

Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution

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Abstract Invasions resulting in the transformation of one ecosystem to another are an increasingly widespread phenomenon. While it is clear that these conversions, particularly between grassland and shrubland systems, have severe consequences, it is often less clear which factors are associated with these conversions. We resampled plots from the 1930s (Weislander VTMs) to test whether two widely assumed factors, changes in fire frequency and nitrogen deposition, are associated with the conversion of coastal sage scrublands to exotic grasslands in southern California. Over the 76-year period, coastal sage scrub cover declined by 49%, being replaced predominantly by exotic grassland species. Grassland encroachment was positively correlated with increased fire frequency and, in areas with low fire frequencies, air pollution (percent fossil carbon as indicated by $\delta^{14}\text{C}$, likely correlated with nitrogen deposition). We conclude that increases in fire frequency and air pollution over the last several decades in southern California may have facilitated the conversion of coastal sage shrubland to exotic grassland systems.

Keywords Mediterranean shrubland · Coastal sage scrub · Grassland encroachment · Biological invasion · Nitrogen deposition · Fire frequency · Air pollution · Wieslander VTM

Introduction

Exotic plant invasions are an increasingly frequent human-induced change across landscapes. Invasions that shift the dominant life form may have particularly serious ramifications, resulting in losses or degradation of ecosystem processes and associated services. In addition to altering diversity by eliminating the dominant species, these conversions often result in permanent disruptions of species interactions and ecosystem structure and function (D'Antonio and Vitousek 1992; Vitousek et al. 1997; Mooney and Hobbs 2000).

While many invasions are linked to human activities, there is considerable debate about the key factors controlling the invasability of communities (Lonsdale 1999; Davis et al. 2000; With 2002; Mack 2003). Observational studies combined with experimental work have advanced our understanding of the factors controlling invasability, most notably disturbance (Hobbs and Huenneke 1992; Burke and Grime 1996; Mack et al. 2000; Hansen and Clevenger 2005; Merriam et al. 2006), resource availability (Davis et al. 2000; Emery and Gross 2007), release from natural enemies (Wolfe 2002; Callaway et al. 2004;

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Colautti et al. 2004), and diversity (Levine 2000; Kennedy et al. 2002). Despite the complexity of most invasions, these studies predominately are short-term (e.g., 1–5 years) and focus on isolating the effects of a single factor. While these studies have been crucial to the progress of invasion biology, they are limited in their ability to determine the relative importance of several causal factors, particularly for invasions with long lag periods between initial colonization and widespread invasion. Due to these time lags and succession, it is also difficult to determine whether the effects of invaders are transient, resulting in short-lived communities that will be replaced with succession, or persistent, resulting in permanent conversion.

Longer-term retrospective analyses at the landscape scale fill this much-needed gap because they can infer the relative roles of multiple concurrent factors in controlling invasions and separate transient from persistent changes in an invaded landscape (Meiners et al. 2002; MacDougall et al. 2004; Rose et al. 2004; Kulmatiski 2006). Unfortunately, long-term records of many invasions, particularly those that offer quantitative measures of species composition, are relatively rare.

Here we address factors associated with annual grass invasion of coastal sage scrub (CSS), an assemblage of mostly soft-leaved, drought-deciduous or seasonally-dimorphic shrubs, since the 1930s. CSS has historically occupied the Pacific coastal ranges extending from north of the San Francisco Bay into Baja California Norte (Holland and Keil 1995). Shrublands not directly threatened by changing land use are being lost to grass invasion, with as little as 40% of shrublands extant in the 1930s remaining relatively uninvaded (Freudenberger et al. 1987; Minnich and Dezzani 1998). Invasion by annual exotic grasses, primarily species from the genera *Bromus* and *Avena*, is thought to be the primary threat to CSS (Freudenberger et al. 1987; Minnich and Dezzani 1998; taxonomy follows Hickman 1993).

The landscape-level factors that favor grass invasion of CSS have been subject of debate, largely characterized by arguments over the role of increased fire frequency versus the role of increased air pollution. In southern California, fire frequency is positively associated with population density and proximity to urban areas (Syphard et al. 2007b). While CSS is adapted to periodic fire (an estimated fire return interval of 40 years; Keeley et al. 2005a), fire

frequencies have increased to unprecedented levels. Increased fire frequency could facilitate the invasion of exotic grasses into CSS (Freudenberger et al. 1987; Keeley et al. 2005a), as frequent fires may favor the exotic grasses over the native shrubs (O'Leary and Westman 1988; Syphard et al. 2006). Increased fire frequency may exceed the tolerance of many woody species, decreasing the density of woody recruits following a fire (Jacobson et al. 2004). This loss would slow the time it takes the shrubland to return to closed canopy, allowing the herbaceous colonizers, particularly exotic annual grasses, to persist. Frequent fires would also decrease the intensity of individual fires, allowing annual grass seed which would have normally been killed by a fire to remain viable (Keeley et al. 2005b). Because annual grasses increase fuel loads due to the accumulation of dry biomass over multiple growing seasons, grass invasion may result in a positive feedback whereby grasses increase and maintain fire frequency beyond the tolerance of woody species, resulting in the long-term persistence of grassland (D'Antonio and Vitousek 1992; Grigulis et al. 2005; Keeley et al. 2005a; D'Odorico et al. 2006).

