime (Keeley 2002). They did not, however, participate in settled agriculture (Nabokov 1989).

Hobbs suggests that La Jolla Valley was cultivated throughout part of its history, a claim that was not supported by further research. The Broome ranch extended nearly 25,000 acres from La Jolla Valley, over the northern tip of the Santa Monica Mountains and into the Oxnard Plain, of which only 4,000 acres were considered farming land (pers. comm., Jeff Maulhardt, historian, 2010, e-mail). It is likely that most of the farming activities took place on the plain. Historical photos dating back to the 1930s show much of the Oxnard Plain entirely dedicated to agriculture. When recalling land use activities on the Broome ranch, descendants and former ranch employees interviewed by Hobbs may not have distinguished between activities on the Oxnard Plain and in La Jolla Valley, thereby leading Hobbs to believe the La Jolla Valley was cultivated. Aerial photos of La Jolla Valley at several other time points, including 1945 and 1960, show no evidence of farming, past or present. Further, the 1934 Wieslander survey did not

classify the valley as under cultivation, despite Hobbs's land-use history indicating that Richard Broome began sharecropping the valley in 1921.

Other evidence undermining the claim that La Jolla was under cultivation includes the fact that there was never any residence in La Jolla Valley, as there was in Serrano. A farm in a location as inaccessible as La Jolla Valley would likely have had at least one person or family living on the land as a caretaker. Also, there are numerous pieces of relic ranching equipment in La Jolla Valley, including cattle grates, pens, and water troughs, but no evidence of farming equipment, which is found extensively in Serrano Valley. Finally, La Jolla Valley lacks the geometric shapes and straight lines in its grassland borders that are often a sign of past tilling. This evidence combines to suggest that La Jolla Valley was likely never under cultivation.

#### Serrano Valley

Hobbs's land use history suggests that the history of anthropogenic activity in Serrano Valley is more complex than that of La Jolla (Hobbs 1983). Before 1900, it had no ownership and was very inaccessible except to neighboring Rancho Guadaluca and Rancho El Conejo. Historical maps of southern California ranchos bear this out (Ventura County Planning Division 2010). The western end of the valley was part of Rancho Guadaluca, and these two ranchos may have run their cattle throughout the valley. Between 1900 and 1910, the valley was opened up to homesteaders in 160-acre plots, most of which were obtained by employees of the nearby ranchos who already knew the land. By 1910, three of the homesteaders cleared their land of shrubs by hand, thus beginning nearly a century of cultivation and soil disturbance in the eastern part of the valley. Beans, corn, oats, and barley were grown on the homesteads, and sheep were

grazed. One of the former homesteaders described the dry farming methods in detail to Hobbs: Sage was removed by hand, with horses and chains helping to remove larger, tougher shrubs. *Malosma laurina* was extremely difficult to remove and eradicate, which occasionally led the homesteaders to resort to burning it. *Salvia leucophylla* was especially targeted for removal because it favors adobe soils, which make excellent farmland. After manual shrub removal, the soil was disked in the fall by horse-drawn diskers, followed by even more intense soil disturbance by a sub-soiler, which uses a single blade to deeply open the soil to rain penetration. The heavy tillage continued as the winter rains began, with mulching taking place between rain events to maintain penetrability, and continued soil work after planting to preserve soil moisture.

In 1932, Japanese farmers, widely present in southern California, began leasing the homesteads for tomato growing using dry farming methods. They remained until the beginning of internment during World War II, in about 1942.

The western end of the valley was first cleared in the mid-1930s, after the Wieslander survey, and used to graze cattle and grow hay, but it was not used for farming early in the century. In 1937, Leo Pruden began acquiring homesteads and by 1956 had purchased the entire valley. He claims that at the time of his arrival in the valley, there were roughly 400 acres (160 ha) of grassland and that he did not clear more than a few additional acres in the periphery of the CSS. He removed shrubs, including the large and woody *Adenostoma fasciculatum* and *Baccharis pilularis*, by tractor. He rotated his land, alternating between grazing his 80-140 cattle per year and growing hay, including oats, barley, broom grass, perennial rye, annual rye, and meadow fescue. Many of these species remain widespread in the valley today. Pruden would disk and plant each part of

the land every two to three years, roughly splitting the valley between grazing and growing hay. Importantly, however, the cattle were not confined to the grassland and were free to roam through the shrubs. Pruden noted they made useful trails through the shrubs in order to graze on native grasses, scratch, and find shade. After a large 1955 fire, state officials dropped exotic grass seeds over the area to help grasses recover from the burn. The valley was last disked in 1976 and last grazed in 1978. The Department of Parks and Recreation acquired the valley in 1980, but has done almost nothing but post a few signs. Much less accessible to hikers than La Jolla, Serrano is quite limited in its recreational use.

Hobbs used aerial photos from six time points between 1938 and 1980, plus the 1934 Wieslander survey, to assess the changes in grassland area (Hobbs 1983). She created the following account of grassland changes: Between 1934 and 1938, 23 ha of shrubs were manually cleared and converted to grassland. This trend reversed slightly between 1938 and 1947, with minor shrub reestablishment. This probably occurred because Pruden, the landowner at the time, found it difficult to travel over the hill from his own ranch (Sierra Vista, to the north) to do regular maintenance. Grassland then began increasing again (by 10 ha) between 1947 and 1965, the period during which Pruden did regular disking. The increase in grassland probably also occurred as a result of the post-fire state grass seeding. By 1977, however, some grassland had given way to shrubs (16 ha). Hobbs posits that Pruden's advancing age may have prevented his continued intense land management. Between the cessation of grazing and 1980, an additional 11 ha of grassland became sparse CSS, and dense CSS gained 22 ha.

Comments on Hobbs's Serrano Valley Land Use History. Hobbs's account of historical land use in Serrano Valley is supported by further research. The 1934 Wieslander survey shows all of the cleared parts of the valley under cultivation. The 1947 imagery shows that roughly 65 percent of the valley has obvious lines of crops or scars from past soil tilling. Ruins of an extensive homestead remain in the valley today, along with farming equipment like diskers, claws, water pumps, and parts of tractors (Figures 2, 3, 4, and 5).



FIGURE 2. Farming equipment in Serrano Valley.





FIGURE 3. Farming equipment in Serrano Valley.



FIGURE 4. Farming equipment in Serrano Valley.



FIGURE 5. Farming equipment in Serrano Valley.

## CHAPTER 4

### METHODOLOGY

This study uses a mixed method approach, employing both photo interpretation of historic aerial images and field transects. In order to integrate the two methods, this study combines historical photos and Hobbs's land use history to interpret the environmental data, caching the proximate ecological results within the larger societal context of twentieth-century southern California (Hobbs 1983). Doing so provides answers that move beyond simple physical relationships and consider the complex web of interactions between human beings and the natural environment.

The methodology for this study was aimed at reproducing and building upon the 1983 work of Hobbs, in that site history, aerial photo interpretation, and field transects are used in combination to paint a complete picture of the vegetation changes in the two valleys. This research differs from Hobbs's work in several ways. First, the two valleys were ranched and/or cultivated during most of Hobbs's study period, which extended from the 1930s to 1980, leaving Hobbs only a few years after release from grazing/cultivation to study the recovery. The current research compares the era of heavy anthropogenic disturbance, including the period of Hobbs's study, to an extended period mostly free from human activity (1980 to present).

Second, a large part of Hobbs's work involved creating detailed land use histories for the sites, compiled from interviews with former ranch employees and land owners,

along with archival research into land records, property titles, and historical photo collections. Rather than recreating the site history, this study took Hobbs's work as a starting point and sought to substantiate it using evidence from historical photos and accounts as previously detailed. Third, aerial photo interpretation is completed digitally rather than manually in this study, thanks to advances in computer technology. Finally, this study compares areas of significant shrub regrowth (recovering boundaries) to areas of minimal shrub regrowth (stable boundaries), using field transects based on the aerial photo interpretation. Hobbs's transects did not target specific regrowth patterns.

The research proceeded in two distinct phases. First, site histories were gathered from Hobbs's work, and historical photos were used to verify and/or clarify the histories. Photos from the mid-twentieth century were georeferenced and used to establish a baseline for grassland extent. Then, photos from four time points between the sites' release from anthropogenic disturbance and the present were input into a geographic information system (GIS), with the goal of delineating the changing grassland areas. The time points were chosen based on availability of imagery and an attempt to space the images evenly across the thirty-year period of study. The rate of conversion from grassland to CSS was calculated over the entire study period and between time points, to produce an average rate of grassland loss over the entire study period, as well as individual averages for the shorter time periods. The results of this work guided the locations of transects across both stable and recovering grassland-CSS boundaries. Environmental characteristics of the two types of borders were then compared to identify any environmental reasons for the stability or location of the boundary.

### Delineation of Vegetation Boundaries

The study area was defined by the extent of the 2007 imagery, which had the most limited coverage of the valleys. The area included 155 ha of grassland in La Jolla and 88 ha of grassland in Serrano. A small part (about 6 ha) of the northwestern portion of La Jolla grassland and a small part (less than 1 ha) of the southeastern part of Serrano grassland were left out of the analysis due to lack of coverage in the 2007 aerial image. Except for this minor limitation, the entire extent of both valleys was studied.

Aerial images of both valleys from 1947, 1976, 1989, 2002, and 2007 were acquired from the United States Geological Survey (USGS) EarthExplorer Web site (United States Geological Survey 2007), a collection of historical photos assembled by Scott Eckardt for his own thesis research at California State University, Long Beach (Eckardt 2006), and the Ventura County Planning Division. Except for the 1947 imagery, these images had already been georeferenced and were readily loaded into ESRI's ArcMap 9.3.1 software for analysis. The 1947 image had to be georeferenced prior to analysis.

Grassland was defined as any area with less than 1 percent shrub cover, which excluded almost all shrubs except for stand-alone pioneers present in the middle of otherwise uniform grassland. This threshold was chosen in order to include the establishment of sparse CSS. For the 1947 Serrano imagery, the only image with obvious crops, cultivated land was included in the grassland delineation. The polygon creation tool was used to digitize polygons around all grassland areas for both valleys and all time points. The calculate areas tool in ArcEditor was then used to determine the area of the

grassland polygons. The summed areas were used to find the rate of grassland change in hectares lost per year.

The rate of grassland change for both valleys for the period from 1947 to 1976 was then compared to the rate of grassland change for the period from 1976 to 2007, and the two valleys were compared to each other, with the goal of evaluating the differences in grassland changes between a time period with anthropogenic disturbance and a time period without such disturbance, and between a valley that was mostly grazed and a valley that was mostly cultivated. Changes for the smaller time periods were also compared.

### Field Sampling

Belt transects were implemented to examine the physical characteristics of the grassland-CSS boundary. These transects were used to identify differences between stable boundaries that have not moved since 1976 and recovering boundaries that have moved considerably due to shrub regrowth. The goal of this field sampling was to determine if environmental factors might explain stable versus recovering boundaries. Purposeful sampling was used to select transect locations for several reasons: The study required comparing stable boundaries to recovering boundaries; boundaries created by geographic features like very steep ravines and vegetation anomalies like oak groves were avoided; and transects had to be safely accessible. The latter was a significant consideration because parts of both valleys are blocked by dense vegetation, including stands of *Malosma laurina*, *Baccharis pilularis*, *Adenostoma fasciculatum* and *Ceanothus megacarpus* that could not be penetrated, as well as otherwise unpleasant species like *Toxicodendron diversilobum* and *Cynara cardunculus*.

Twelve transects were conducted in each valley, six across stable boundaries and six across recovering boundaries. Each transect included 25 m of grassland and 25 m of shrubland. The boundary between grasses and shrubs was located visually, and 25 m were measured out from that point into the grassland and into the shrubland. In most cases, there was a transition zone between grasses and shrubs that was neither completely grass nor completely shrubs. To address this ambiguity, the center of the ecotone was located, and 25 m measured out from that point in each direction. The size of the ecotone was also recorded. For each transect, a GPS unit was used to obtain start and end coordinates of the transects, and slope, aspect, and location of CSS on the slope were recorded. Photos were taken at each end, down the line of the transect.

