Global Ecology and Conservation 2 (2014) 190–203

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA

Robert D. Cox [a,*], Kristine L. Preston [b,1], Robert F. Johnson [b], Richard A. Minnich [c], Edith B. Allen [d]

[a] Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409, United States
[b] Center for Conservation Biology, University of California, Riverside, CA 92521, United States
[c] Department of Earth Sciences, University of California, Riverside, CA 92521, United States
[d] Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521, United States

ARTICLE INFO

Article history:
Received 3 June 2014
Received in revised form 12 September 2014
Accepted 13 September 2014
Available online 26 September 2014

Keywords:
Nitrogen deposition
Critical load
Coastal sage scrub
Exotic grass
Invasion
Vegetation type conversion

ABSTRACT

In California, USA, coastal sage scrub (CSS) vegetation is being converted to exotic annual grassland, and several causes have been suggested. In order to investigate the importance of environmental variables in the conversion and recovery of CSS, particularly nitrogen deposition within the context of historical fire intervals, we employed an information theoretic approach. Prior studies have not assessed both conversion and recovery, and did not analyze nitrogen critical load for vegetation type conversion. We included measures of climate, topography, vegetation, land use, nitrogen deposition, and fire in our analysis, and found that 34% of CSS study sites were converted to exotic grassland between 1930 and 2009. Converted sites had higher nitrogen deposition with a critical load of 11 kg N ha^{-1} yr^{-1}, also had shallower slopes, and were more west-facing. A smaller number of sites (24%) recovered to CSS, and these sites had about 2.5 times more CSS and 4.5 times less grassland in the surrounding landscape. CSS conservation and restoration efforts are most likely to be successful when focused on sites with <11.0 kg N ha^{-1} yr^{-1} and low invasion of exotic grasses. Analyses such as this that identify important threats may be useful in region-wide plans to conserve unique vegetation types.

1. Introduction

Invasion of native vegetation by exotic species is an accelerating and global issue that is receiving increasing attention (Fox, 1990; D'Antonio and Vitousek, 1992; Vitousek et al., 1997; Lenz et al., 2003; Brooks et al., 2004; D'Antonio et al., 2009; Spear et al., 2013). Vegetation conversion at this scale likely has several interacting causes, and many possible factors have been implicated including fire (Minnich and Dezzani, 1998; Brooks and Pyke, 2001), grazing by domestic livestock (Burcham, 1957; HilleRisLambers et al., 2010), fragmentation (Zink et al., 1995), competition (Eliason and Allen, 1997; Fleming et al., 2009), and nitrogen deposition (Fenn et al., 2003, 2010; Bobbink et al., 2010; Stevens et al., 2009; Clark et al., 2013). These

---

[*] Corresponding author. Tel.: +1 806 784 2841.
E-mail address: robert.cox@ttu.edu (R.D. Cox).

[1] Current address: US Geological Survey, 4165 Spruance Road, Ste 200, San Diego, CA 92101, United States.

http://dx.doi.org/10.1016/j.gecco.2014.09.008

are causal factors for decline of several plant communities in southern California, but especially of coastal sage scrub (CSS), which is considered one of the most threatened vegetation types in North America (Noss et al., 1995). CSS vegetation was often converted to agriculture in the late 19th to early 20th century, and increasing fire, air pollution, and urbanization during the last half of the 20th century resulted in large-scale and rapid conversion to exotic annual grassland (Klopatek et al., 1979; Allen et al., 1998; Minnich and Dezzani, 1998; Allen et al., 2005). Estimated losses of CSS habitat range from 60 to 90%, and the CSS that remains is often heavily invaded by exotic grasses (Westman, 1981; O'Leary, 1995; Minnich, 2008).

CSS ranges from Baja California in Mexico north to coastal central California, up to 100 km inland (Westman, 1981; Rundel, 2007). It is composed of several species of generally soft-leaved shrubs and subshrubs that are seasonally dimorphic such as *Artemisia californica* (California sagebrush) and *Salvia apiana* (white sage), combined with a diverse group of native understory annuals, and exotic annuals including grasses in the genera *Bromus, Avena, Hordeum,* and *Vulpia,* and forbs in the genera *Erodium* and *Brassica* and others (Westman, 1981; DeSimone, 1995; Rundel, 2007). CSS lies in the Mediterranean-climate region of California, one of the global hotspots of biodiversity (Myers et al., 2000). It is habitat for a large number of endangered, threatened, or "special concern" species under the US Endangered Species Act (Sawyer and Keeler-Wolf, 1995; Bowler, 2000; CNPS, 2001; Preston et al., 2012), and is therefore a priority for local and federal government restoration and conservation efforts (Bowler, 2000; Rubinoff, 2001).

Two causes of CSS conversion that have received major attention are frequent fire and nitrogen deposition (Allen et al., 2005; Talluto and Suding, 2008; Fleming et al., 2009). A model of nitrogen deposition has been developed for California at a 4 km scale (Fenn et al., 2010) that enables setting critical loads of N deposition for management purposes. A critical load (CL) is defined as the level of a pollutant below which there is no detrimental ecological effect (Fenn et al., 2010; Pardo et al., 2011; Blett et al., 2014). Up to 30 kg N ha^{-1} yr^{-1} are deposited on some areas of CSS vegetation, mostly as dry deposition during the dry Mediterranean-climate summer (Fenn et al., 2010). Oxidized N is the predominant form from urban combustion sources, with lower amounts of reduced N from agriculture (Padgett et al., 1999; Fenn et al., 2003). Increasing fire frequencies have also impacted CSS, and areas that burn are more likely to be dominated by exotic grasses (Talluto and Suding, 2008; Fleming et al., 2009). In addition, grasses are likely to promote more frequent fires, thus perpetuating a cycle of grass dominance (D'Antonio and Vitousek, 1992; Minnich and Dezzani, 1998; Cione et al., 2002; Keeley et al., 2005a). The relationship between invasive grasses, fire, and loss of native CSS is exacerbated by nitrogen deposition that increases exotic grass biomass more rapidly than native plants (Weiss, 1999; Allen et al., 2005; Fenn et al., 2010; Kimball et al., 2014). Earlier analyses of N deposition impacts (Talluto and Suding, 2008) did not assess CL because values of N deposition were not available until more recently, or used species loss rather than large-scale vegetation-type conversion as a criterion for CL (Fenn et al., 2010; Pardo et al., 2011).