Alternatively, others have argued that invasion is driven by pollution effects arising from nitrogen deposition that favors exotic grasses (Minnich and Dezzani 1998; Wood et al. 2006). Nitrogen deposition rates from air pollution in the Los Angeles region are among the highest in the US, with coastal regions experiencing fairly low deposition rates compared to inland valleys and mountains (Padgett et al. 1999; Fenn et al. 2003). While increased nitrogen is often speculated to be associated with loss of CSS, the little experimental evidence that exists is conflicting (Padgett and Allen 1999; Stylinski and Allen 1999; Suguenza et al. 2006; Wood et al. 2006). General theories of invasion ecology predict that increased N availability should promote the invasion of fast-growing annual plants into systems dominated by slow-growing perennials (Dukes and Mooney 1999; Davis et al. 2000). Empirical studies in California (Huenneke et al. 1990; Maron and Conors 1996) and elsewhere (Burke and Grime 1996; Wedin and Tilman 1996) have shown that high soil N availability favors non-native annual grasses over native perennials, possibly because annuals are more capable of increasing growth in response to increased N availability compared to native perennials adapted to low soil N (Grime 1979; Chapin et al. 1986).

The debate about the importance of fire and nitrogen in driving the invasion of annual grasses into perennial-dominated ecosystems has largely gone unresolved because of the difficulty in comparing the relative strengths of these processes at appropriate spatial and temporal scales. While studies of fire effects are relatively straightforward at large spatial scales, most focus on the early successional period immediately following the disturbance (Keeley et al. 2005b). Grass invasion immediately following fire does not necessarily portend continued decadal dominance of exotic grasses. Because it is difficult to manipulate fire frequency, most studies rely on existing field patterns. In comparison, it is difficult to get long-term estimates at the proper spatial resolution for N deposition, particularly dry deposition (Weiss 1999; Fenn et al. 2003), and soil-based indicators of deposition are notoriously poor (Stylinski and Allen 1999). Consequently, most studies testing the nitrogen mechanism have been performed in the greenhouse or at a small number of field sites (Padgett and Allen 1999; Suguenza et al. 2006; Wood et al. 2006). Thus, it is difficult to compare results across studies, and simultaneous tests of both mechanisms are rare. In a notable exception, Keeley et al. (2005a) found that fire history, compared to regional nitrogen deposition, better predicted annual grass invasion in southern California. However, this work focused on early successional changes—grass invasion 5 years following fire—and used nitrogen deposition estimates with low spatial resolution (36 km, Tonnesen et al. 2003). A further complication is that interactions between fire, nitrogen, and local soils and microclimate may contribute to patterns of invasion in this system (e.g., Minnich and Dezzani 1998).

Here, we compare these past results to longer-term records of grass invasion into CSS. We resurveyed CSS plots originally surveyed in the early 1930s, allowing us to assess the factors related to persistent annual grass invasion. We used radiocarbon ($\delta^{14}\text{C}$) as a biomarker of fossil fuel burning, allowing us greater precision in inferring the influence of air pollution and associated atmospheric nitrogen deposition (Shore et al. 1995; Alessio et al. 2002; Bukata and Kyser 2007; Hsueh et al. 2007) at these sites. We compiled detailed fire history for each plot, as well as information on soils and climate.

This unique record enables us to test a hypothesis that reconciles some of the current debate about the

causes of annual grass invasion in this system: CSS sites most likely to be invaded by exotic annual grasses are those with short fire return intervals combined with high levels of nitrogen deposition from atmospheric pollution. High fire frequency may cause the demise of shrubs, allowing the initial recolonization process to be dominated by exotic grasses (Jacobson et al. 2004; Keeley et al. 2005a). The extent to which these exotic grasslands are successional and eventually replaced by shrubland could depend on atmospheric pollution (Eliaison and Allen 1997; Wood et al. 2006). In this study, we used a 70 year retrospective analysis to test the prediction that CSS sites with high levels of atmospheric pollution, when combined with high fire frequencies, have a high probability of converting to exotic grasslands.

Methods

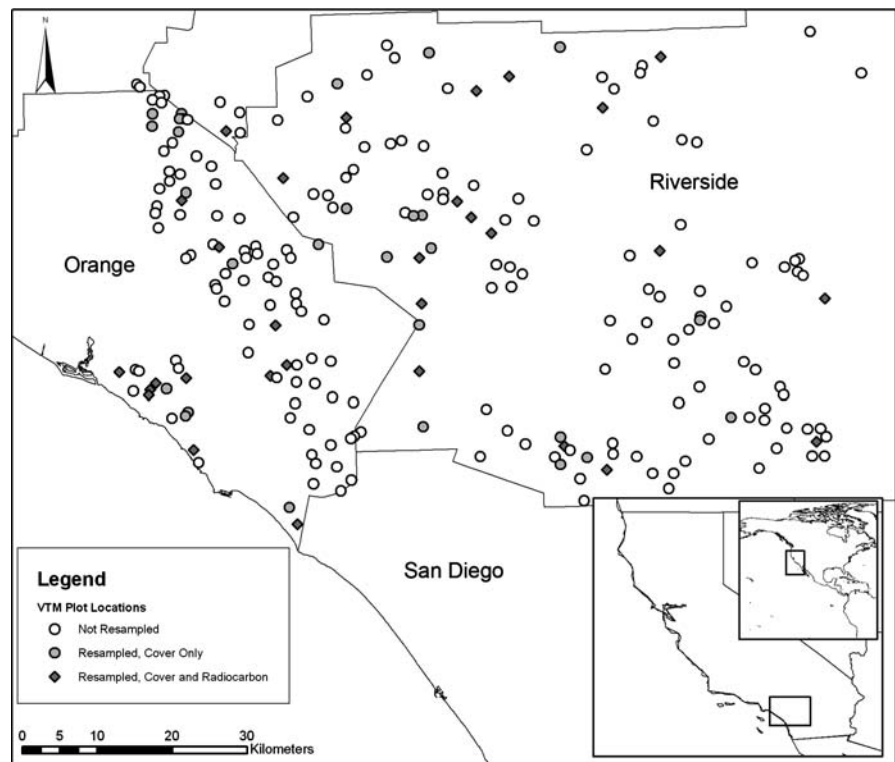
In the early 1930s, the US Forest Service conducted an extensive vegetation mapping project that included placing more than 13,000 0.04-ha plots in forests, shrublands, and grasslands of California, called the Wieslander Vegetation Type Map (VTM) Survey. The survey collected detailed information on species composition, cover and environmental characteristics. These data present a unique opportunity to study conversion processes in CSS over the last 70 years.