A 1-square-meter quadrat constructed from PVC pipe was laid next to the transect line every 5 m. In each of the quadrats, the percentage of bare ground and individual species cover was recorded. Any species that entered the vertical 1-square-meter column created by the quadrat square was counted. Therefore, some percent covers were more than 100 percent due to species overlap. Height for each shrub species was also recorded, as a stand-in for shrub age, and any juveniles were noted.

Soil samples were collected from the quadrats at the boundary (0 m), 5 m, and 10 m into the grassland and 5 m and 10 m into the shrubland. Soil samples were collected using a soil auger from a depth of 6 inches in each of these five quadrats. Three soil compaction measurements were also obtained from the same quadrats. Selected soil samples from three stable boundary transects and three recovering boundary transects were analyzed for their carbon-to-nitrogen ratio and particle size. For the carbon-to-nitrogen ratio analysis, the samples were baked to remove all moisture and treated with

sulfuric acid vapors to eliminate organic matter, and then run through a carbon hydrogen nitrogen (CHN) analyzer. For particle size analysis, the samples were treated with hydrogen peroxide to remove organic matter, and subsequently filtered through a 63 micron sieve to separate sand from clay and silt. Clay and silt were then separated by creating a mixture of clay, silt, and water, and allowing the silt to settle. This procedure provided a percent of total weight for sand, silt, and clay for each sample. These percentages do not add up to 100 percent, however, due to the removal of the organic matter.



## CHAPTER 5

### RESULTS

This chapter combines the results of the remote sensing and field analyses to describe the processes that these two grassland valleys have undergone over the last half century. Maps of the two valleys with grassland areas delineated are included for 1947, 1976, 1989, 2002, and 2007. As expected, the mapping reveals shrub return over time after the valleys were released from anthropogenic disturbance. The valleys showed significant differences in their rates of return, however, illustrating the unique effects of grazing versus cultivation. The field sampling and data analysis revealed details about the differences between stable and recovering boundaries, but they also led to further questions, which must be addressed in future research.

It should be noted that the purpose of this analysis was not to repeat Hobbs's detailed mapping of the changes in vegetation over smaller periods of time as a result of land management decisions. Rather, this study compared two periods, one of mostly heavy anthropogenic disturbance and one of almost no disturbance, and two valleys, one mostly grazed and one mostly cultivated. Similarly, the field research was not intended to define the differences between grassland and CSS, something Hobbs already endeavored to do. Rather, it examined the differences between stable and recovering boundaries, in an effort to understand why shrubs return in some areas but not others.

### Grassland Changes

The changes in grassland area for both valleys were analyzed between each time point, and over the entire period before and after release from anthropogenic disturbance. La Jolla's grassland changes are shown in Figures 6, 7, 8, 9, and 10. Serrano's grassland changes are shown in Figures 11, 12, 13, 14, and 15. The rates of grassland loss discussed below are annual averages based on the available imagery from the indicated time points, and therefore should not be taken as precise annual rates.

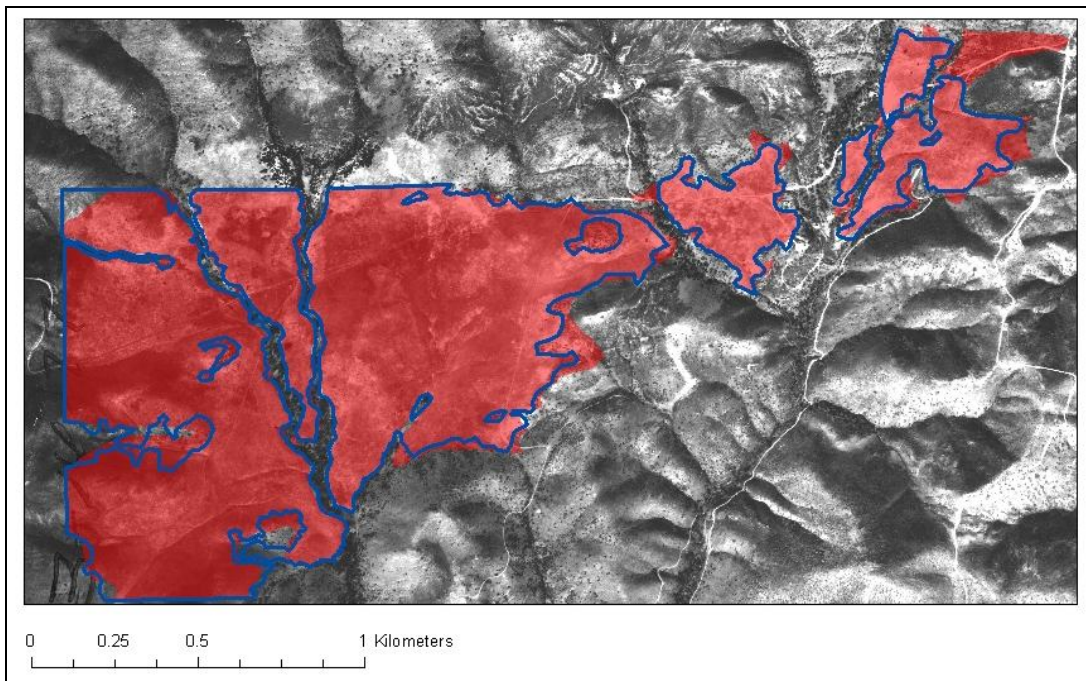


FIGURE 6. Extent of La Jolla Valley grassland in 1946 (shaded in red) and 1976 (outlined in dark blue).

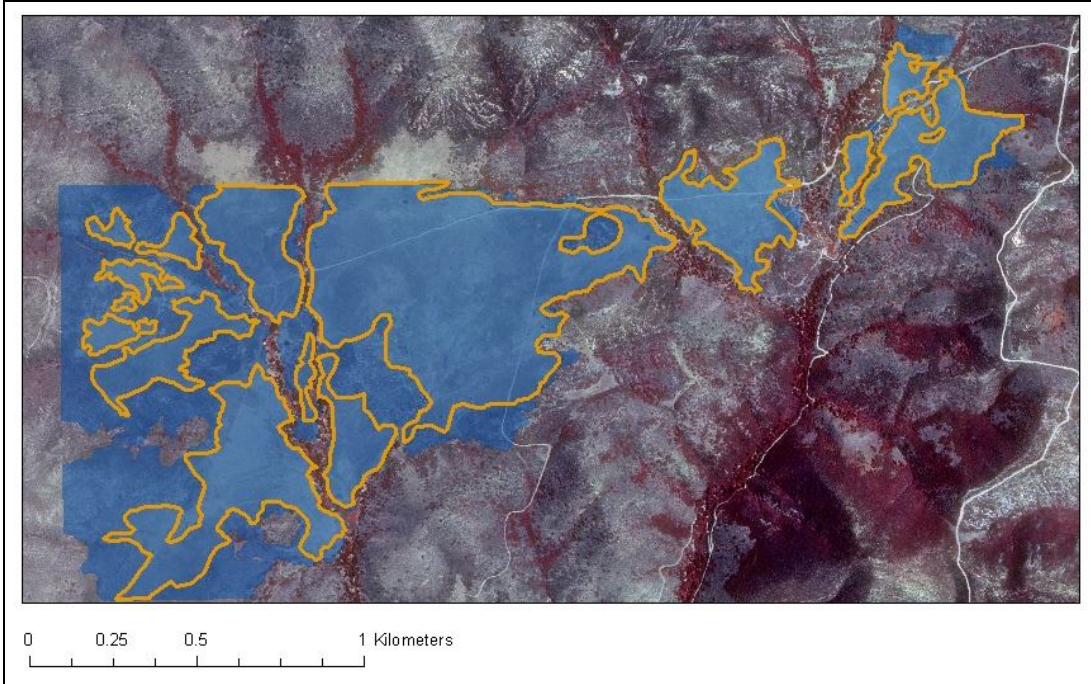


FIGURE 7. Extent of La Jolla Valley grassland in 1976 (shaded in dark blue) and 1989 (outlined in orange).

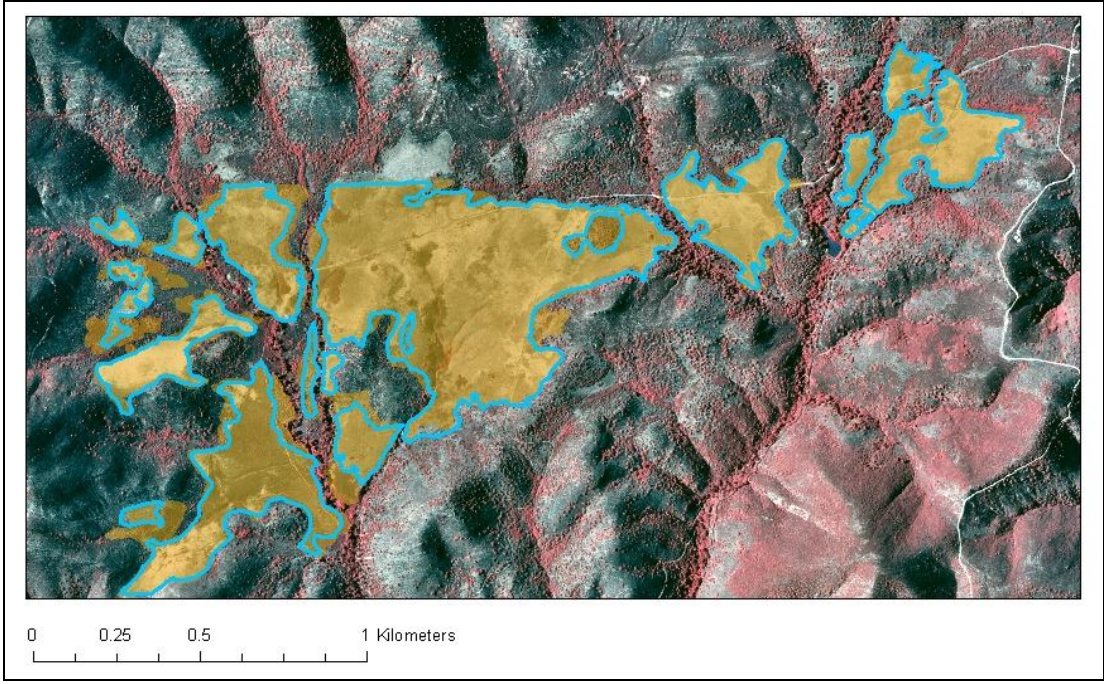


FIGURE 8. Extent of La Jolla Valley grassland in 1989 (shaded in orange) and 2002 (outlined in light blue).

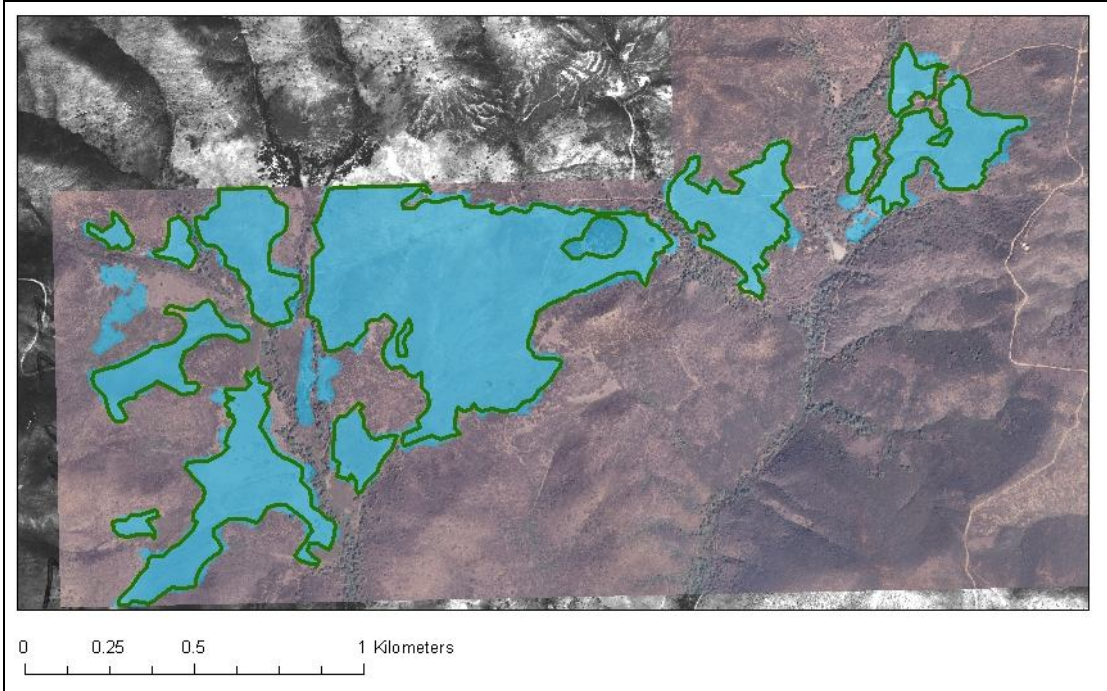


FIGURE 9. Extent of La Jolla Valley grassland in 2002 (shaded in light blue) and 2007 (outlined in green).