Our analyses of CSS conversion expand on existing studies by using N deposition values coupled with other variables to set a CL of N for management purposes. We include multiple landscape-scale variables that interact with N deposition including fire, topography, surrounding vegetation, and land-use that may affect the balance between CSS, exotic annual grassland, and conversion between the two. Our analyses compared historic 1930 with current vegetation maps to show both conversion to and recovery from exotic annual grassland. As one of North America's most endangered ecosystems CSS is subject to major restoration efforts (Allen et al., 2000; Bowler, 2000), in part because natural succession seldom results in recovery of native vegetation (Freudenberger et al., 1987; Stylinski and Allen, 1999). We hypothesized that conversion from coastal sage scrub to exotic grassland would be positively associated with nitrogen deposition, aspect, and percent agriculture, development and exotic grassland in the surrounding landscape. We also hypothesized that conversion would be negatively related to fire return interval, percent slope and percent of coastal sage scrub in the surrounding landscape. We expected the opposite relationships for passive recovery of coastal sage scrub from grassland. Such analyses could provide insight into the drivers behind CSS conversion, and also provide information about where conservation and restoration efforts might be most effective. We developed models of CSS conversion to exotic grassland, and of CSS recovery from exotic grassland that incorporate those variables, and compared models to identify those that best approximate the actual data.

2. Material and methods

2.1. Modeling approach

We employed an information theoretic approach to compare models reflecting alternative hypotheses about the importance of various environmental variables in the conversion of coastal sage scrub to exotic grassland between 1930 and 2009 (Burnham and Anderson, 2002; Borgmann and Rodewald, 2006; Hunter et al., 2006). Similarly, we constructed and evaluated models analyzing recovery of CSS from exotic grassland at locations that were mapped in 1930 as grassland or agriculture and had recovered to coastal sage scrub or remained grassland in 2009. We selected environmental variables for modeling that characterized climate, topography, vegetation, land use, fire, and nitrogen deposition.

2.2. Environmental variables used in modeling

The study area encompasses approximately 460,400 hectares in western Riverside County, California (Fig. 1). The study area was defined by the availability of both a digitized 1930 Wieslander Vegetation Type Map (Wieslander, 1935; VTM,

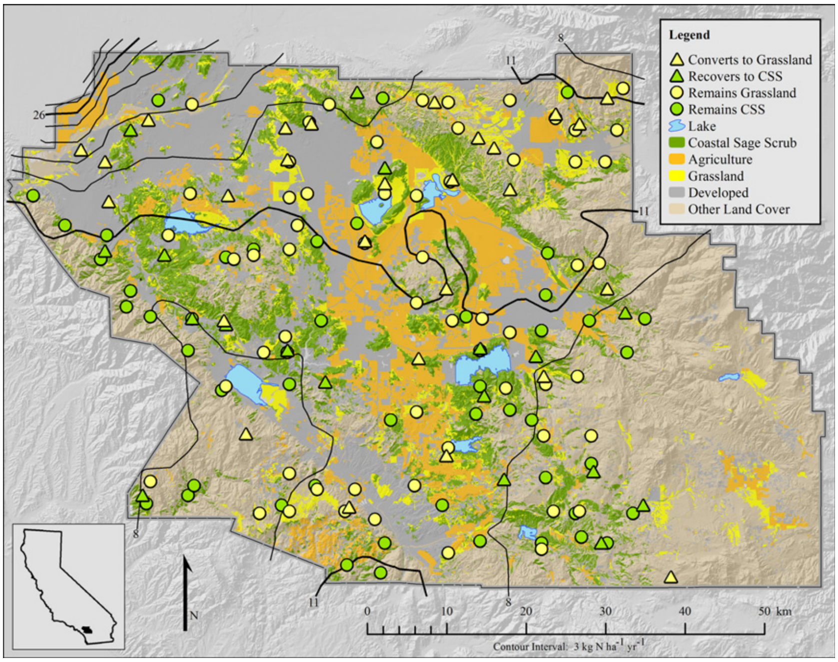


Fig. 1. Location of study area in western Riverside County, California, USA and sampling plots used in modeling conversion of coastal sage scrub to exotic grassland and recovery/natural succession of coastal sage scrub from grassland or agriculture between 1930 and 2009.

2006) and a current digital vegetation map (Klein and Evens, 2005; Evens and Klein, 2006). This study area includes the more arid extent of coastal sage scrub (mean (±SE): 352 ± 7.2 mm) versus that found in southern California from Ventura County south to the international border (mean (±SE): 451 ± 0.4 mm).

Using Geographic Information Systems (GIS) software (ESRI, 2009), we calculated values from digital GIS layers for various measures of climate, topography, vegetation, land use, nitrogen deposition, and fire (Table 1). Variables were calculated for 250 m × 250 m sample plots selected from a grid across the study area (Fig. 2). Plots were nested within 4000 m cells determined by the coarsest resolution GIS layers used to calculate climate and nitrogen deposition variables.