Study area and site selection

Our study area was located in cismontane southern California and included central and southern Orange County and western Riverside County. Elevations of our study sites ranged from 90 m to 850 m. Mean annual precipitation in the region ranges from 23 to 60 cm/year. Much of the study area experienced greater than average precipitation during the study period. Land use history in the region is complex, with most natural areas persisting in a matrix of suburban development, agriculture, and disturbed habitat dominated by exotic annual grasses and forbs.

We identified 232 plots that were dominated (>50% cover) by CSS shrubs when the plots were sampled in the original survey (Fig. 1). These plots were stratified into categories by fire frequency (CDF

Fig. 1 Map of study area in southern California, USA, including all historical VTM points present in coastal sage scrub in the study area, as well as plots that were resampled for vegetative cover only or for vegetative cover and radiocarbon. Plots shown include plots that may have been developed since the 1930s survey. Black lines indicate county boundaries



2005) and air pollution (EPA 2004); study sites were then randomly selected within each category. We selected an initial sample of 60 VTM plots. Sites on private property were sampled if property owners granted permission, otherwise we substituted another randomly selected VTM site. We also substituted any sites that had been developed. Six plots from the final sample showed clear evidence of recent (1–2 year old) heavy disturbance, such as off-road vehicle use, plowing, disking, and high-intensity grazing. We excluded these plots from analysis, resulting in a final sample size of 54. This sample size is comparable to other landscape-scale surveys in CSS (Minnich and Dezzani 1998; Keeley et al. 2005a).

Sampling methodology

We resampled VTM plots between February and April 2005. We chose sampling methods to replicate as closely as possible the methods used by the original VTM crews (Wieslander et al. 1933). VTM crews visually selected plot locations from ridge tops and other vantage points, choosing locations that appeared to be representative of the community type being

sampled. This non-random placement of plots may have produced a bias in the original survey. However, because of the large number of plots and the large area over which the study was conducted, any original biases in site selection are likely to be small in comparison to variability due to the geographic location of the plots.

VTM crews mapped plot locations on topographic maps based on USGS 15-min quadrangles published in 1898, but left no permanent markers, making exact plot relocation impossible. We utilized a digitized version of the VTM map (R. Taylor, US National Park Service) when relocating plots. Plot locations on the original maps were indicated by hand-drawn circles with real-world radii of up to 300 m (Franklin 2002; Keeley 2004).

To relocate plots, we used ArcGIS 9.0 (ESRI, Redlands, CA) to identify all areas within 300 m of the digitized plot locations that had the same slope (± 10 degrees) and aspect (± 15 degrees) as recorded on the original datasheet. We chose 300 m to match the size of the largest of the hand-drawn circles on the original maps. This radius should also sufficiently account for most of the error present in the topographic maps used by the VTM crews. This

procedure produced an area containing the most probable locations for the original plot.

To provide a better estimate of mean vegetative cover for the entire area being sampled, we sampled two replicate plots for each VTM plot location and averaged the cover measurements for these plots to obtain a composite resample plot. If the potential resampling area was too small to contain two replicate plots, we sampled a single plot. This method has been employed in previous studies using the VTM (Minnich et al. 1995; Minnich and Dezzani 1998; Taylor 2004) and has been criticized by Keeley (2004) who noted that small-scale variability in shrub cover could be so high that any attempt to discern the fate of a single VTM plot would be meaningless unless the plot could be relocated with extreme precision. To address this concern, we compared the variability in shrub cover between our replicate samples to the variability between the modern composite and the original VTM plot.

VTM plots were 40 m by 10 m (0.04 ha), and each plot was further divided into 100 2.0 m by 2.0 m cells. Cells with less than 50% cover were considered bare ground. In cells with greater than 50% vegetative cover, the VTM crews recorded the single most dominant species in that cell. The crews then counted the number of cells dominated by each species and recorded that number as percent cover. We repeated this method when resampling plots. To avoid confusion with other common methods for measuring cover, cover measurements from both original and resample plots will be hereafter referred to as “percent VTM Cover.”