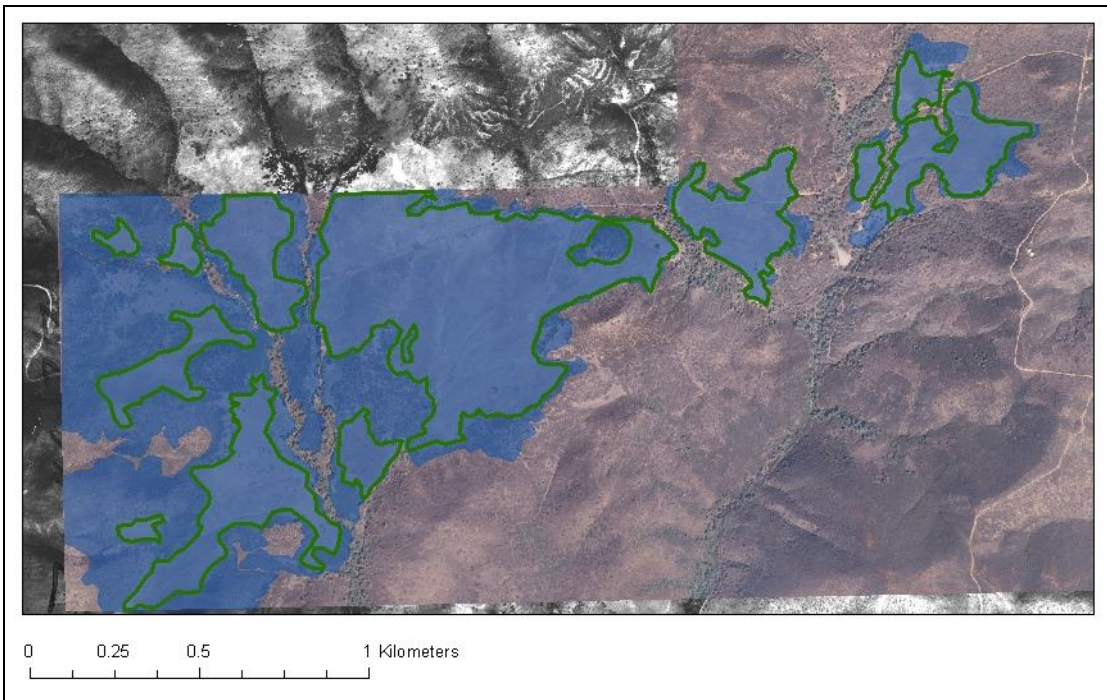


FIGURE 10. Extent of La Jolla Valley grassland in 1976 (shaded in dark blue) and 2007 (outlined in green)

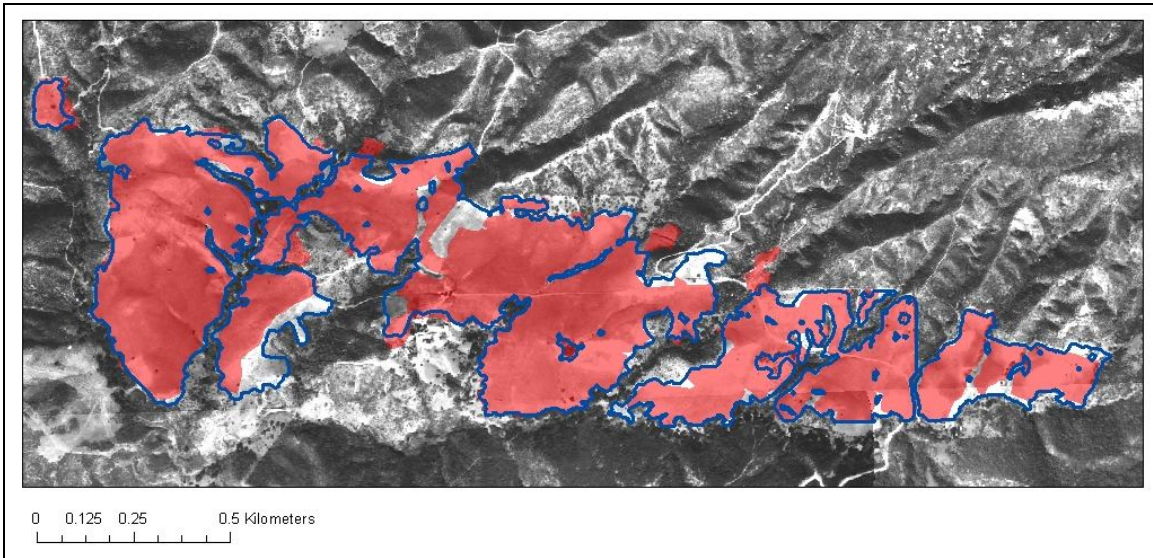


FIGURE 11. Extent of Serrano Valley grassland in 1947 (shaded in red) and 1976 (outlined in dark blue).

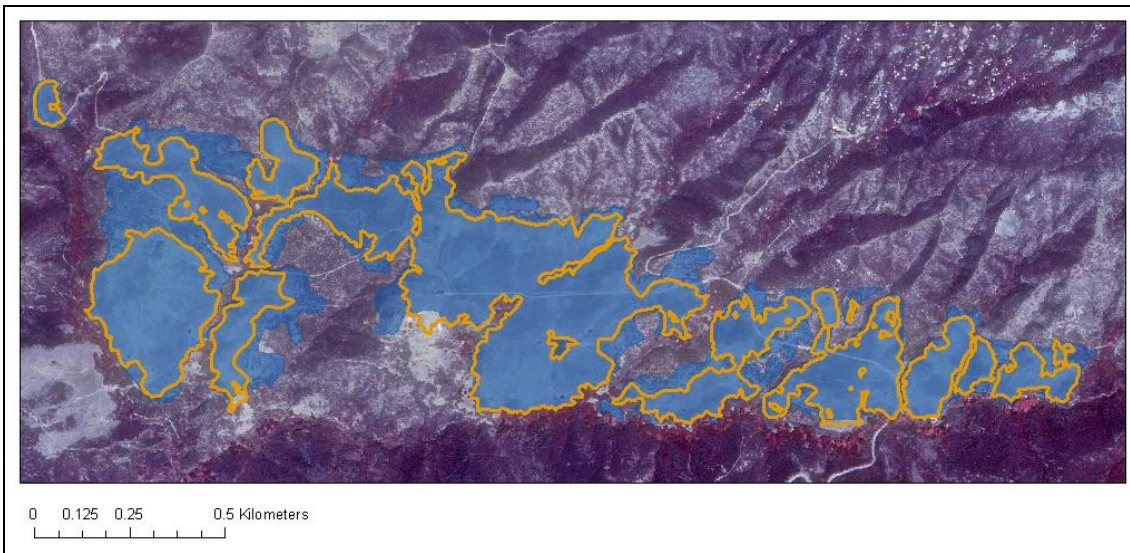


FIGURE 12. Extent of Serrano Valley grassland in 1976 (shaded in dark blue) and 1989 (outlined in orange).

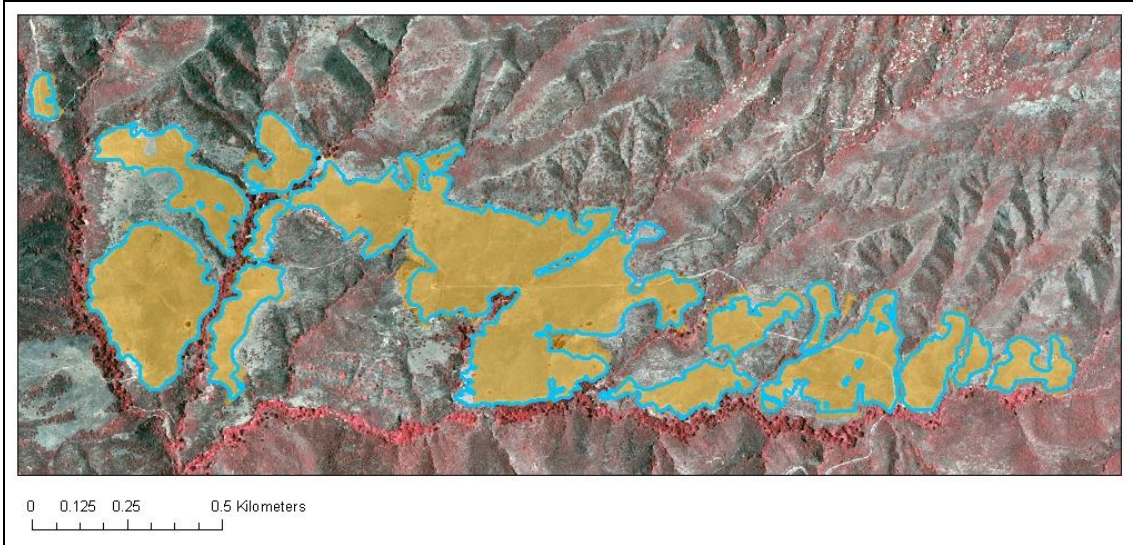


FIGURE 13. Extent of Serrano Valley grassland in 1989 (shaded in orange) and 2002 (outlined in light blue).

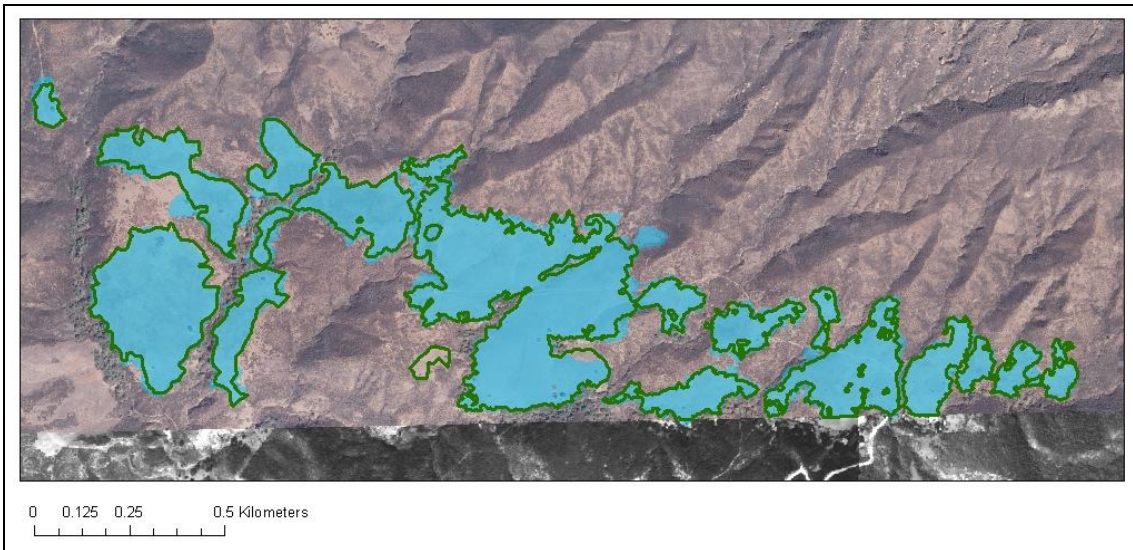


FIGURE 14. Extent of Serrano Valley grassland in 2002 (shaded in light blue) and 2007 (outlined in green).