Climate variables were obtained from PRISM digital climate layers (OSU, 2006), and topographic variables were calculated using a 30 m Digital Elevation Model (USGS, 2004). We used the 2002 California Department of Fish and Game (CDFG) vegetation map for western Riverside County (Klein and Evens, 2005; Evens and Klein, 2006) for current vegetation and land use variables. We calculated the percentage of selected land use and vegetation types within 2250 m × 2250 m neighborhoods centered on the 250 m sample plot (Table 1, Fig. 2, Table A.1).

We extracted nitrogen deposition values (reduced plus oxidized N) for 2002 from the CMAQ (Community Multiscale Air Quality) model calculated at a 4000 m × 4000 m scale and encompassing the 250 m sample plots (Tonnesen et al., 2007; Fenn et al., 2010; Table 1, Fig. 2). The model is based on air pollutant emissions inventories available from the Environmental Protection Agency and the Western Regional Air Partnership (Tonnesen et al., 2007). These emissions are chemically transformed using an air chemistry model and moved across the Los Angeles air basin with a meteorological model. Nitrogen deposition in the study area ranges from 5.7 to 23.8 kg N ha^{-1} yr^{-1} (Fenn et al., 2010).

We obtained digital data representing fire perimeters derived from a United States Geological Service (USGS) compilation of Landsat imagery from 1984 through 2005 (USGS 2008). The USGS fire perimeters do not include fires smaller than 405 hectares. To add smaller fires and to provide a more extensive history of fires, we supplemented the USGS fire perimeters with mapped perimeters from 1944 through 2007 obtained from the California Fire and Resource Assessment Program and varying in extent from 0.12 to 27,540 hectares in area. The largest of these fires lies mostly outside the study extent so that the portion of the largest fires covers no more than approximately 12,000 ha within the study area (FRAP; CDF, 2008). After merging these two datasets, we calculated the time since the most recent fire for each 250 m sample plot (Table 1). We omitted from our analyses sample plots that burned after 2003, since inland CSS vegetation communities in these areas likely take longer than 6 years to fully recover (Fleming et al., 2009; Keeley et al., 2005b), such that grass dominance at such sites could be a function of short successional time rather than vegetation-type conversion. This means that our analysis considers CSS conversion and recovery in areas that have not burned recently, and for which the fire return interval may be approximately equal to the natural fire return interval of CSS, which is about 30–40 years (Keeley et al., 2005b).

To quantify vegetation changes over the eighty year period, we compared sample plots between a 1930 vegetation map with the 2002 CDFG vegetation map updated to reflect 2009 conditions for the set of modeling sample plots. For the historic vegetation, we digitized 1930 Wieslander Vegetation Type Maps (VTMs; Wieslander, 1935; VTM, 2006) for western Riverside County which were drawn at a scale of 1:125,000 and enlarged to 1:62,500 for recording field observations. To calculate

Table 1
Environmental variables used in modeling conversion and recovery of coastal sage scrub in western Riverside County.

Type of variable	Variable vode	Description of environmental variables used in modeling
Topography[1]	EAST	Median value of eastern aspect [East = sin(aspect)] for an 8 × 8 cell neighborhood at 30 m resolution within the 250 m sample plot. Domain: −0.999 to 0.998. Due east is 1.000 and due west is −1.000.
	NORTH	Median value of northern aspect [North = cos(aspect)] for an 8 × 8 cell neighborhood at 30 m resolution within the 250 m sample plot. Domain: −0.999 to 1.000. Due north is 1.000 and due south is −1.000.
	SLOPE	Median slope for an 8 × 8 cell neighborhood at 30 m resolution encompassing the sample point. Unit: degrees above horizontal.
Climate[2]	PRECIP	Average annual precipitation (mm) from 1931–2000 extracted at the center of the 4000 m cell.
	TEMPMAX	Average maximum temperature (°C) for the month of July from 1931–2000 extracted from the center of the 4000 m cell.
	TEMPMIN	Average minimum temperature (° C) for the month of January from 1931–2000 extracted from the center of the 4000 m cell.
Vegetation[3]	CHAP	Landscape-scale; percent chaparral within a 2250 m × 2250 m neighborhood encompassing the 250 m sample plot.
	CSS	Landscape-scale; percent coastal sage scrub (as above).
	GRASS	Landscape-scale; percent of exotic grassland (as above).
Land Use[3]	AG	Landscape-scale; percent of agricultural lands within a 2250 m × 2250 m neighborhood encompassing the 250 m sample plot.
	DEV	Landscape-scale; percent of developed lands (as above).
Fire[4]	TIMEFIRE	Time since most recent fire assessed for the 250 m sample plot.
Nitrogen[5]	NITRO	Total nitrogen deposition (wet & dry) in kg N/ha/yr obtained from Tonnesen et al. (2007) model, from the center of the 4000 m cell.

[1] National Elevation Dataset, 1 arc-second (30m) resolution (USGS, 2004).
[2] PRISM temperature and precipitation data, 2.5 arc-minute (4000 m) resolution (OSU, 2006).
[3] Vegetation map of western Riverside County, 6 m resolution resampled to 30 m (Klein and Evens, 2005).
[4] Fire perimeters from FRAP, vary from 0.12 to 27,540 ha minimum fire extents, depending on the date of fire and the source (CDF, 2008) and MTBS, 30 m resolution (USGS, 2008).
[5] Community Multiscale Air Quality model year 2002 output, 4000 m resolution (Tonnesen et al., 2007).

current vegetation and land use variables we used the CDFG vegetation map at a scale of 1:12,000. We updated the 2002 CDFG map with satellite imagery to delineate urban and rural development through 2005 (Preston and Rotenberry, 2007). We further updated status of fire history, vegetation, and land use at sample plots selected for modeling using 2002 through 2009 Google Earth aerial imagery. Based upon these maps and the Google Earth assessment we selected our modeling plots from the grid of plots (Fig. 2) within the study area.