We identified all trees, shrubs, and subshrubs to species using Hickman (1993). Shrubs and subshrubs were classified as CSS or chaparral using Holland and Keil (1995). Species that commonly occur in both communities were classified as CSS. The original VTM crews did not identify grasses and ground-level herbaceous plants to species. During resampling, we categorized herbaceous species as exotic annuals, exotic perennials, native annuals, and native perennials. Because the original VTM survey did not distinguish between native and exotic cover of herbaceous species, we lumped all herbaceous vegetation when analyzing changes from the original survey. For analyses that did not use the original survey, we used only exotic annuals. We refer to this measure of exotic annual cover as “grass cover” as

indicative of exotic grassland rather than shrubland systems.

Freudenberger et al. (1987) wrote that CSS and exotic-dominated grassland in the Los Angeles basin have dynamically changing boundaries. Because the original VTM crews deliberately sampled areas that contained mostly shrubs, changes observed since the 1930s in the present study may be a result of these changing boundaries, without a change in the relative proportions of each community. To address this issue, we randomly selected 31 resample plots and used modern orthophotos to digitize polygons of grassland and shrubland patches within 300 m of the plots. Each polygon was assigned one of five levels of grassland cover (0%, 25%, 50%, 75%, and 100%). Both grassland and CSS were readily distinguished from each other and other vegetation types on the photographs. We then computed the area of each stand to approximate the grassland cover of the landscape.

Factors associated with grassland invasion

To describe the fire history at each sampling site, we calculated the mean fire return interval using a GIS layer of fire perimeters (CDF 2005). Sites that had no fires in the 76 years since the VTM survey were assigned a fire return interval of 80 years. We also analyzed the minimum time interval between any two fires and the time since the most recent fire as alternate measurements of fire frequency.

The CDF fire perimeter database covers public and private lands throughout California. While this dataset represents the best available fire history data for California, it has inherent biases. In particular, the dataset may not include fires less than 300 acres, older fires, and those occurring on non-USFS lands. However, the use of this database had important advantages over the alternative of measuring stand age in the field. Because we were interested in the long-term history of these sites, measurement of modern (2005) stand age only would represent the most recent fire return interval and not give information about average or minimum fire return interval.

To test the hypotheses concerning whether differences in nitrogen deposition rates relate to annual grassland invasion, we collected samples of leaf tissue from the annual grass species *Avena fatua*, *Bromus diandrus*, *B. madritensis*, and *B. hordeaceus*. These

species were selected because their widespread presence in southern California ensured that samples of at least one species would be available at each plot. Because we concentrated on annual species, these measures indicate the fossil carbon incorporated in leaf tissue over a single year, avoiding the influence of differentially aged individuals (Hsueh et al. 2007). In using this approach, we assume that the influence of fossil fuel-derived CO₂ during the year of sampling are associated with a larger cumulative impact over the 76-year resampling interval. Historic levels of atmospheric NO_x loads have increased in the Los Angeles Basin since the 1930s, with the highest levels in the 1970s (Egerton-Warburton et al. 2001). Although small-scale patterns of NO_x pollution have likely been influenced by local factors (e.g., new construction), large-scale spatial patterns are thought to have remained consistent over this period (Fenn and Bytnerowicz 1997). Approximately 10 g of tissue from each of 1–3 species was collected from within each plot, or if annual grasses were not present within the plot, from within 200 m of the plot. Samples were bulked for analysis. We analyzed leaf tissue from 30 plots for $\delta^{14}\text{C}$ at the Keck Carbon Cycle Accelerator Mass Spectrometer (KCCAMS), University of California, Irvine (Santos et al. 2004). These plots were chosen at random from the original sample of 54 plots (Fig. 1). From observed $\delta^{14}\text{C}$ values, we calculated the % fossil carbon incorporated into leaf tissue (following Hsueh et al. 2007). Although this is not a direct measurement of N deposition, N deposition in southern California originates predominantly from fossil fuel combustion (Padgett et al. 1999; Fenn et al. 2003), and so atmospheric concentrations of anthropogenic N are likely to be correlated with concentrations of fossil carbon. Because we measured $\delta^{14}\text{C}$ at each site, we expect that the spatial resolution of this data is much greater than model-based estimates, as there are only a few dry deposition sampling stations within the study area.

To determine if local topography had any effect on grassland invasion, we used data recorded on the original VTM datasheets to compute an index of northness (Borchert et al. 1989) using the following equation:

$$\text{northness} = \cos(\text{aspect}) * \sin(\text{slope}) \quad (1)$$

We also addressed the effects of elevation, mean annual precipitation, and soil type on grassland

invasion. Elevation was derived from a three meter resolution digital elevation model. The GIS layer of mean annual precipitation was obtained from CDF (2005). The data were originally digitized from 1:1,000,000 isohyetal maps.

Soil data were obtained from digitized versions of USDA soil surveys. From the surveys, we included available water capacity (a measure of water that is available to plants), soil rooting depth (the estimated depth to which roots can penetrate the soil), soil texture (measured as % sand and % silt in the surface layer), and soil pH as continuous variables in our models. We also included soil parent material as a categorical variable. With the exception of rooting depth and parent material, all variables refer to the surface soil layer. Because the continuous soil variables (available water capacity, rooting depth, % sand, % silt, and pH) were highly intercorrelated, we simplified them using principal components analysis and included the transformed axes as predictors in our regression models.