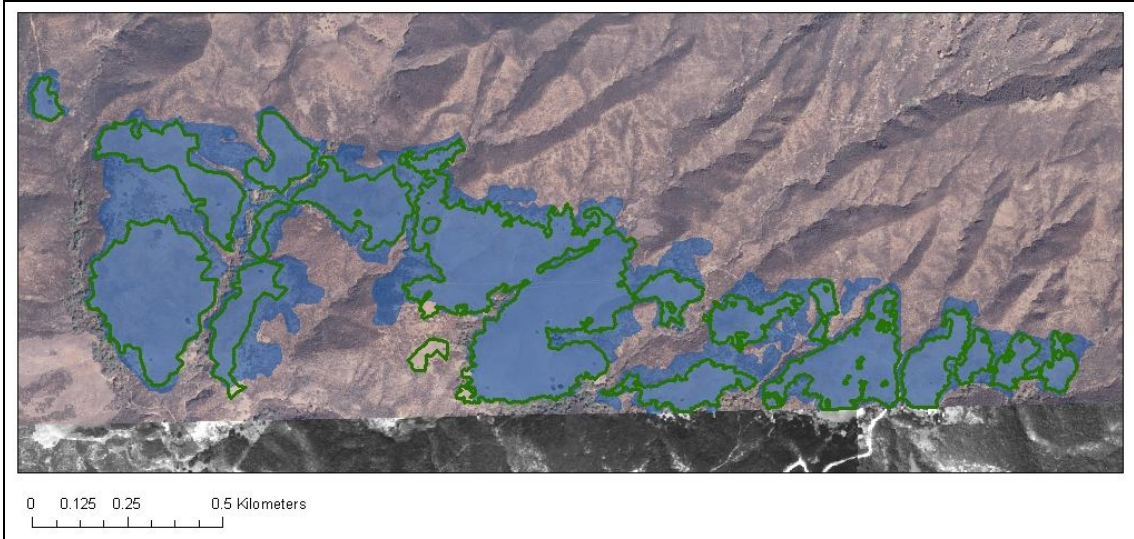


FIGURE 15. Extent of Serrano Valley grassland in 1976 (shaded in dark blue) and 2007 (outlined in green).

### La Jolla Valley

In La Jolla Valley, shrubs actually increased in the valley at an average rate of 0.47 ha per year between 1947 and 1976. This period includes eighteen years of grazing, and eleven years without human activity. Between 1976 and 1989, a thirteen-year period free of grazing, 50.60 ha of grassland converted to shrubs. This is the highest rate of shrub regrowth in La Jolla Valley for any time period studied, at an average rate of 3.90 ha per year. The next time period studied, 1989 to 2002, showed a significant drop in the conversion of grassland to shrubs, with only 7.11 ha of grassland returning to CSS over the thirteen-year period. The final time period studied, between 2002 and 2007, showed shrubs moving into an additional 9.97 ha of grassland, at an average rate of 1.99 ha per year. Over the entire post-grazing period of study, 1976 to 2007, La Jolla Valley lost

67.73 ha of grassland, an average rate of 2.18 ha per year, four and a half times the average rate during active grazing. These findings are presented in Table 1.

TABLE 1. La Jolla Valley Grassland Changes

Period	Grassland (ha)	Grassland Change (ha)	Average Rate of Grassland Change (ha per year)	Land Use
1947 to 1976	1947: 169.37 1976: 155.68	-13.69	-0.47	Grazing, fire in 1957, 1973
1976 to 1989	1989: 105.03	-50.65	-3.90	None
1989 to 2002	2002: 97.92	-7.11	-0.55	Fire in 1993
2002 to 2007	2007: 87.95	-9.97	-1.99	None
1976 to 2002	--	-67.73	-2.18	--

### Serrano Valley

Between 1947 and 1976, when Serrano Valley was both grazed and cultivated, including significant soil disturbance through disking and mulching, grassland gained 6.66 ha of land, at an average rate of 0.23 ha per year. The 1947 aerial image shows a large portion of the valley under cultivation and evidence of tilling over most of the area classified as grassland (Figure 16).

The period between release from grazing and cultivation and the present saw the loss of 28.43 ha of grassland, an average rate of 0.91 ha per year. Examination of the other time points in this period showed Serrano following a similar path to that of La Jolla (Table 2). The first thirteen years after release from grazing and cultivation, from



1976 to 1989, saw 22.89 ha of grassland loss. This average rate of 1.76 ha per year is the highest rate of grassland loss, just as it is in La Jolla Valley.



FIGURE 16. Evidence of cultivation in Serrano Valley in 1947.

TABLE 2. Serrano Valley Grassland Changes

Period	Grassland (ha)	Grassland Change (ha)	Average Rate of Grassland Change (ha per year)	Land Use
1947 to 1976	1947: 81.98 1976: 88.64	+6.66	+0.23	Grazing, farming, fire in 1951, 1973
1976 to 1989	1989: 65.75	-22.89	-1.76	None
1989 to 2002	2002: 64.70	-1.05	-0.08	Fire in 1993
2002 to 2007	2007: 60.22	-4.48	-0.90	None
1976 to 2002	--	-28.43	-0.91	--

During the next time period studied, 1989 to 2002, Serrano Valley shrub regrowth also slowed, with only 1.05 ha of grassland ceding to shrubs, at an average rate of 0.08 ha per year. The rate picks back up between 2002 and 2007, with 4.48 ha of grassland loss, at an average rate of 0.90 ha per year. The average rates of grassland loss for both valleys are shown in Figure 17.

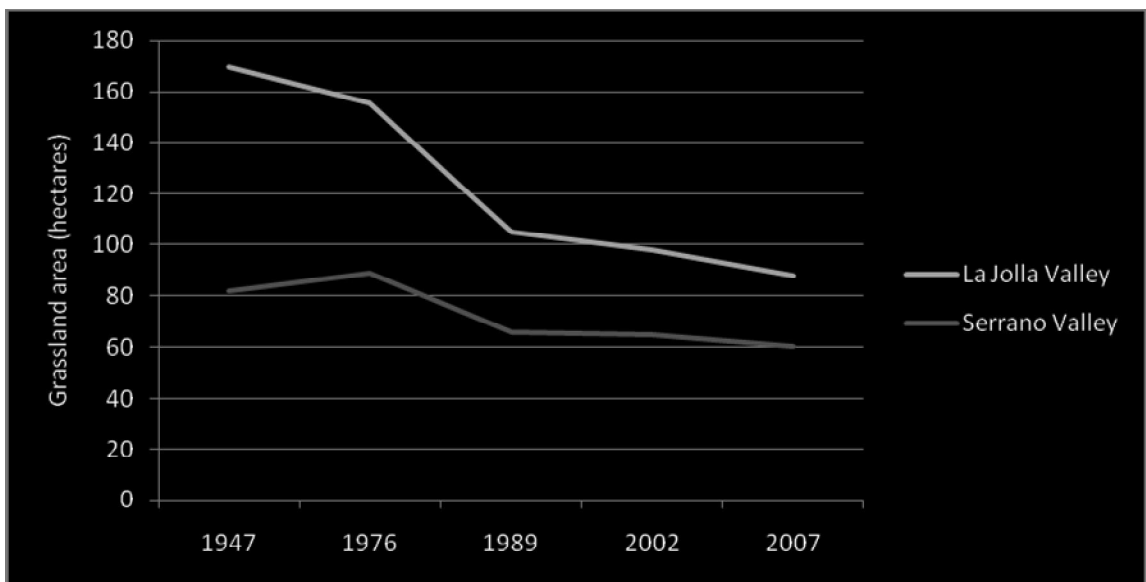


FIGURE 17. Change in area of grassland for La Jolla and Serrano Valleys 1947 to 2007.

It is important to consider not just at the raw numbers but also the percentage of grassland change, because total area of the grassland in the two valleys was significantly different at the starting point of the comparison. La Jolla had 169.37 ha of grassland in 1947, and Serrano had only 81.98 ha. This disparity was due primarily to the different topography in the two valleys.

The differences between the valleys are less pronounced but still noteworthy when percentage of change is considered (Table 3). Grassland in La Jolla contracted by about 8 percent during the time of human activity, and grassland in Serrano expanded by about the same percentage. Both valleys experienced a major contraction in their grassland areas immediately following release from grazing and cultivation, with La Jolla losing 32 percent and Serrano losing 26 percent of their grassland areas. Grassland loss slowed during the next time period (1989 to 2002) in both valleys but increased again in the most recent time period (2002 to 2007), though at a small fraction of the rate immediately following release from grazing or cultivation. Over the entire period without anthropogenic disturbance, grassland decreased by 43 percent in La Jolla and by 32 percent in Serrano. Although the percentage changes are not as dramatic as the raw numbers, these findings still show La Jolla grassland giving way to shrubs at a rate about 1.3 times faster than Serrano.

TABLE 3. Percentage Change in Grassland Area for La Jolla and Serrano Valleys

Time Period	Grassland Area Change	
	La Jolla	Serrano
1947 to 1976	-8.08 %	+8.12 %
1976 to 1989	-32.50 %	-25.83 %
1989 to 2002	-6.77 %	-1.60 %
2002 to 2007	-10.20 %	-6.92 %
1976 to 2007	-43.50 %	-32.07 %

### Boundary Differences

The study also investigated whether there were differences in the environmental, vegetation, and edaphic attributes of recovering versus stable boundaries, using field data.

#### Environmental Characteristics

Elevation, slope, and aspect were examined to see if any of these variables explained recovering versus stable boundaries. An unpaired t-test showed that the difference in elevation between stable and recovering boundaries was not significant. Similar results were found for slope and aspect, as presented in Table 4.

TABLE 4. Results of Unpaired T-Test Comparing Slope, Elevation, and Aspect in Recovering and Stable Boundaries

	Recovering Mean	Recovering SD	Stable Mean	Stable SD	<i>P</i>
Elevation (m)	243.00	4.97	254.25	20.66	0.3185
Slope (°)	17.16	10.87	18.18	5.69	0.7654
Aspect (°)	210.92	50.95	193.85	93.64	0.5690

Aspect was converted to a binomial classification, with aspects between 0° and 90° and between 270° and 360° classified as north-facing, or cool, slopes and aspects between 90° and 270° classified as south-facing, or warm, slopes. Despite differences in the frequency of recovering and stable boundaries on warm and cool slopes, a chi-square test showed that these differences were not statistically significant ( $P=0.2359$ ). Finally, the location of CSS on the slope was examined. Transects were binomially classified as having CSS upslope from grassland or not having CSS upslope from grassland. The

latter category included instances both of CSS downslope from grassland, as in the case of a ravine, and CSS next to grassland, as in the case of a boundary parallel to the slope (Figure 18). A chi-square analysis showed that CSS occurred upslope from grassland on significantly more recovering boundaries than stable boundaries. The results of these two chi-square analyses are shown in Table 5.



FIGURE 18. Example of vegetation boundary parallel to slope.

TABLE 5. Frequency of Warm Slopes and Upslope CSS in Recovering and Stable Boundaries

	Recovering	Stable	<i>P</i>
Warm slopes	11	6	0.2359
Upslope CSS	10	3	0.0416*

\* significant at  $P < 0.05$

### Soil Characteristics

A limited set of soil samples was tested for carbon-nitrogen ratio, particle size analysis, and compaction. Carbon-to-nitrogen ratios were averaged across stable and recovering boundaries. An unpaired t-test was used to determine that there was no significant difference in these ratios between stable and recovering boundaries, as shown in Table 6.

TABLE 6. Results of Unpaired T-Test for Carbon-to-Nitrogen Ratios in Recovering and Stable Boundaries

	Recovering Mean (%-mol)	Recovering SD	Stable Mean (%-mol)	Stable SD	<i>P</i>
All	8.26	3.04	9.00	4.01	0.9000
CSS	7.33	2.24	7.46	2.15	0.9223
Grassland	8.95	2.06	11.24	3.09	0.2193
Ecotone	11.07	3.87	6.87	0.25	0.5120

Samples from the same transects analyzed for carbon-to-nitrogen ratios were analyzed for percent content by weight of three different particle sizes: Sand, clay, and silt. An unpaired t-test showed that, when all recovering boundaries were compared to all

stable boundaries, percent content of sand was significantly different, as was, to a lesser extent, percent content of silt, with recovering boundaries favoring less sandy and more silty soils. When separate analyses were performed according to vegetation cover type, the effect was less apparent, with a significant difference showing only in percent content of silt in samples obtained from CSS. These results are presented in Table 7.