2.3. Selection of modeling plots

Conversion of CSS to exotic grass—In order to analyze influential factors in the conversion of CSS to exotic grass, we used the VTM map to identify sample plots in the grid that were classified as coastal sage scrub in 1930. We then selected only those plots that were classified as either coastal sage scrub or exotic grassland in the 2002 composite CDFG vegetation map (Table A.1), and then deleted plots that had burned between 2003 and 2009 to include only locations that had sufficient time to recover to coastal sage scrub. We reduced spatial autocorrelation by selecting one sample plot per 16 km^2 which is the N deposition and precipitation cell size (Table A.1). Next we used Google Earth to inspect the selected sample plots to determine if there were fires not detected in the digital fire history and land use or vegetation changes between 2002 and 2009 within the 250 m sample plot. We omitted any plots that had been converted to agriculture or development or that were no longer coastal sage scrub or exotic grassland. The different scaling of the 1930 and 2002 maps resulted in uncertainty of vegetation identity of some plots that fell on ecotones with chaparral or other vegetation, which were also omitted.

The CDFG map classifies a polygon as a shrubland when there is 10% or greater shrub cover and many polygons identified as coastal sage scrub can be dominated by exotic annual grasses. This lessens the distinction between plots that converted to exotic grassland versus those remaining as coastal sage scrub. Because we were interested in those plots that remained intact as coastal sage scrub with low invasive cover we further screened the dataset to exclude coastal sage scrub plots that were indicated by the CDFG map to be highly invaded by exotic grasses. We excluded 250 m sample plots where the amount of exotic grassland exceeded the amount of coastal sage scrub, as this indicated a local landscape highly degraded by exotic annual grasses. We also used another feature of the CDFG map that classified categories of exotic cover and deleted any plots from the modeling subset where the amount of exotic cover in coastal sage scrub polygons was greater than 25%.

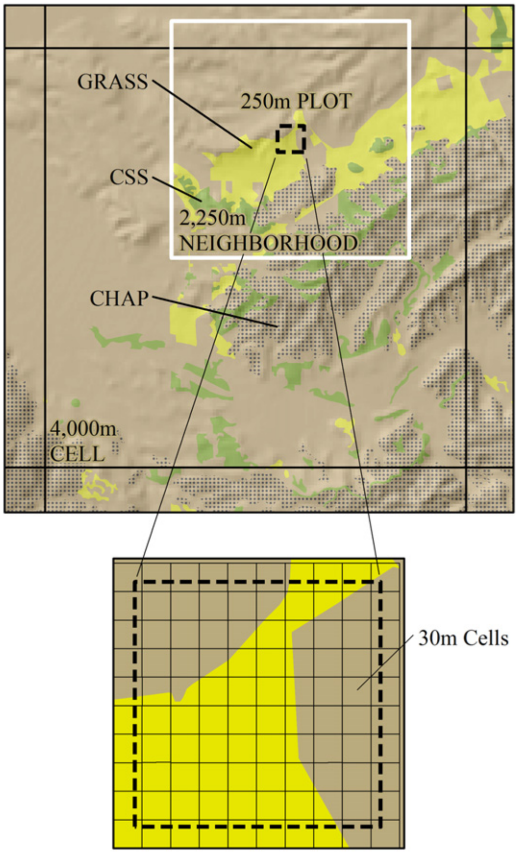


Fig. 2. Example of nested grid method to select a sample plot. The plot illustrated was from a continuous grid of 250 m plots across the study area. The sampled plot chosen was closest to the center of the 4000 m NITRO and PRECIP cell, while meeting other selection criteria per Table 1 and Table A.1. At this map scale, only a selection of vegetation cover types (grass, CSS and chaparral) is displayed; other map units, e.g., agriculture or urban, are not shown.

Coastal sage scrub recovery from exotic grass—We used the VTM map to select from the grid of plots those that were classified as either grassland or agriculture in 1930. Using the composite CDFG map we then selected only plots that had recovered to coastal sage scrub or remained as exotic grassland. As before, we further screened the dataset and removed records classified as coastal sage scrub in the composite CDFG map but which had less than 25% coastal sage scrub within the 250 m sample plot or had more grassland than coastal sage scrub. We were interested in comparing those plots where coastal sage scrub was now dominant and reflected recovery from exotic grass or abandoned agriculture. We also removed current grassland records where the amount of chaparral habitat within the sample plot was greater than the amount of grassland. In this latter case, conversion of chaparral to grassland reflects different processes than coastal sage scrub type conversion to grassland and was not the objective of our analyses. We used the remaining grid plots ($n = 151$) as our modeling dataset, representing 2009 (with most recent burn date of 2003) coastal sage scrub plots that had recovered from grassland or agriculture in 1930 and plots that had remained as exotic grassland.

2.4. Model construction and evaluation

An information theoretic approach compares models with different combinations of variables to find the model or collection of models that best approximates the "truth" which cannot be known from empirical data (Burnham and Anderson, 2002). We avoided taking an exploratory approach to model construction and did not construct models with all possible subsets of variables or interactions between variables. The models to be compared were constructed *a priori* based upon scientific knowledge (Burnham and Anderson, 2002). For our analyses, we developed a set of logistic regression models with different combinations of environmental variables hypothesized to be associated with conversion of coastal sage scrub to exotic grassland in the last eighty years.