Statistical analysis

To confirm that sampling paired replicate plots adequately incorporates variability within each VTM sampling site, we used paired *t*-tests to compare the difference in VTM cover of the two most dominant species between replicate plots to the difference between the composite modern plots and the original plots. To test whether shifting boundaries of shrubland and grasslands could bias the results, we compared grassland cover within 300 m of each plot (estimated from aerial photo interpretation) and grassland cover observed within the corresponding resample plots using a paired *t*-test.

We compared percent VTM cover of grasses in the 2005 resampling with original 1930s VTM data using paired *t*-tests. VTM cover of shrub species was not analyzed separately because it was highly correlated with VTM cover of grasses.

We used multiple regression models to analyze the effects of all predictor variables on the change in herbaceous cover (from original VTM to resampling) and the modern % VTM cover of exotic annual grasses (using resample plot data only). Percent cover values were transformed using an arcsine transformation. We calculated the relative change in herbaceous cover since the VTM survey using a natural log ratio as follows:

$$\text{Log ratio} = \ln((\text{modern} + 0.1)/(\text{historic} + 0.1)) \quad (2)$$

Positive log ratio values indicate a relative increase in grassland cover since the 1930s, zero indicates no change, and negative values indicate a relative decrease.

We initially included only main effects in our regression models, and we selected the most descriptive model using a stepwise algorithm that minimized Akaike's information criterion (AIC). We then added two-way interaction terms for all variables that were included in the initial models, and used a similar stepwise procedure to eliminate interaction terms. Because we only sampled $\delta^{14}\text{C}$ from a subset of plots, we analyzed the effects of $\delta^{14}\text{C}$ and interactions involving $\delta^{14}\text{C}$ in separate models. These models initially included $\delta^{14}\text{C}$ and all variables and interactions that were present in the final model using all sampled plots, and the most descriptive models were selected by eliminating predictors until AIC was minimized. Soil parent material, a categorical variable, was simplified by combining categories with parameter estimates with overlapping standard errors. Response variables and model residuals were examined for spatial autocorrelation by using Moran's I correlograms with the SAM software package (Rangel et al. 2006).

Results

Resampling accuracy

Potential resampling areas that were within 300 m of the mapped plot locations and matched the slope and aspect on the original datasheet averaged 3.01 ha. Variability in percent VTM cover between replicate plots was significantly lower than the variability between the composite plot and the original VTM survey plot for both the most dominant ($t_{51} = -7.3$, $P < 0.001$) and the second most dominant species ($t_{41} = -3.1$, $P = 0.004$).

Grassland cover observed on modern aerial photographs within 300 m of plot locations did not significantly differ from the grassland cover recorded within resample plots ($t_{30} = 0.73$, $P = 0.5$). The mean difference in grassland cover between resample plots and digitized aerial photographs was less than 11% (95% CI: $-10.5\% < \mu < 5.0\%$).

Table 1 Change in vegetation since the 1930s VTM survey

	% VTM cover	
	1929–1934	2005
Coastal sage scrub	78.5 (3.2)	40.1 (4.7)
Total herbaceous cover	12.4 (2.8)	53.5 (5.0)
Exotic annual herbaceous	–	49.4 (4.9)
Native annual herbaceous	–	4.0 (2.3)
Native perennial herberbaceous	–	0.1 (0.1)
Chaparral	0.76 (0.51)	3.9 (2.2)
Other vegetation types	0.51 (0.42)	0.07 (0.06)
Total vegetative cover	92.2 (1.5)	97.5 (0.55)

Cover values are mean VTM cover with SEM. The original VTM survey did not divide total herbaceous cover into subcategories, as we have done in the present survey

Invasion of grasslands into CSS

Mean CSS cover at VTM sites significantly decreased from 78.5% in the 1930s original survey to 40.1% in the present study ($t_{53} = 8.4$, $P < 0.001$), while herbaceous cover increased from 12.4% to 53.5% ($t_{53} = 7.1$, $P < 0.001$; Table 1). There was a small but significant increase in total vegetative cover from 92.2% to 97.5% ($t_{53} = 3.3$, $P = 0.002$; Table 1).

Factors related to grassland invasion

The variables for soil rooting depth, texture, pH, available water capacity, and permeability were transformed using PCA. The first principal component explained 48% of the variance and was positively correlated with % silt, pH, available water capacity, and rooting depth, and negatively correlated with % sand. The second principal component explained an additional 26% of the variance and was positively correlated with % silt and negatively correlated with all other factors, although the strongest effects were for rooting depth and % sand. The third principal component explained 12% of the variance and was positively correlated with rooting depth and % silt and negatively correlated with pH (Table 2).

Fire return interval appeared as a predictor of both the relative change (from 1930s to 2005) in herbaceous cover and the modern (2005) cover of exotic annual grasses. The change in herbaceous cover was negatively correlated with fire return interval, indicating that plots with higher overall fire frequency showed a larger magnitude increase in grass cover

Table 2 Strength of factor loadings for the principal components analysis for soil variables

	Principal components		
	First	Second	Third
Available water capacity	0.5162	-0.2114	0.2187
Rooting depth	0.3053	-0.6288	0.5063
% Sand	-0.5386	-0.3653	0.1626
% Silt	0.3365	0.6175	0.4521
pH	0.4869	-0.2124	-0.6819
Proportion variance explained	0.475	0.262	0.123

($P < 0.01$, $r^2 = 0.12$; Fig. 2, Table 3). Change in herbaceous cover was not correlated with any other environmental variables we included in our models.