TABLE 7. Results of Unpaired T-Test for Soil Particle Size for Recovering and Stable Boundaries

	Recovering Mean (%-content)	Recovering SD	Stable Mean (%-content)	Stable SD	<i>P</i>
All – Sand	48.92	15.82	34.62	11.29	0.0081**
All – Silt	37.90	8.25	44.60	7.37	0.0262*
All – Clay	19.55	13.51	21.45	8.07	0.6443
CSS – Sand	52.09	13.14	35.32	15.36	0.0695
CSS – Silt	33.32	8.80	46.36	7.03	0.0195*
CSS – Clay	14.32	5.12	20.00	10.41	0.2579
Grass – Sand	48.12	21.28	33.67	10.24	0.1651
Grass – Silt	42.11	7.78	41.61	6.76	0.9078
Grass – Clay	25.72	19.59	24.72	6.08	0.9076
Ecotone – Sand	44.21	11.15	35.11	6.09	0.2827
Ecotone – Silt	38.11	4.75	47.10	9.88	0.2285
Ecotone – Clay	17.68	0.096	17.79	5.81	0.9849

\* Significant at  $P < 0.05$ ; \*\* Significant at  $P < 0.01$

Soil compaction readings were collected for roughly half the transects. Three readings were taken in each sampled quadrat and then averaged to yield a single compaction score for each quadrat. These data were averaged again to find compaction scores in grassland for stable boundaries and for recovering boundaries, in CSS for stable boundaries and for recovering boundaries, and in the transition zone for stable and for

recovering boundaries. An unpaired t-test showed that there were no statistically significant differences in soil compaction between stable and recovering boundaries, nor were there any differences in soil compaction for any of the vegetation covers, as shown in Table 8.

TABLE 8. Results of Unpaired T-Test for Soil Compaction for Stable and Recovering Boundaries

	Recovering Mean (kg/cm <sup>2</sup> )	Recovering SD	Stable Mean (kg/cm <sup>2</sup> )	Stable SD	<i>P</i>
All	1.68	1.04	1.25	0.64	0.1120
CSS	1.67	1.05	1.38	0.52	0.5076
Grass	1.89	1.27	1.11	0.71	0.1538
Ecotone	1.29	0.41	1.25	0.81	0.9329

### Vegetation Characteristics

The study also investigated differences between recovering and stable boundaries in vegetation types, characteristics, and dynamics, including ecotone width, percent vegetation cover, shrub height, species composition, and other variables.

Recovering boundaries had significantly broader ecotones than stable boundaries when the two valleys were analyzed together. When each valley was analyzed separately, however, only La Jolla Valley showed a statistically significant difference in ecotone width (Table 9).

Some grassland-CSS boundaries have no vegetation cover (bare soil) between the two vegetation types (Figure 19). Transects were classified as having a bare soil ecotone,



defined as less than 15 percent vegetation cover, or not having a bare soil ecotone. When both valleys were analyzed together using a chi-square analysis, no significant difference was found in vegetation coverage. However, when the valleys were examined separately, a strong statistically significant difference in vegetation coverage was found between recovering and stable boundaries in La Jolla Valley (Table 10).

TABLE 9. Results of Unpaired T-Test for Ecotone Width for Recovering and Stable Boundaries

	Recovering Mean (m)	Recovering SD	Stable Mean (m)	Stable SD	<i>P</i>
Both Valleys	5.76	3.41	2.13	2.66	0.0081*
La Jolla	6.23	3.93	0.83	0.17	0.0072*
Serrano	5.29	3.10	3.43	3.39	0.3493

\* Significant at  $P < 0.01$



FIGURE 19. Bare soil ecotone between grassland and CSS.

TABLE 10. Frequency of Bare Soil Ecotones in Recovering and Stable Boundaries

	Recovering	Stable	<i>P</i>
Both valleys	5	10	0.2359
La Jolla Valley	1	6	0.0416*
Serrano Valley	4	4	1.0000

\* Significant at  $P < 0.05$

Shrub heights were measured in the 0 m, 5 m, and 10 m CSS quadrats for each transect as a stand-in for shrub age. Three species of shrubs that occurred in both recovering and stable boundaries were measured, *Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia mellifera*. No significant differences in shrub height were found between recovering and stable boundaries (Table 11).

TABLE 11. Results of Unpaired T-Test of Shrub Height for Recovering and Stable Boundaries

	Recovering Mean (cm)	Recovering SD	Stable Mean (cm)	Stable SD	<i>P</i>
<i>Artemisia californica</i>	100.47	44.81	115.35	33.02	0.3906
<i>Eriogonum fasciculatum</i>	67.43	21.26	61.59	26.67	0.6662
<i>Salvia mellifera</i>	138.00	29.67	137.26	32.88	0.9718

Species composition was examined to determine if recovering and stable boundaries favor different shrub species. A number of species appear in one type of boundary and not the other. *Adenostoma fasciculatum*, *Malacothamnus fasciculatus*, and *Cercocarpus betuloides* appears in eighteen, five, and four stable transect quadrats,

respectively, but in zero recovering transect quadrats. *Baccharis pilularis* appears in twelve recovering transect quadrats, but in zero stable transect quadrats. A chi-square analysis showed that recovering and stable boundaries have statistically significant differences in their species composition ( $P=0.001$ ). The frequencies of species occurring in each type of boundary were significantly different for the species listed in Table 12.

TABLE 12. Frequency of Species in Recovering and Stable Boundaries

	Stable	Recovering	<i>P</i>
More common in recovering boundaries			
<i>Artemisia californica</i>	21	40	0.0292*
<i>Mimulus aurantiacus</i>	2	10	0.0280*
<i>Eremocarpus setigerus</i>	3	12	0.0279*
<i>Eriogonum fasciculatum</i>	12	26	0.0384*
More common in stable boundaries			
<i>Salvia mellifera</i>	28	4	0.0001**
<i>Ceanothus megacarpus</i>	6	1	0.0480*
<i>Yucca whipplei</i>	8	1	0.0150*

\* Significant at  $P < 0.05$ ; \*\* Significant at  $P < 0.01$

Mean percent cover of each species was then examined. A statistically significant difference in percent cover was found for only one species, *Nassella spp.* ( $P=0.002$ ). In other words, *Nassella spp.* (native needlegrass) appears in a similar number of quadrats for stable and recovering boundaries, but it covers more of each of those quadrats in recovering boundaries. Note that two species of *Nassella spp.* occur in the valleys, *Nassella pulchra* (purple needlegrass) and *Nassella lepida* (foothill needlegrass). They are difficult to distinguish from each other and almost impossible to distinguish when

seeds have dropped and the foliage has been grazed close to the ground, so the species were combined into a single category in this study.

Transect data was also examined to determine if there were differences in percentage of native species for recovering and stable boundaries. As expected, CSS for both types of boundaries contained the most native species, followed by the transition zones. No significant differences were found in percentage of native species for recovering and stable boundaries.

Finally, data were examined for native shrub species occurring in grassland quadrats to determine which species tend to pioneer into the grassland. Recovering and stable boundaries had similar numbers of individual plants pioneering into the grassland, as well as similar species. These data are presented in Table 13.

TABLE 13. Native CSS Species Found in Grassland

Species	Occurrences in Grassland	Boundary Type	Distance from Boundary into Grassland (m)
<i>Eremocarpus setigerus</i>	13	Recovering	5
		Recovering	10
		Recovering	15
		Recovering	20
		Recovering	5
		Recovering	10
		Recovering	15
		Recovering	20
		Recovering	20
		Recovering	25
		Stable	5
		Stable	10
		Stable	25

TABLE 13. Continued

Species	Occurrences in Grassland	Boundary Type	Distance from Boundary into Grassland (m)
<i>Eriogonum fasciculatum</i>	5	Recovering	15
		Stable	10
		Stable	15
		Stable	20
		Stable	25
<i>Hazardia squarrosa</i>	4	Recovering	5
		Stable	20
		Stable	25
		Stable	25
<i>Artemisia californica</i>	3	Recovering	5
		Recovering	15
		Stable	15
<i>Salvia leucophylla</i>	2	Recovering	5
		Recovering	10
<i>Salvia mellifera</i>	1	Stable	5
<i>Baccharis pilularis</i>	1	Recovering	10

## CHAPTER 6

### DISCUSSION

The results of the mapping of grassland changes over time indicate that (1) cultivation has more significant long-term effects on native shrub return than does grazing, (2) the most significant shrub return occurs immediately following release from anthropogenic disturbance, and (3) cultivation results in a type conversion to a new steady state of exotic grassland, while grazing does not. These findings confirm the first two hypotheses of this study. The results of the transect data analysis show that there are physical differences between recovering and stable boundaries, supporting the third hypothesis. Together, these results indicate that the ability of native shrubs to reestablish in exotic grasslands, and the rate at which this recovery takes place, are most likely determined by a combination of physical factors and land use history factors, which are themselves a function of the societal context of land use in twentieth-century southern California.

#### Grassland Changes

The changes in the sizes of grassland areas in the two different valleys demonstrate the divergent long-term impacts of grazing and cultivation on native shrub recovery. La Jolla Valley's rate of shrub return of 0.47 ha per year during active grazing between 1947 and 1976 is a strong indication that grazing does not suppress shrub regrowth as many have claimed. This period even included six years classified as

“heavily overgrazed by cattle” by Hobbs on the basis of her interview with a Broome relative (1983, 41). These data should not suggest that Axelrod was correct in his hypothesis that overgrazing causes shrubs to invade grassland (Axelrod 1978), but they do indicate that active cattle grazing may have less impact on grassland-CSS relations than previously thought.

Grazing does have some impact, however. The large increase in grassland loss after release from grazing (2.18 ha per year between 1976 and 2007) shows that grazing does something to maintain the grassland and has more effect than no activity at all. This in-between impact of grazing, neither fully suppressing nor promoting shrub regrowth, is reflected in the disagreement in the literature. Research variously claims that grazing promotes exotic grasses over native forbs (Kimball and Schiffman 2002), leads to permanent grassland only with continued anthropogenic intervention (Westman 1976), leads to invasion of grassland by shrubs (Axelrod 1978), or has different impacts on different species compositions (Hatch et al. 1999). These disparities in opinion are also evidence of the complex web of factors influencing California coastal vegetation communities, including the impacts of and interactions among fire, grazing, cultivation, development, conversion to park land, and environmental factors like soil and hydrology.

The next time period after release from grazing, 1989 to 2002, reflects a sharp slowing of grassland loss in La Jolla Valley to only 0.55 ha per year. Although shrubs are expected to return more slowly over time, this steep decline may be associated with the Green Meadows fire of 1993, which burned nearly 40,000 acres, including both La Jolla and Serrano Valleys (California Department of Forestry and Fire Protection 2007). The waning effects of the fire are seen in the uptick in the shrub recovery rate to 1.99 ha

per year for the final time period studied, 2002 to 2007. As previously noted, fire is also known to set off a burst of diversity one to two years after the burn (Keeley, Fotheringham, and Baer-Keeley 2005). This effect may have been stronger in La Jolla Valley, where seed bank and below-ground biomass survived decades of grazing, but not Serrano, where repeated tilling would have destroyed these means of recovery.

Cultivation appears to have very different long-term effects on native shrub recovery than does grazing. Unlike La Jolla Valley, Serrano Valley gained grassland between 1947 and 1976. Some of these gains may have been directly attributable to human intervention, since Hobbs's account describes the active clearing of CSS around the edges of the Serrano Valley grassland (Hobbs 1983). The cultivation of the valley would also have prevented the regrowth of shrubs, which would have had little chance to establish in the two to three years between disking that one of the landowners described to Hobbs (Stromberg and Griffin 1996).

After release from human activity, Serrano Valley follows a similar trend of shrub regrowth as La Jolla, but always at a slower pace. Once Serrano was free from anthropogenic disturbance, CSS returned to the valley, but at a relatively low rate. Although cessation of cultivation has obviously allowed shrubs to returned to some parts of the grassland, shrubs return at a rate almost one and a half times slower than La Jolla Valley. The highest rate of shrub return occurred immediately following release from anthropogenic activity, followed by a slowing down most likely due to the Green Meadows Fire in 1993, and then another slight pick-up after the Green Meadows Fire.

The fact that the highest rate, by several fold, of grassland loss occurs immediately following release from anthropogenic disturbance suggests that there are



certain areas particularly receptive to shrub regrowth due to their land-use history, and once released from grazing or cultivation, these areas are rapidly recolonized by shrubs. This conclusion is supported by Hobbs's findings of shrubs returning at a rate of 3.5 ha per year (higher than any rate found in this study) in the first three years after Serrano Valley was released from anthropogenic disturbance (Hobbs 1983). The rate suggests that shrubs can quickly fill in these ideal areas, only to slow down over time as fewer locations suitable for shrub regrowth are left available.