To analyze the conversion of CSS to exotic grass, we constructed a global model which included all selected variables and compared its performance with models consisting of subsets of the selected variables as well as the global model with the addition of an interaction between nitrogen deposition and aspect, both important variables in a prior study on CSS conversion (Talluto and Suding, 2008). A second set of logistic regression models analyzed natural succession or recovery of coastal sage scrub in 2009 from an initial state in 1930 of exotic grassland or agriculture. Our analyses were conducted using

R version 3.0.2 (R Core Team, 2013) and SAS statistical software (SAS Institute, 2013). For every environmental predictor, we ran a logistic regression model for conversion and for passive recovery response to assess residuals for normality. Predictor variables with Pearson Residuals $\leq$3.0 and ≥ -3.0 were included in models.

To evaluate model performance and select the best approximating model(s), we used Akaike's information criterion (AICc; Burnham and Anderson, 2002) adjusted for small sample sizes. We chose the model with the lowest AIC$_c$ value and subtracted this value from the AIC$_c$ values of other models to calculate a difference in AIC$_c$ (Δ_i) for each model. We calculated Akaike weights (ω_i) for each model representing the probability that the model is the actual best approximating model for the data sample considered. We also calculated an evidence ratio based on model weights for pairwise comparisons of the top performing model relative to each other model. The evidence ratio for each pairwise comparison gives the probability that the top-ranked model is likely to be correct relative to the other model under comparison. For each set of analyses, we evaluated the overall fit of the global model using log likelihood ratios. Based upon cumulative Akaike weights, we identified $\geq$95% confidence subsets of best approximating models for each set of analyses. To avoid multicollinearity issues, we did not include independent variables with bivariate correlations $>$0.70 in the same model (Tabachnick and Fidell, 2001). We screened for multicollinearity after models were constructed, eliminating models from further consideration that had variable tolerances $<$0.10 or condition index values $>$30. To replace models exhibiting multicollinearity, we constructed new models with a subset of the original variables, excluding those variables that were not as relevant to our interest in identifying anthropogenic factors associated with conversion and restoration of CSS. We imported the residuals of the global model into GIS and conducted a Moran's I spatial autocorrelation analysis to see if there was significant spatial autocorrelation.

For the $\geq$95% confidence subset of best performing models we identified variables that were important in distinguishing between locations converting from coastal sage scrub to grassland versus those remaining the same. We identified important variables as those in which the predictor variable contributed substantially to the probability of conversion to exotic grassland. We used the GLM Predict function in R version 3.0.2 (R Core Team, 2013) to plot the probability of conversion for the best performing model as a function of a single predictor variable with all other predictors held constant at their mean value. Similarly, we identified important variables in the top-ranking models distinguishing between grassland/agriculture locations that recovered to coastal sage scrub or remained grassland.

3. Results

Using the model selection criteria we reduced the number of plots to 151 for analysis of CSS conversion and recovery between 1930 and 2009 (Table A.1). These plots were spread out across the landscape at a density of no more than one sampling location per 16 km^2. There was no spatial autocorrelation in the residuals for the global models for conversion (Moran's Index: −0.029; z-score: −0.879; p-value: 0.379) or for restoration (Moran's Index: −0.041; z-score: −1.566; p-value: 0.117).

3.1. Coastal sage scrub conversion to exotic grassland

From the initial dataset of plots that were CSS in 1930, we selected those plots that represented relatively intact coastal sage scrub resulting in 76 plots that were approximately normally distributed to use in our modeling (Table A.1, Fig. 1). Of these, 34.2% converted to exotic grassland, while 65.8% remained relatively intact coastal sage scrub.

Chaparral and climate variables (climate is consistent across this region) were highly correlated with other variables resulting in multicollinearity. Therefore, we excluded these variables from the global model as they were not considered to be as important in predicting type conversion as variables that were included in the model. The resulting global model was the best performing model in predicting conversion of coastal sage scrub to exotic grassland and had a weight (ω_i) of 1.0 (Table 2). The global model with interaction between nitrogen and north was omitted from the model set due to poor model fit. Using maximum likelihood and the logit transform function, the y-intercept and parameter estimates of best fitting data were determined for the global model predicting the probability of CSS conversion (Table 3).

The most important variables in the global model were those that contributed substantially to the probability a sample plot that was CSS in 1930 would convert to exotic grassland in 2009. This was determined by using the R GLM Predict function to plot the probability of conversion for the global model as a function of a single predictor with all other variables in the model held constant at their mean values (Fig. 3a–i). The Predict function analysis shows that nitrogen deposition values of 6–11 kg N ha^{-1} yr^{-1} contributed little to the probability of converting (probability $<$0.03; Fig. 3a). There was a sharp increase in slope of the curve above 11 kg N ha^{-1} yr^{-1}, suggesting a rapid rate of increase in conversion to grassland above this value. At 12.0 kg N ha^{-1} yr^{-1} the probability was 0.11 and at 20 kg N ha^{-1} yr^{-1} it reached 1.0 (Fig. 3a). Hill slopes of $>$10% contributed little to the probability of converting, whereas hill slopes of $\leq$5% had a probability equal to 1.0 (Fig. 3b). Converted sample plots in our modeling dataset had on average higher levels of nitrogen deposition (mean (±SE) 11.8 (±0.5) vs. 9.3 (±0.3) kg N ha^{-1} yr^{-1}) and shallower hill slopes (6.7° (±0.8) vs. 15.2° (±1.2) than sample plots that remained coastal sage scrub. Plots facing due west had a probability of 0.25 of converting to exotic grassland (Fig. 3c). At plots that had burned within the last 10 years, the probability was 0.23 for conversion (Fig. 3e). Plots with $\geq$80% of grassland in the surrounding landscape had probability of 0.56 of converting to exotic grassland (Fig. 3i). The remaining variables (north, development,

Table 2
Models relating climate, topography, native vegetation, nitrogen deposition, land use and fire to the conversion of coastal sage scrub to exotic grassland over an 80 year period. Models highlighted in bold form >95% confidence subset of best approximating models with the highest ranking model shaded in gray. *K* represents the number of model parameters, Δ_i is the difference in AIC$_c$ values for each model relative to the model with the lowest AIC$_c$, ω_i is the model weight, and ω_i/ω_1 is the evidence ratio. The model weight represents the probability that the model is the best approximating model and the evidence ratio is the relative likelihood that the top ranked model is the best performing model compared to another model in the set. Variables are defined in Table 1.