Modern grass cover was negatively correlated with fire return interval ($P < 0.001$, $r^2 = 0.35$; Fig. 2, Table 3), and there was a significant negative interaction between fire return interval and the second principal component for soil type ($P < 0.01$, $r^2 = 0.17$). Minimum fire interval (the smallest amount of time between any two fires) was also positively related to modern grass cover (Table 3). However, there was also a significant interaction between

minimum fire interval and the first soil principal component. When minimum fire interval was low, siltier, deeper soils with higher water holding capacity were more likely to have higher grass cover than at high minimum fire interval.

As expected, site-specific topography and geology also influenced modern grass cover. Grass cover increased on more north facing slopes, and on igneous, latite-porphyry, gabbro, and metamorphosed sandstone derived soils. Modern grass cover was also positively correlated with the first soil principal component and negatively correlated with the third, indicating a positive correlation with % silt, soil water holding capacity, pH, and soil depth, and a negative correlation with % sand (Table 3).

Modern grass cover was positively correlated with % fossil carbon, but only in areas with long fire return intervals (% fossil carbon and fire return interval interaction, $n = 30$, interaction $r^2 = 0.29$, $P < 0.01$; Fig. 2, Table 3). At short fire return intervals, % fossil carbon had no effect on grass cover. At long fire return intervals (low fire frequency), grass cover increased with % fossil carbon (Fig. 3).

Modern grass cover showed significant spatial autocorrelation at the shortest lag distances of 8.9,

Fig. 2 Partial residual plots showing the effects of selected predictors on change in herbaceous cover (a) and grass cover in modern plots (b–d). With the exception of change in herbaceous cover (a), y values show the residuals from a model containing all significant predictors except the variable plotted on the x-axis. Change in herbaceous cover is plotted as a log ratio, with positive values indicating a relative increase in herbaceous cover. Residuals were not plotted for this model because only one predictor was included in the model. Fitted lines show relationships that were significant in the multiple regression models

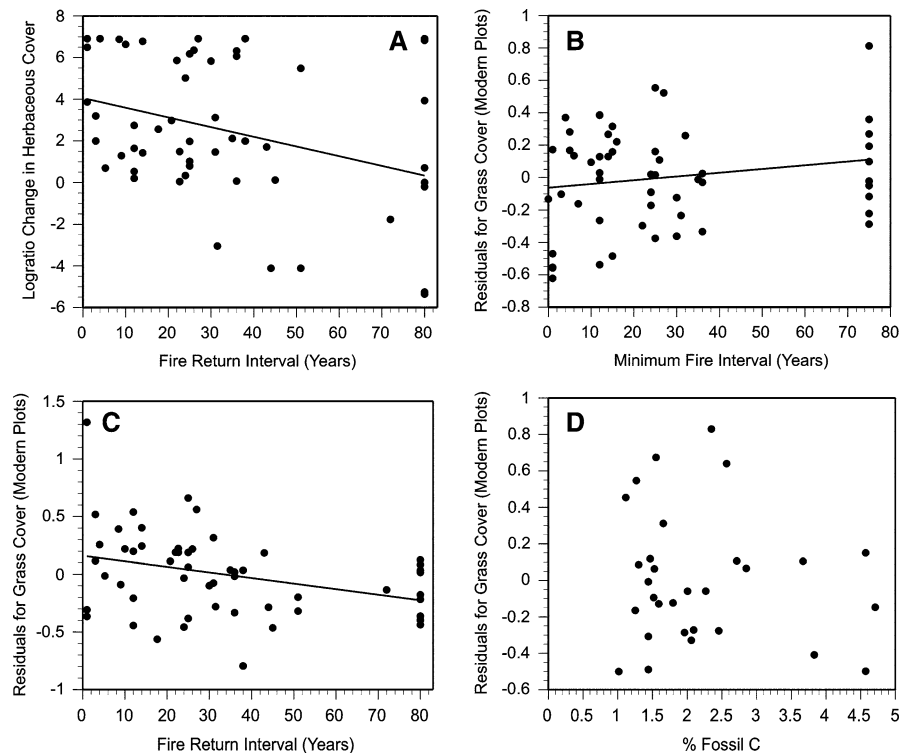


Table 3 Parameter estimates and explanatory power from multiple regression models that minimized AIC for each response variable

	Parameter estimates (proportion variance explained)	
	Change in herbaceous cover	Modern grass cover
Northness	–	0.43 (0.11)*
First principal component (soil type) ^a	–	0.21 (0.29)***
Second principal component (soil type)	–	–0.01 (0.00)
Third principal component (soil type)	–	–0.13 (0.10)*
Soil parent material ^b	–	0.75 (0.41)***
Fire return interval (FRI)	–0.047 (0.12)**	–0.014 (0.35)***
Minimum fire interval (F _{min})	–	0.0073 (0.11)*
% Fossil carbon	–	–0.11 (0.04)
F _{min} * first principal component (soil type)	–	–0.0031 (0.12)*
FRI * fossil C	–	0.0073 (0.29)**
FRI * second principal component (soil type)	–	–0.0048 (0.17)**

The total proportion of variance explained was 0.12 for change in herbaceous cover and 0.67 for modern grass cover

^a Principal components for soil type: First: positively correlated with % silt, pH, water holding capacity, and rooting depth; negatively correlated with % sand. Second: positively correlated with % silt; negatively correlated with % sand and rooting depth. Third: negatively correlated with pH

^b Parent material is a dummy variable; a value of 1 indicates the presence of igneous, mica-schist, latite porphyry, gabbro, or metamorphosed sandstone, and a value of 0 indicates all other types. Asterisks indicate significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

22.3, and 30.7 km (Moran's $I = 0.20$, -0.16 , and 0.22 ; $P = 0.02$, 0.02 , and 0.005 , respectively). We found no significant spatial autocorrelation in change in herbaceous cover or in the residuals for either model.