It remains to be seen if this rate will drop to zero before the grassland is entirely gone, leaving some part of the valley as a steady-state exotic grassland, or if the rate will simply slow until the grassland is entirely replaced by shrubs. Evidence throughout California cannot answer this question definitively. Much of the state was variously cultivated and/or grazed over the last several centuries, but it is difficult to find any large area that has been free of anthropogenic disturbance for a long enough period of time (e.g., more than one-hundred years) to truly test this hypothesis. Only returning to places like La Jolla and Serrano Valleys in another fifty years will tell us if these exotic grasslands are a permanent feature of the California landscape, or if the state is slowly returning to its more natural native shrub vegetation.

It is likely that the impacts of cultivation will continue to outweigh those of grazing. The rate of grassland loss in Serrano proceeded at roughly 75 percent of that in La Jolla over the last thirty years, but this difference fluctuates over the shorter time periods. Specifically, the difference between the rates was more substantial in the most recent period from, 2002 to 2007, than it was for the earlier period 1976 to 1989. This slowing of the rate of shrub return is more pronounced for Serrano Valley, as shrubs

quickly fill in areas that are least disturbed by cultivation and then may be unable to establish in areas that have been heavily cultivated.

This hypothesis is borne out by the fact that, by 1989, shrubs had invaded most of the parts of Serrano Valley that were not under cultivation in 1947 (Figure 20). The areas obviously under cultivation in the 1947 imagery (Figure 16) are the same areas that remain grassland today. These portions of the valley may represent the new steady-state exotic grassland, while shrubs continue to recover slowly around the edges, which did not experience the same level of disturbance. La Jolla Valley shrub regrowth, on the other hand, proceeded in a more uniform fashion, with shrubs invading the grassland from most edges, not appearing to favor any particular area. Elsewhere, as noted, others have documented how intense mechanical disturbance and/or cultivation prevent shrub return even after very long periods (Davis 1994; Stromberg and Griffin 1996).

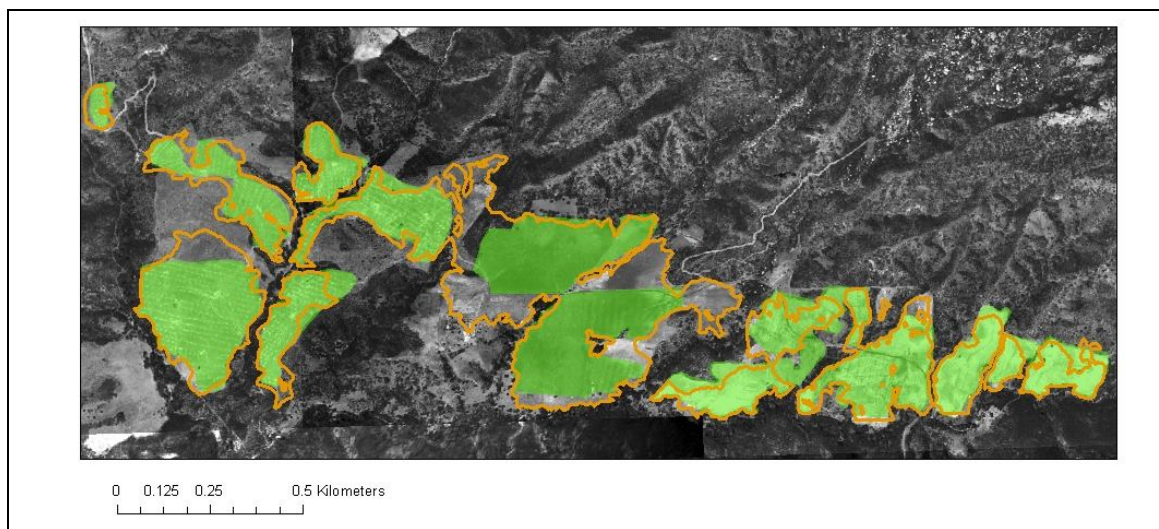


FIGURE 20. Extent of Serrano Valley 1989 grassland (outlined in orange) and 1947 cultivated land (shaded in light green).

The varying impacts of grazing and cultivation have significant implications for restoration and land management. The findings of this study indicate that restoration of native shrub populations in exotic grasslands may be more successful in areas that were previously grazed than in areas that were cultivated with intense mechanical disturbance. In a state that has lost a large portion of its native vegetation communities to exotic grasses, a tool to prioritize restoration efforts would be extremely useful. Land use history may therefore help guide these restoration decisions. Also, it is important to know the long-term effects of different land use activities on native vegetation communities when considering the environmental impact of these activities. The effects of cultivation are clearly more pronounced than those of grazing.

The reasons for the differing long-term impacts of grazing and cultivation remain unclear. One hypothesis centers on the role of arbuscular mycorrhizal (AM) fungi, which grow in plant roots and form a mutualist relationship with the host plant. CSS is known to host such fungi (Vogelsang and Bever 2009). The breaking up and mixing of soil destroys and then retards the reestablishment of AM fungi (e.g., McGonigle and Miller 1996). Li, Li, and Zhao, for example, noted this phenomenon in southwestern China, where AM fungi density was highest in a never-cultivated field, low for an old field, and lowest for cultivated land (Li, Li, and Zhao 2007).

Further evidence for the role of AM fungi includes the fact that (1) exotic California grasslands have significantly less AM fungi than CSS, (2) exotic species rely less upon mutualist relationships like that between AM fungi and CSS, (3) soil rife with

AM fungi can inhibit nonnative growth, and (4) nonnative plants are poorer hosts for AM fungi than is CSS (Vogelsang and Bever 2009). These factors contribute to a positive feedback loop whereby the initial destruction of AM fungi by soil disturbance allows exotic grasses to establish, and the inability of exotic grasses to host AM fungi additionally reduces the presence of AM fungi, further favoring grasses over native shrubs (Vogelsang and Bever 2009). Cultivation activities like tilling and mulching most likely destroy AM fungi, while grazing most likely does not. Although this hypothesis does not provide a definitive answer to our question of why shrubs return to some areas and not others, it does address the divergent rates of native shrub return for areas cultivated and areas grazed.

In addition to destroying AM fungi, soil tilling associated with cultivation may also disrupt and root crowns and seed banks of CSS. CSS can respond well after fire because some CSS species resprout from root crowns or tubers after a fire and other CSS species grow from the seed bank already present in the soil, sometimes many decades old (Zedler, Gautier, and McMaster 1983). Tilling would disrupt or destroy both below-ground biomass and seed banks, making recovering after fire very difficult. This hypothesis is supported by the fact that the biggest difference between rates of grassland loss in La Jolla Valley and Serrano Valley is for the period that included the Green Meadows Fire of 1993. Serrano's percent loss of grassland for the period is only a quarter of La Jolla's, suggesting that the benefits of post-fire recovery are seen in the valley that was grazed more so than in the valley that was cultivated.

### Boundary Differences

The results of this study indicate several differences between recovering and stable grassland-CSS boundaries. It should be noted, however, that with such a small number of samples, most of the statistical analyses should be taken as preliminary results to be confirmed with further research. The findings indicate trends that can help direct future inquiries in the complex exploration of native shrub return.

One finding is that shrubs are more likely to return when the CSS is upslope from grasses. DeSimone and Zedler found similar results, showing shrubs generally invaded grassland at a slower rate when CSS is downslope from grassland (DeSimone and Zedler 2001). It is hypothesized that CSS is more likely to appear upslope from grass on recovering boundaries because shrub seeds, which are quite large compared to grass and forb seeds, may tend to move downhill. Moving downhill gives shrub seeds a chance to enter, germinate, and grow in the neighboring grassland. Although CSS species have been described as wind-dispersed (Wells 1962), DeSimone and Zedler in studying the species *Salvia apiana*, *Eriogonum fasciculatum*, *Artemisia californica*, and *Lotus scoparius*, found no evidence of seeds traveling more than 5 m from their source (DeSimone and Zedler 2001). When CSS is downslope from grassland or next to grassland, it would not have the advantage of slope to help seeds enter the grassland. Of course, this theory does not apply to all CSS species, such as those that propagate primarily through resprouting, or those with very small seeds, so it has limited applicability. In areas that were previously cultivated or heavily mechanically disturbed, however, there would be no remaining shrub biomass from which new individuals could sprout, making dispersed seeds all the more important.

Another finding is that CSS is more likely to recover in less sandy, more silty soils, a finding that conflicts with research suggesting that shrubs favor coarser soils. The fact that this study finds shrubs more easily recover in the very type of soil other research shows they do not favor again illustrates the complexity of the problem. This discrepancy indicates that soil may not be the answer; historical land use decisions were based on soil type, which may lead researchers to conflate the effects of land use history and soil characteristics.

On-the-ground indicators of recovering boundaries include broad ecotones with denser vegetation and more native bunch grass, while stable boundaries are marked by bare soil ecotones. This study suggests that the broad ecotone is reflective of the slow process by which shrubs invade grassland, creating a buffer between the two vegetation types that is a mix of shrubs and grasses (Figure 21). Hobbs argued a similar point: Narrow ecotones are associated with higher disturbance levels, while broad ecotones illustrate the slow advancing of shrubs into the grassland (Hobbs 1986).



FIGURE 21. Broad ecotone with mix of shrubs and grasses.

Conversely, the bare soil ecotone indicative of the stable boundaries suggests that there is a point beyond which the shrubs cannot grow despite the lack of competition from exotic grasses, and where grasses also cannot grow. The appearance of the bare ground surrounding the shrubs mimics the effect seen in allelopathy, something *Salvia leucophylla* may engage in (Halsey 2004). However, allelopathy in *S. leucophylla* has been contested, and other CSS species are not known to practice such inhibition of other plant growth. This bare area occurs near various CSS species and is often more than 1 m wide. More research is needed to explain this phenomenon.

The difference in species composition for recovering and stable boundaries was quite marked, with traditionally chaparral species like *Adenostoma fasciculatum*, *Ceanothus megacarpus*, and *Cercocarpus betuloides* found almost exclusively in stable boundaries. Because these species did not appear in recovering boundaries, no comparison of shrub height could be made. While it is not fair to compare shrub height across different species, the vegetation in stable boundaries was generally taller and denser and more closely resembled chaparral than did the vegetation in the recovering boundaries, which tended to be more open and low. The vegetation communities in stable boundaries have been present for at least sixty-three years, so more individuals have been able to grow and to grow to greater heights, making the vegetation both taller and thicker. Further, the fact that these boundaries are unmoving may indicate that something is inhibiting shrub seed dispersal into the grassland, leaving seeds to germinate within CSS and allowing that area to become denser. Because recovering boundaries are constantly moving forward into the grassland, the boundary inherently has younger

vegetation. These communities have simply not had the time to grow as tall and thick as communities in stable boundaries.

An attempt was made to record the presence of juvenile shrubs in stable and recovering boundaries, but not enough juveniles were observed to support a statistical analysis. Anecdotally, however, it should be noted that juveniles were observed in both types of boundaries. The difference was in the location of juveniles: In stable boundaries, juveniles were seen within the CSS, and in recovering boundaries, juveniles were seen in the ecotone and in the grassland. Again, this may be due to seed dispersal. Research focusing specifically on juvenile shrubs could confirm this trend.

The higher frequency of *Artemisia californica* in recovering boundaries is somewhat surprising. Although *A. californica* is known to have relatively light seeds, which are easier to disperse (DeSimone and Zedler 2001), the ubiquity of this species in CSS makes its favoring of recovering boundaries unexpected; one would think it would be so common in all CSS that there would not be a statistically significant difference in its presence between boundary types. The higher frequency of *A. californica* in recovering boundaries again suggests that recovering boundaries more closely resemble CSS, while stable boundaries more closely resemble chaparral. However, the traditional explanations for the different locations of CSS and chaparral, such as aspect, slope, substrate, and elevation, do not explain the location of recovering and stable boundaries. Therefore, one cannot make the assumption that chaparral leads to stable boundaries. It is possible that the stability of the boundary may have led to the development of chaparral, rather than chaparral causing the boundary to be stable.