Model type	Model parameters	K	Δ_i	ω_i	ω_i/ω_1
Global Model[*]	**EAST, NORTH, SLOPE, TIMEFIRE, NITRO, AG, DEV, CSS, GRASS**	**11**	**0.000**	**1.000**	
Topography	EAST, NORTH, SLOPE	5	21.585	0.000	344,828
Vegetation	CHAP, CSS, GRASS	5	24.886	0.000	>344,828
Nitrogen	NITRO	3	33.394	0.000	>344,828
Climate	PRECIP, TEMPMIN, TEMPMAX	5	48.696	0.000	>344,828
Land Use	AG, DEV	4	48.727	0.000	>344,828
Fire	TIMEFIRE	3	48.896	0.000	>344,828

[*] CHAP and climate variables excluded from the global model because of multicollinearity.

Table 3
Maximum likelihood parameter estimates and standard errors determining the shape of the predictive function for the top performing logistic regression model to distinguish between coastal sage scrub plots that converted to grassland and those remaining as coastal sage scrub.

Variable	Parameter estimate	SE
Intercept	−1.53	3.08
EAST	−4.08	1.45
NORTH	−0.58	1.32
SLOPE	−0.93	0.37
NITRO	1.27	0.49
TIMEFIRE	−0.11	0.06
AG	−0.04	0.05
DEV	−0.04	0.03
CSS	−0.01	0.04
GRASS	0.07	0.05

agriculture, and coastal sage scrub) were included in the top ranked model but did not contribute substantially (probability <0.05) to the probability of conversion. Our sample of plots represented a natural fire interval, with average of 41.4 ± 3.1 (SE) years since the most recent fire for plots that remained CSS and an average of 42.4 ± 3.1 (SE) for plots that converted from CSS to grassland.

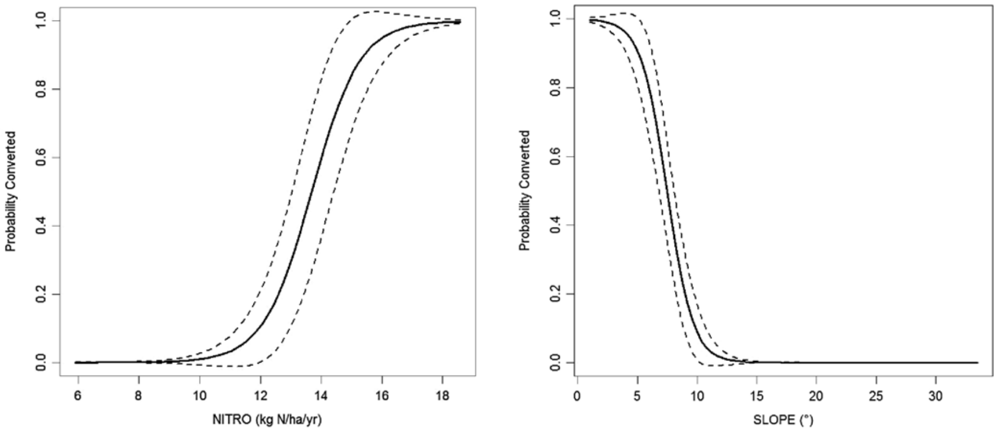
3.2. Natural succession from grassland and agriculture to coastal sage scrub

We identified a total of 75 locations that had been agriculture or exotic grassland in 1930 and either remained grassland or recovered to intact coastal sage scrub over the eighty year period (Fig. 1). There were far fewer records of natural succession (22.7%) than of those remaining exotic grassland (77.3%).

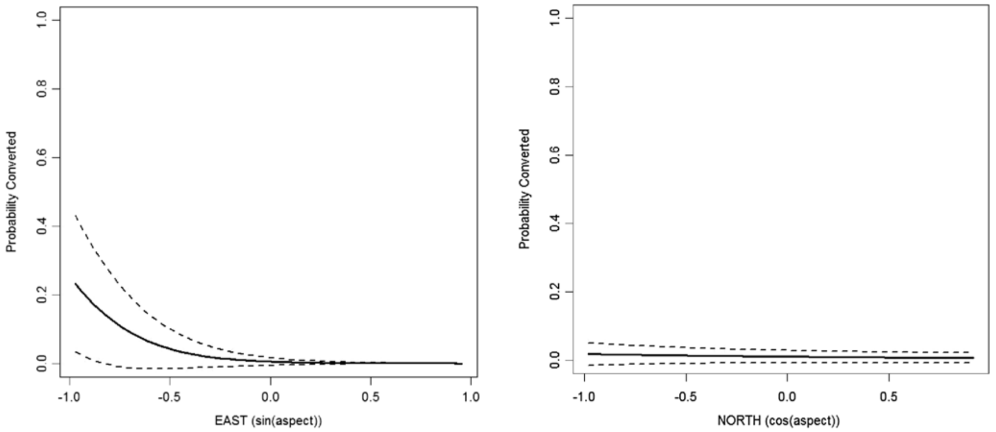
Unlike the conversion analysis, the top performing model predicting natural succession or recovery of coastal sage scrub included only vegetation variables with a weight of 0.88 (Table 4). Table 5 lists the y-intercept and parameter estimates for the logistic function predicting passive recovery of coastal sage scrub at the sample plots. Only two variables showed substantial contributions to the recovery of CSS from grassland and agriculture when other variables were held constant at their mean values (Fig. 4a–c). Recovered plots had 4.5 times less grassland within 2250 m neighborhoods (4.9% vs, 22.3%) and 2.5 times more CSS (35.5% vs. 14.3%). Plots with 60% CSS cover in the surrounding area had a probability of 0.46 of recovery and this probability increased to 0.95 at 80% CSS cover (Fig. 4a). Sample plots with little or no exotic grassland in the neighborhood had a probability of recovery of 0.76, whereas probabilities were <0.01 as percent grass in the neighborhood increased to 20% (Fig. 4b).