Discussion

Grassland invasion

Cover of coastal sage shrub species substantially declined in the study area since the 1930s VTM survey. Grasses increased in mean cover by nearly

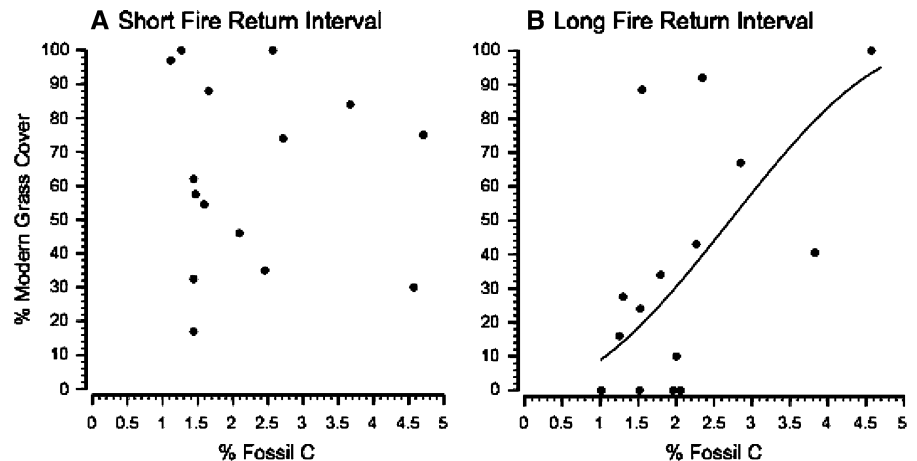
four-fold over the 70 year interval, from 12% to 50%, while mean shrub cover declined from 79% to 40% (Table 1). Most (48%) coastal sage VTM plots that we resampled were dominated by exotic annual grasses, and only 15% were uninvaded. Other studies have found similar rates of decline in CSS (Freudenberger et al. 1987; Minnich and Dezzani 1998), strongly suggesting widespread invasion of annual grasses in this system.

As we hypothesized, we found evidence supporting the association of fire, air pollution, and an interaction between fire and pollution with the conversion of CSS to exotic annual grassland. The long-term decline in CSS was positively associated with high fire frequency, indicating that CSS is intolerant of frequent disturbance from fire. Work has shown that frequent fires can lead to successional grassland invasion (Jacobson et al. 2004; Keeley et al. 2005a). Our results confirm that this trend persists over many years and may lead to a persistent invaded state. Air pollution, approximated using ^{14}C as a bioassay, was also positively correlated with annual grass invasion. While fire was consistently a stronger predictor of grass invasion regardless of pollution, pollution was associated with grass invasion only in areas of low fire frequency (Table 3). Thus, it appears that CSS sites with high fire frequency are most at risk of long-term dominance of exotic grass. Secondly, sites with a lower fire frequency in areas with high air pollution are also at risk.

Fire frequency

In sites that had been frequently burned, grass cover increased dramatically since the 1930s. Studies in other systems have found that fire facilitates the invasion of annual grasses into woody systems (Freudenberger et al. 1987; D'Antonio and Vitousek 1992; Haidinger and Keeley 1993; Knapp 1996; Keeley 2000; Briggs et al. 2005; Keeley et al. 2005a, b). Our observations of widespread conversion of CSS to grassland since the 1930s, and the association of this change with increased fire frequency, suggests that fire-facilitated invasion may contribute to long-term conversion in this system. In CSS, we expect that frequent fire is associated with both increased ability of grasses to competitively exclude recruiting shrubs (as hypothesized by Minnich and Dezzani (1998) and positive

Fig. 3 Relationship between % fossil carbon (assayed by measuring foliar ^{14}C content) and grass cover in modern resample plots at high (a) and low (b) fire frequency. The fitted line was obtained by dividing the data into high and low fire frequency at the median fire return interval (25.5 years) and performing a simple linear regression of fossil carbon on arcsine transformed grass cover



feedbacks with greater grass cover causing fuel accumulation and increased fire frequency (D'Antonio and Vitousek 1992; Keeley et al. 2005a). The ability of invading grasses to increase fire frequency, resulting in eventual dominance of grasses, has been demonstrated in other woody systems (Grigulis et al. 2005; D'Odorico et al. 2006), and warrants further study in CSS. Although we were only able to compare two points in time in this analysis, fire frequency has been consistently higher than expected through much of that time interval (Keeley et al. 2005a, b; Syphard et al. 2007a). It is therefore likely that this observed relationship between fire and CSS loss represents a continuous change over that period. More detailed time series analyses of annual grass invasion and fire events would be necessary to more conclusively determine whether positive feedbacks are important in this system and whether the observed changes have been continuous and persistent over time.