As in much land use history research, it is difficult to separate environmental effects from anthropogenic effects, because ranchers and farmers made land use decisions based on their natural environment. For example, farmers may have avoided steep slopes and rocky soils when tilling. They burned large shrubs like *Malosma laurina*, which was said to be almost impossible to remove (Hobbs 1983). Burning this shrub would have been somewhat ineffective, since it resprouts from remaining below-ground biomass, and landowners would have been forced to address the shrub year after year (Rundel and Gustafson 2005). Such difficulties may have led landowners to avoid areas with *M. laurina* and similarly large, deep-rooted chaparral species, leading to a preponderance of such species in stable boundaries today. Vegetation management decisions may also have been based on knowledge of specific plants. For example, farmers may have been particularly aggressive in removing purple sage based on the knowledge that it favors adobe soils, which are good for cultivation (Hobbs 1983).

The higher frequency of *Salvia mellifera* in stable boundaries may be indicative of its role as an associate of *Adenostoma fasciculatum* in the transition between chaparral and sage scrub (Rundel and Gustafson 2005). Although *S. mellifera* tended to appear at the transition from grasses to chaparral in the La Jolla and Serrano valleys, its role as a transition species may stand. Most of the literature claims that CSS occurs between grassland and chaparral, so there is less work exploring the direct relationship between the two vegetation communities. Further, Westman found that *S. mellifera* favored courser soils, which are characteristic of the stable boundaries and not the recovering boundaries (Westman 1983). This preference for coarser soil may have prevented *S. mellifera* from growing very frequently in the recovering boundaries.

*Nassella spp.* had a higher percent cover in recovering boundaries than in stable boundaries. This may be due to the fact that *Nassella pulchra* actually benefits from herbivory, both in terms of growth and in terms of seed germination (Dyer 2002; Dyer 2003; Bartolome 2004). The recovering boundaries are in areas that were once grazed, so the *Nassella pulchra* populations in recovering boundaries may have benefited when cattle and sheep were present, with their population gains sustained to the present.

Identification of the species that are more common in recovering boundaries and in grassland adjacent to recovering boundaries has significant implications for restoration efforts. Such efforts in southern California are often directed at returning native shrubs to exotic grasslands, and these species may help to begin this process. Because they are more commonly found in recovering boundaries, *Mimulus aurantiacus*, *Artemisia californica*, and *Eriogonum fasciculatum* may be better at successfully establishing themselves in an ecotone. The latter two were also found in grassland quadrats. In major restoration projects, a huge amount of time and resources go toward eliminating the exotic vegetation community prior to promoting the native species. If these CSS species can successfully establish in exotic grasslands, it may be possible to significantly reduce the removal of exotic species prior to restoration. *Eremocarpus setigerus*, a native annual herb, is of special note because it is more common in recovering boundaries and was found in thirteen grassland quadrats, more than any other native species. Whether *E. setigerus* in some manner paves the way for other CSS species to establish, or it thrives in the same types of conditions as recovering CSS, it can be used as an indicator of exotic grassland areas that may be unusually receptive to CSS restoration.

The processes involved in the grassland-shrubland dynamics are complex, so one cannot assume that native shrub species found in grassland are necessarily pioneers that will lead to further native shrub growth. The recovery of *Artemisia californica*, for example, may actually promote grasses over shrubs; Yelenik and Levine found that *A. californica* increased nitrogen and phosphorus in the soil, and these resulting higher soil nitrogen levels favor grasses (Yelenik and Levine 2010). Thus it is vital to understand these myriad factors and relationships between species and the environment when planning restoration projects.

## CHAPTER 7

### CONCLUSIONS

The changes in the size of the grasslands in the La Jolla and Serrano Valleys over time clearly indicate that cultivation has more significant long-term impacts on native shrub recovery than does grazing. The considerable manipulation of the natural environment required to support cultivation is both more chronic and more acute than anything done to support grazing. Further, California native species have evolved to handle herbivory, a native disturbance, but not cultivation, an exotic disturbance (Stylinksi and Allen 1999). Of course, the level of herbivory present when livestock were grazing during the twentieth century was heavier than the grazing of deer and other native animals with which native shrubs may have evolved (Stromberg, Corbin, and D'Antonio 2007), which is reflected by the fact that shrubs retracted during some active livestock grazing. These effects, however, remain less significant than those of cultivation.

It is clear that both valleys experienced a type conversion from CSS to exotic grassland during the earlier part of the twentieth century. Whether this type conversion is permanent and whether it is maintained after cessation of anthropogenic activity are less clear. While we cannot yet infer that the impact of cultivation is permanent, it continues to have a marked impact on vegetation more than thirty years after cessation. Other research has extended this impact to seventy years (Stromberg and Griffin 1996). Thus,

it appears that, while grazing temporarily inhibits native shrubs, cultivation results in a type conversion of CSS to a new steady-state vegetation community of exotic grassland. In a region with a long and continuing history of both grazing and cultivation, and in which many parklands are former ranches and farms, it is important to understand what today's activities will mean for native vegetation twenty-five, fifty, and one hundred years from now.

No restoration activities have taken place in these valleys since their release from anthropogenic disturbance in 1965 and 1978. Despite the lack of human intervention, the native shrub species have returned to a considerable portion of both valleys, with 43.5 percent of La Jolla Valley's grassland and 32.1 percent of Serrano Valley's grassland giving way to shrubs. Although restoration efforts are valiant and needed, the best tool for native plant return in California may be time, and the best guide to native shrub recovery may be land use.

The results of the field sampling were in general agreement with Hobbs and other research in finding that factors like slope, elevation, aspect, soil nitrogen, and soil compaction could not explain the recovery of CSS to some areas and not others (Hobbs 1983). The finding that CSS recovers more successfully when it is upslope of grassland is also in agreement with the literature. The complete explanation for recovering and stable boundaries remains unclear and requires further research, preferably with more fine-scale land use histories and a larger number of field samples.

The field sampling accomplished another, related goal—namely, it may be useful in identifying unique characteristics of stable and recovering boundaries. Such identification allows these boundaries to be recognized without the benefit of historical

imagery or any prior data. If land managers can identify which areas are already recovering, by spotting broad ecotones or CSS upslope from grassland, for example, they may focus their restoration efforts in places they know are receptive to shrub regrowth rather than waste time in areas that may never recover.

None of the research in this study is meant to imply that the grasslands are not in some way natural, or that they do not have some environmental value. It is obvious from personal experience that the exotic grasslands host myriad animals, including rodents, lizards, rattle snakes, gopher snakes, red fox, deer, coyote, and even mountain lion. Observations of some of these animals and their scat, burrows, game trails, bedding areas, and skeletal remains suggest that the valleys support rich and lively mammal and reptile populations. In the consideration of land management and restoration efforts, it is important not to assign value to a particular vegetation community based on our own biases.

Together, the mapping and field sampling illustrate interactions between the proximate physical factors directly affecting vegetation communities, and the ultimate societal factors resulting in land use decisions that indirectly impact grassland and CSS. Although the Chumash tribe used La Jolla Valley, it was not until the arrival of Mexicans and Europeans in California and the resulting introduction of agriculture that the vegetation in the valleys truly began to change. The homesteading laws, changing of ownership, and economic context have all had roles in the history of these areas. Where once the land was entirely natural and relatively free from human manipulation, it came to support the anthropogenic interventions represented by ranches and farms, and then transitioned back to something in-between. The valleys are now a hybrid entity, a

product of both nature and society, neither entirely natural nor entirely humanized. They defy the dichotomy of landscapes separated into those of natural origins and those of human origins (Duvall forthcoming) and represent a true cultural landscape (Sauer 1950).

This study opens the door to additional research on several levels. First, the transects conducted during field sampling could be returned to periodically in the future, with the goal of continuing to measure the return of shrubs and determining if the ecotones become pure CSS over time. Additional new transects would also improve the statistical analysis and possibly allow for an interesting examination of shrub height as a stand-in for shrub age. Most importantly, the hypothesis that AM fungi is destroyed by tilling, thereby inhibiting CSS reestablishment, must be explored through the collection of extensive soil samples and microscopic examination of these samples, two activities beyond the scope of this project. If it is determined that this lack of AM fungi prevents CSS from regrowing, the introduction of AM fungi could become a major tool in the CSS restorationist's toolbox, as it already is for those working with other vegetation communities.

As the world's populations urbanize, many rural agricultural areas are left behind to return to their natural condition, while others remain permanently humanized through type conversion to a new steady state. The processes behind and dynamics of this rewilding must be understood, not only to facilitate the return of native species and prevent the dominance of exotic species but also to predict changes in a landscape over time. Understanding how and why these changes take place, and what human activities result in permanent landscape changes, will help to direct restoration resources to the places they will be most beneficial. Such knowledge can also guide decisions about the

conversion of former human landscapes to parkland, and inform us about the impact natural and human disturbance like fires and erosion on society. It is possible that areas subjected to certain kinds of human activity, especially those similar to native natural disturbance, may simply be left to their own devices to return to a near-natural state. It is also possible that some anthropogenic activities leave the land forever changed and unnatural to some degree.



## REFERENCES

## REFERENCES

- Anderson, R. C. 1990. The historic role of fire in North American grassland. In *Fire in North American tall grass prairie*, eds. S. L. Collins and L. L. Wallace, 8-18. Norman, OK: University of Oklahoma Press.
- ArcGIS Version 9.3.1. ESRI: Redlands, CA, USA.
- Atwood, J. L., and R. F. Noss. 1994. Gnatcatchers and development: A “train wreck” avoided? *Illahee* 10 (2):123-30.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-83.
- Axelrod, D. I. 1978. The origin of coastal sage vegetation, Alta and Baja California. *American Journal of Botany* 65 (10):1117-31.
- Barry, W. J. 1972. *The Central Valley Prairie, Volume I*. Sacramento, CA: California Department of Parks and Recreation.
- . 1976. *Point Mugu State Park Resource Inventory*. Sacramento, CA: California Department of Parks and Recreation.
- Bartolome, J. W., J. S. Fehmi, R. D. Jackson, and B. Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California’s coast range grassland. *Restoration Ecology* 12 (2):279-89.
- Baskin, J. M., and C. C. Baskin. 1997. Methods of breaking seed dormancy in the endangered species *Iliamna corei* (Sherff) Sherff (Malvaceae), with special attention to heating. *Natural Areas Journal* 17 (4): 313-23.
- Beckman, J. P., and J. Berger. 2003. Rapid ecological and behavioral changes in carnivores: The responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology* 261 (2):207-12.
- Behnke, R., and I. Scoones. 1993. Rethinking range ecology. In *Range ecology at disequilibrium*, eds. R. Behnke, I. Scoones, C. Kerven, 1-30. London, U.K.: Overseas Development Institute.
- Blaikie, P., and H. Brookfield. 1987. *Land degradation and society*. New York: Routledge.

- Pickett, S. T. A., and P. S. White. 1986. *Ecology of natural disturbance and patch dynamics*. San Diego: Academic Press.
- Butzer, K. W. 1990. The Indian legacy in the American landscape. In *The making of the American landscape*, ed. M. P. Conzen, 27-50. Boston, MA: Unwin Hyman.
- California Department of Forestry and Fire Protection. 2007. Fire and Resource Assessment Program. <http://frap.fire.ca.gov/> (last accessed 07 December 2010).
- Callaway, R. M., and F. W. Davis. 1991. Vegetation dynamics, fire, and the physical environment in coastal Central California. *Ecology* 74 (5):1567-78.
- Carlton, G. C., and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79 (4): 1305-19.
- Carrington, M. E., and J. E. Keeley. 1999. Comparison of post-fire seedling establishment between scrub communities in Mediterranean and non-Mediterranean climate ecosystems. *Journal of Ecology* 87:1025-36.
- Cione, N. K., P. E. Padgett, and E. B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in Southern California. *Restoration Ecology* 10 (2):376-84.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199 (4335), 1302-10.
- Coleman, H. M., and J. M. Levine. 2007. Mechanisms underlying the impacts of exotic annual grasses in coastal California meadow. *Biological Invasions* 9:65-71.
- Cox, R. D., and E. B. Allen. 2008. Composition of soil seed banks in Southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecology* 198:37-46.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. In *Invasive species in a changing world*, eds. H. A. Mooney and R. J. Hobbs, 65-94. Washington, DC: Island Press.
- D'Antonio, C. M., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservations: research needs. In *Conservation biology: Research priorities for the next decade*, eds. M. E. Soulé and G. H. Orians, 59-97. Washington, DC: Island Press.
- Davis, C. M. 1994. Succession in California shrub communities following mechanical anthropogenic disturbance. M.S. Thesis, San Diego State University.
- Dean, J., P. Laris, C. Rodrigue, and M. Ferris. An 80-year record of the disturbance regime of California coastal sage scrub on the Palos Verdes Peninsula. Paper presented at Southern California Academy of Sciences, Los Angeles, CA, 8 May 2010.