4. Discussion

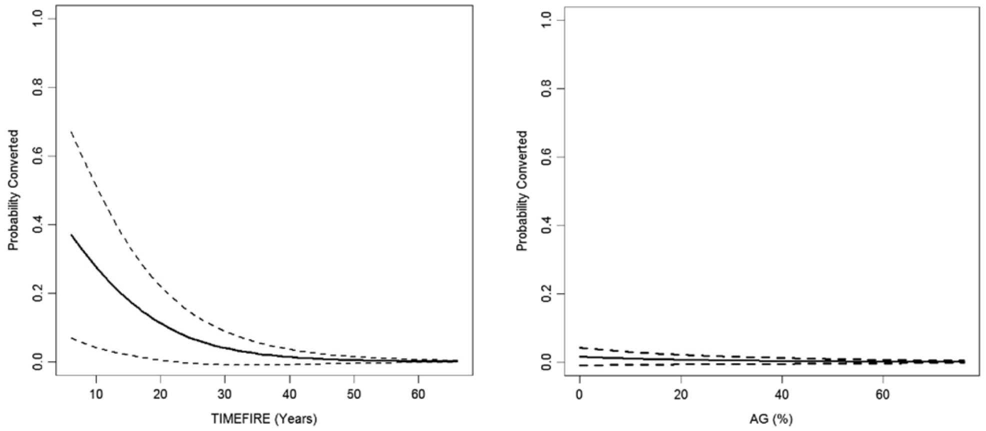
At fire intervals close to those hypothesized as normal for undisturbed CSS, this endangered vegetation type appears most vulnerable to conversion to exotic grassland in areas with elevated levels of nitrogen deposition and on shallow west-facing slopes. Experimental evidence for vegetation-type conversion comes from nitrogen fertilization studies that caused increased exotic grass and decreased shrub cover (Kimball et al., 2014). Talluto and Suding (2008) also found that deposition of nitrogen could contribute to CSS conversion under a normal fire regime. However, their analyses were based on leaf δ^{14}C as a surrogate for pollution that originates from combustion, while our analysis used the more recently developed CMAQ model of N deposition for California (Fenn et al., 2010). Using these modeled data, we calculated that sample plots with <11 kg N ha^{-1} yr^{-1} were less likely to convert from CSS to exotic grassland, and we suggest that this is the critical load



(a) Nitrogen. (b) Slope.



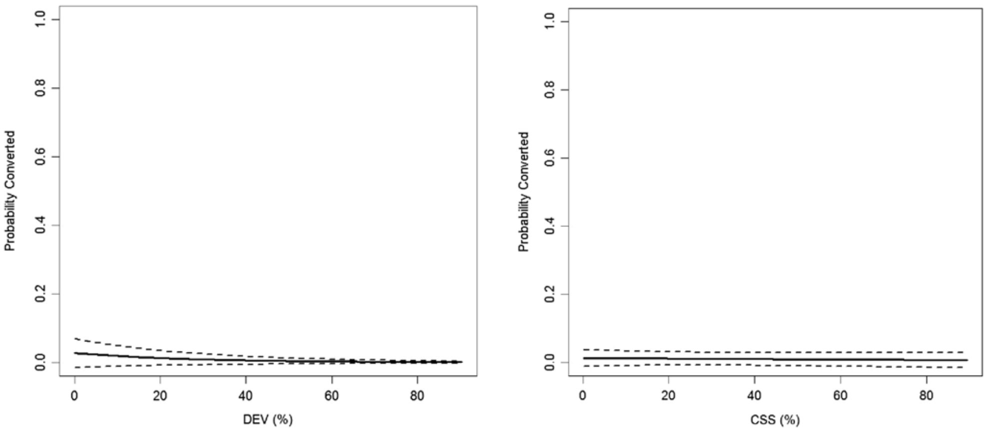
(c) East. (d) North.



(e) Time since most recent fire. (f) Agriculture.