Nitrogen deposition

Grass cover was associated with the amount of fossil carbon incorporated in plant tissue, but only when fire frequency was low (Fig. 3, Table 3). This supports our hypothesis that grass invasion is associated with nitrogen deposition in this system because both fossil carbon and anthropogenic nitrogen in southern California originate primarily from fossil fuel combustion (Padgett et al. 1999; Fenn et al. 2003). Our use of ^{14}C as a biomarker is one of the first fine spatial scale analyses of the association of air pollution to vegetation patterns. Tissue ^{14}C is likely

indicative of several factors, including the direct effects of greater N availability due to N deposition, higher ozone levels, and effects indirectly associated with air pollution such as land use history (Westman 1979; Lambers and Poorter 1992; Wedin and Tilman 1996; Stevens et al. 2004; Hsueh et al. 2007; Syphard et al. 2007a). More research is needed to determine whether air pollutants other than nitrogen can influence the conversion of CSS and other shrublands to annual grassland.

Although pollution effects were weaker than fire effects in our models, it is difficult to determine if this corresponds to the relative strengths of these mechanisms or if it is due to the different temporal scales at which these variables were measured. Our bioassay of air pollution only sampled a single growing season; therefore our ability to infer changes over the entire study period is limited by the assumption that fossil fuel pollution in the present is correlated to long-term trends in nitrogen deposition. Unless methods become available to retroactively study nitrogen deposition with high spatial resolution, retrospective analyses of nitrogen deposition such as this one must make this assumption. Historical pollution levels likely result from a combination of large-scale spatial patterns, which are thought to have changed little since the 1930s (Fenn and Bytnerowicz 1997), and smaller-scale variation derived from local land-use patterns. Our sampling method cannot distinguish between these two sources of variation in pollution levels, so it is likely that our observations reflect both the longer-term trend in N deposition and shorter-term variation introduced at a more local scale.

Based on successional studies of grassland invasion (Jacobson et al. 2004; Keeley et al. 2005a; Wood et al. 2006), we hypothesized that higher levels of N deposition would facilitate grassland the most in areas of high fire frequencies, in opposition to the association we found. This difference may point to the difference between short-term successional work and longer-term dynamics. It may be that annual grass invasion is rapid after fire, regardless of N deposition or other pollution effects. Alternatively, N deposition without associated high fire frequencies may slowly promote grass invasion. If so, a study of short duration may not be able to pick up this longer-term trend, even though its cumulative effects could be substantial over several decades. Finally, the effects of increased fire frequency may be greater in magnitude than those of N deposition, resulting in near total conversion at high fire frequency regardless of N deposition.

Environmental associations

As we expected, fire and pollution were not the only factors that were associated with grassland invasion; particular environments were at risk of conversion regardless of disturbance history. Sites with high silt, pH, water holding capacities, and deep soils were all correlated with increased modern grass cover. The interaction between soil and fire return interval indicated that these effects were stronger when fire return interval was high, suggesting that sites with environmental conditions favorable to annual grasses were prone to invasion despite infrequent fire, but that sites with frequent fire tend to be invaded regardless of environmental conditions. Sites on north facing slopes also had higher grass cover. Igneous, latite-porphyry, gabbro, mica-schist, and metamorphosed sandstone derived soils were all associated with increased grass cover (Table 3). Most of these relationships are consistent with the natural distribution of CSS across the landscape and likely indicate that areas with less optimal conditions for CSS are more likely to undergo conversion.

Resampling accuracy

By using slope and aspect information recorded on the VTM datasheets, we were able to reduce potential resampling areas from 28.3 ha (the area of a 300 m radius circle) to an average of 3.01 ha per plot. This

figure is likely a high estimate, as it includes areas of matching slope and aspect that VTM crews were unlikely to sample due to small size or inaccessible local topography. Other studies that have attempted to relocate VTM plots have reported similar relocation accuracies in their methods, although they have not always specified how the figures were determined (Minnich et al. 1995; Minnich and Dezzani 1998; Taylor 2004). In contrast to Keeley's (2004) study, we found low variability between replicate resample plots, suggesting that sampling replicate plots is an appropriate method for accounting for spatial uncertainty in relocating historical plots in this system. We also found no evidence that dynamic borders between grassland and CSS influenced our results; proportions of grassland and CSS in our sample plots was not significantly different than proportions interpreted from aerial photographs of the surrounding landscape.

Conclusions

Shrub cover in CSS appears to have substantially declined in the last 70 years, with a corresponding increase in the cover of annual grassland. Continued rapid urbanization in southern California means that CSS will almost certainly continue to decline in the future. Furthermore, differences among CSS subtypes represent a significant fraction of the total diversity within this ecosystem, and the poor representation of these subtypes in reserves (Davis et al. 1994; Davis et al. 1995; Taylor 2004), coupled with high rates of loss due to urban encroachment and grassland invasion may make some loss in both species and subtype diversity inevitable. Future increases in human population density in rapidly growing portions of southern California will likely result in increases in both fire frequency and nitrogen deposition rates, which, coupled with increasing pressures from urban conversion and fragmentation, may speed the loss of CSS. Our results suggest that restoration and conservation efforts in CSS and other shrublands threatened by annual grass invasion will not be successful unless fire frequency and nitrogen availability can be reduced.

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