- Denevan, W. 1992. The pristine myth: The landscape of the Americas in 1492. *Annals of the American Association of Geographers* 82:369-85.
- Denslow, J. S. 1985. Disturbance-mediated coexistence of species. In *The ecology of natural disturbance and patch dynamics*, eds. S. T. A. Pickett and P. S. White, 307-23. Academic Press: Orlando, FL.
- DeSimone, S. A., and P. H. Zedler. 2001. Do shrub colonizers of Southern California grassland fit generalities for other woody colonizers? *Ecological Applications* 11 (4):1101-11.
- Dowding, J. E., and E. C. Murphy. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: A conservation perspective. *Biological Conservation* 99:47-64.
- Duvall, C. Forthcoming. Biocomplexity from the ground up: Vegetation patterns in a West African savanna landscape. *Annals of the Association of American Geographers*.
- Dyer, A. R. 2002. Burning and grazing management in California grassland: Effect on bunchgrass seed availability. *Restoration Ecology* 10 (1):107-11.
- . 2003. Burning and grazing management in California grassland: Growth, mortality, and recruitment of *Nassella pulchra*. *Restoration Ecology* 11 (3):291-96.
- Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* 43 (2):316-33.
- Eckardt, S. 2006. Assessment of wildfire frequency and coastal sage scrub vegetation dynamics in the Santa Monica Mountains of Southern California. M.A. Thesis, California State University, Long Beach.
- Erickson, C. L. 2006. The domesticated landscapes of the Bolivian Amazon. In *Time and complexity in historical ecology*, eds. W. B. Balée and C. L. Erickson, 235-78. New York: Columbia University Press.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. *Botanical Review* 57:1-32.
- Fairhead, J., and M. Leach. 1996. *Misreading the African landscape: Society and ecology in a forest-savanna mosaic*. Cambridge, U.K., and New York: Cambridge University Press.
- Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* 80:753-72.

- Freudenberger, D. O., B. E. Fish, and J. E. Keeley. 1987. Distribution and stability of grasslands in the Los Angeles Basin. *Bulletin of the Southern California Academy of Sciences* 86:13-26.
- Gaston, K. 2005. Biodiversity and extinction: Species and people. *Progress in Physical Geography* 29:239-47.
- Goode, S. 1981. The vegetation of La Jolla Valley. M.S. Thesis, California State University, Los Angeles.
- Google Earth Version 5.2.1. Google: Mountain View, CA, USA.
- Halsey, R. W. 2004. In search of allelopathy: An eco-historical view of the investigation of chemical inhibition in California coastal sage scrub and chamise chaparral. *Journal of Torrey Botanical Society* 131 (4):343-67.
- Harms, R. S., and R. D. Hiebert. 2006. Vegetation response following invasive tamarisk (*Tamarix* spp.) removal and implications for riparian restoration. *Restoration Ecology* 14:461-72.
- Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* 121:99-106.
- Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7 (4):376-81.
- Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17 (6):1694-1702.
- HilleRisLambers J., Yelenik S. G., Colman B. P., and Levine J. M. 2010. California annual grass invaders: The drivers or passengers of change? *Journal of Ecology* 98 (5):1147-56
- Hobbs, E. R. 1983. Factors controlling the form and location of the boundary between coastal sage scrub and grassland in Southern California. Ph.D. Dissertation, University of California, Los Angeles.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Keeley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68 (2):434-43.
- . 2002. Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography* 29:303-20.
- . 2005. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20 (2):375-84.

- Keeley, J. E., C. J. Fotheringham, and M. Baer-Keeley. 2005. Factors affecting plant diversity during post-fire recovery and succession of Mediterranean-climate shrublands in California, USA. *Diversity and Distributions* 11:525-37.
- Keeley, J. E., C. J. Fotheringham, and M. Morais. 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284 (5421):1829-32.
- Keeley, J. E., and S. C. Keeley. 1984. Postfire recovery of California coastal sage scrub. *American Midland Naturalist* 111 (1):105-17.
- Kimball, S., and P. M. Schiffman. 2002. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* 17 (6):1681-93.
- Kotchen, M., and O. Young. 2007. Meeting the challenges of the anthropocene: Toward a science of coupled human-biophysical systems. *Global Environmental Change* 17:149-51.
- Laris, P. 2008. An anthropogenic escape route from the "Gulliver syndrome" in West African savanna. *Human Ecology* 36 (6):789-805.
- . Forthcoming. Humanizing savanna biogeography: Linking human practices with ecological patterns in a frequently burned savanna of southern Mali. *Annals of the Association of American Geographers*.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* 44:427-33.
- Li, L. F., T. Li, and Z. W. Zhao. 2007. Differences of arbuscular mycorrhizal fungal diversity and community between a cultivated land, an old field, and a never-cultivated field in a hot and arid ecosystem of southwest China. *Mycorrhiza* 17 (8):655-65.
- Liu, H., and S. Koptur. 2003. Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: Impacts of the urban-wildland interface. *American Journal of Botany* 90 (8):1180-87.
- Macfadyen J. D. 2009. Breaking sod or breaking even? Flax on the northern great plains and prairies, 1889-1930. *Agricultural History* 83 (2):221-46.
- Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasion: Characteristics and consequences. In *Biological invasions: A global perspective*, eds. J. A. Drake and H. A. Mooney, 155-79. New York: John Wiley and Sons.
- Mack, R., D. Simberloff, W. Lonsdale, H. Evens, M. Clout, and F. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:698-710.
- MacDonald, G. M. 2003. *Biogeography: Space, time and life*. New York: John Wiley and Sons.

- McDonnell, M. J., and S. T. A. Pickett. 1993. *Humans as components of ecosystems: The ecology of subtle human effects and populated areas*. New York: Springer-Verlag.
- McGonigle, T. P., and M. H. Miller. 1996. Development of fungi below ground in association with plants growing in disturbed and undisturbed soils. *Soil Biology and Biochemistry* 28 (3):263-69.
- Mckinney, M. L., and F. A. La Sorte. 2007. Invasiveness and homogenization: Synergism of wide dispersal and high local abundance. *Global Ecology and Biogeography* 16:394-400.
- McNaughton, S. J. 1968. Structure and function in California grasslands. *Ecology* 49:962-72.
- Micallef, S. B. 1998. Grazing effects on the grassland vegetation of Mount Diablo State Park, California. M.S. Thesis, San Francisco State University.
- Minich, R. A., and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* 29 (4):366-91.
- Nabokov, P. 1989. Reconstituting the Chumash: A review essay. *American Indian Quarterly* 13 (4): 535-43.
- Neumann, R. 2003. The production of nature: Colonial recasting of the African landscape in Serengeti National Park. In *Political ecology: An integrative approach to geography and environment-development studies*, eds. K. Zimmerer and T. Bassett, 240-55. New York: The Guilford Press.
- O'Leary, J. F., and W. E. Westman. 2008. Regional disturbance effects on herb succession patterns in coastal sage scrub. *Journal of Biogeography* 15:775-86.
- Qian, H., and R. E. Ricklefs. 2006. The role of exotic species in homogenizing the North American flora. *Ecology Letters* 9:1293-98.
- Robbins, P. 2004. Comparing invasive networks: Cultural and political biographies of invasive species. *Geographical Review* 94:139-56.
- Rodrigue, C. M. 2004. The construction of scrub in California and Mediterranean borderlands: Climatic and edaphic climax or anthropogenic artifact? *American Geophysical Union*: San Francisco. 16 December 2004. (Biogeosciences, Paper no. B41B-0113).
- Rundel, P. W. 2007. Sage scrub. In *Terrestrial vegetation of California*, eds. M. Barbour, A. Schoenherr, and T. Keeler-Wolf, 208-28. Berkeley: University of California Press.
- Rundel, P. W., and R. Gustafson. 2005. *Introduction to the plant life of Southern California*. Berkeley and Los Angeles: University of California Press.

- Sauer, C. O. 1950. Climax, fire, and man. *Journal of Range Management* 3 (1):16-21.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in Savannas. *Annual Review of Ecology and Systematics* 28:517-44.
- Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications* 13 (3):575-92.
- Siemann, E., and W. E. Rogers. 2003. Herbivory, disease, recruitment limitation, and success of alien and native tree species. *Ecology* 84:1489-1505.
- Sprugel, D. 1991. Disturbance, equilibrium and environmental variability: What is 'natural' vegetation in a changing environment? *Biological Conservation* 58:1-18.
- Stromberg, M. R., J. D. Corbin, C. M. D'Antonio. 2007. *California grasslands: Ecology and management*. Berkeley and Los Angeles: University of California Press.
- Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* 6 (4):1189-1211.
- Stylinksi, C. D., and E. B. Allen. 1999. Lack of native species recovery following severe exotic disturbance in Southern California shrublands. *Journal of Application Ecology* 36:544-54.
- Talluto, M. V., and K. N. Suding. 2007. Historical change in coastal sage scrub in Southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology* 23:803-15.
- Underwood, E. C., S. L. Ustin, and C. M. Ramirez. 2006. A comparison of spatial and spectral image resolution for mapping invasive plants in coastal California. *Environmental Management* 39:63-83.
- United States Geological Survey. 2007. Earth Explorer. <http://edcsns17.cr.usgs.gov/EarthExplorer/> (last accessed 07 December 2010).
- Vale, T. 2002. *Fire, native peoples, and the natural landscape*. Washington, D.C.: Island Press.
- Ventura County Planning Division. 2010. Ventura, CA.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13.
- Vogl, R. J. 1976. An introduction to the plant communities of the Santa Ana and San Jacinto Mountains. In *Plant communities of Southern California*, ed. J. Latting, 77-98. Sacramento, CA: California Native Plant Society.



- Vogl, R. J., and P. Schorr. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. *Ecology* 53(6):1179-88.
- Vogelsang, K. M., and J. D. Bever. 2009. Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology* 90(2):399-407.
- Walker, P. 2005. Political ecology: Where is the ecology? *Progress in Human Geography* 29:73-82.
- Wells, P. V. 1962. Vegetation in relation to geological sub-stratum and fire in San Luis Obispo Quadrangle, California. *Ecology* 32:79-103.
- Western Regional Climate Center. 2010. Historical Climate Information. <http://www.wrcc.dri.edu/climatedata.html> (last accessed 13 December 2010).
- Westman, W. E. 1976. Vegetation conversion for fire control in Los Angeles. *Urban Ecology* 2:119-37.
- . 1981. Factors influencing the distribution of species of California coastal sage scrub. *Ecology* 62(2):439-55.
- . 1983. Xeric mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. *Vegetatio* 52(1):3-19.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266-74.
- White, K. L. 1966. Old-field succession on Hastings Reservation, California. *Ecology* 47:865-68.
- . 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. *Ecology* 48:949-55.
- Wilson, E. O. 1992. *The diversity of life*. Cambridge: The Belknap Press.
- Woinarski, J. C., and A. J. Ash. 2002. Responses to vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecology* 27:311-23.
- Wolkovich, E. M., R. A. Virginia, D. T. Bolger, K. L. Cottingham, and D. A. Lipson. 2010. Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. *Global Change Biology* 16(4):1351-65.
- Worster, D. 1990. The Ecology of order and chaos. *Environmental History Review* 14:1-18.
- Yelenik, S. G., and J. M. Levine. 2010. Native shrub reestablishment in exotic annual grasslands: Do ecosystem processes recover? *Ecological Applications* 20(3):716-27.

Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64(4):809-18.

Zimmerer, S., and K. Young. 1998. Introduction: The geographical nature of landscape change. In *Natures geography: New lessons for conservation in developing countries*, eds. S. Zimmerer and K. Young, 3-22. Madison, WI: University of Wisconsin Press.