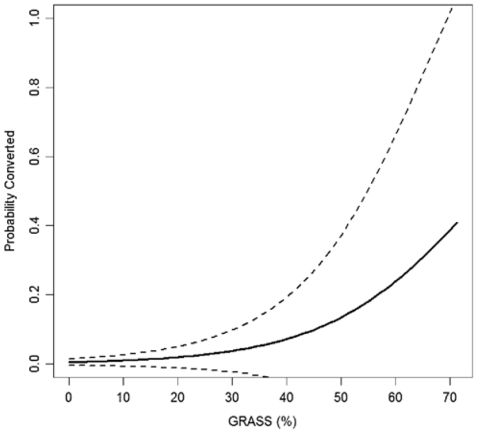
Fig. 3. Probability of converting from coastal sage scrub in 1930 to exotic grassland in 2009 as a function of single predictor variables included in the best approximating model with all other variables held constant at their mean value.

of N for conversion of CSS to grassland. In an analysis that used declining species diversity as a criterion for response to N deposition, 10 kg N ha^{-1} yr^{-1} was estimated to be the CL for loss of native forb richness and mycorrhizal fungal richness across the same CSS gradient (Fenn et al., 2010; Pardo et al., 2011). Thus the conversion to exotic annual grassland and the loss of native plant and fungal diversity can both be attributed to a similar level of N deposition (10 to 11 kg N ha^{-1} yr^{-1}).



(g) Development.

(h) Coastal sage scrub.



(i) Exotic annual grassland.

Fig. 3. (*continued*)

Table 4

Models relating climate, topography, native vegetation, nitrogen deposition, land use and fire to the natural succession of coastal sage scrub from exotic grassland and agriculture over an 80 year period. Models highlighted in bold form >95% confidence subset of best approximating models with the highest ranking model shaded in gray. K represents the number of model parameters, Δ_i is the difference in AIC$_c$ values for each model relative to the model with the lowest AIC$_c$, ω_i is the model weight, and ω_i/ω_1 is the evidence ratio. The model weight represents the probability that the model is the best approximating model and the evidence ratio is the relative likelihood that the top ranked model is the best performing model compared to another model in the set. Variables are defined in Table 1.

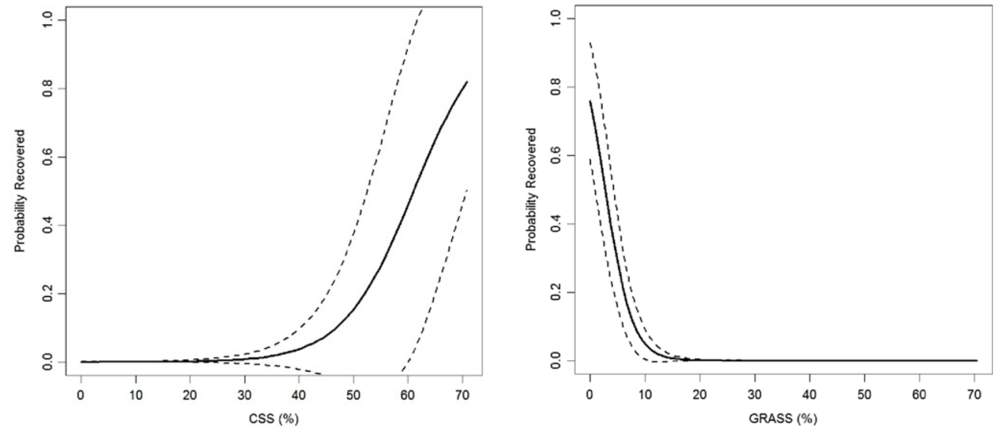
Model type	Model parameters	K	Δ_i	ω_i	ω_i/ω_1
Vegetation	**CHAP, CSS, GRASS**	**5**	**0.000**	**0.884**	
Global Model[*]	**EAST, NORTH, SLOPE, NITRO, AG, DEV, CSS, GRASS**	**10**	**4.063**	**0.116**	**8**
Topography	EAST, NORTH, SLOPE	5	29.218	0.000	2114,833
Nitrogen	NITRO	3	50.382	0.000	>2114,833
Fire	TIMEFIRE	3	55.090	0.000	>2114,833
Land Use	AG, DEV	4	54.318	0.000	>2114,833
Climate	PRECIP, TEMPMIN, TEMPMAX	5	55.984	0.000	>2114,833

[*] CHAP and climate variables excluded from the global model because of multicollinearity.

Table 5

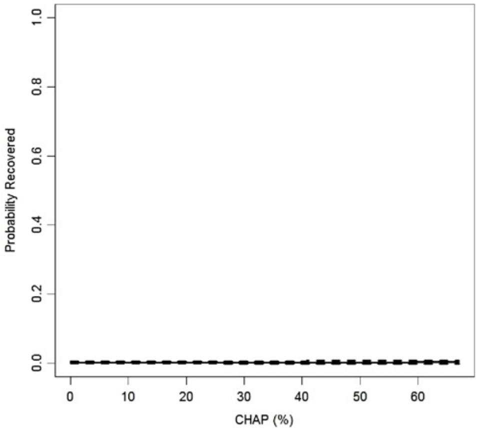
Maximum likelihood parameter estimates and standard errors determining the shape of the predictive function for the top performing logistic regression model to distinguish between grassland plots that passively recovered to coastal sage scrub and those remaining as grassland.

Variable	Parameter estimate	SE
Intercept	−1.96	1.54
CHAP	0.01	0.03
CSS	**0.15**	**0.05**
GRASS	**−0.42**	**0.14**



(a) Coastal Sage Scrub.

(b) Grassland.



(c) Chaparral.

Fig. 4. Probability of passively recovering from grassland in 1930 to coastal sage scrub in 2009 as a function of individual predictor variables included in the best approximating model with all other variables held constant at their mean value.

Like Freudenberger et al. (1987) and Callaway and Davis (1993), we also found that CSS can be resilient to disturbance, recovering from exotic grasses, though at relatively low rates. While nitrogen levels affected conversion to exotic grassland, nitrogen levels did not significantly influence recovery from exotic grass domination. This suggests that recovery of CSS may also be controlled by other factors such as interactions of invasive and native plants (Eliason and Allen, 1997) or disturbance history of a site (Stylinski and Allen, 1999). Recovered patches were more likely to occur in areas with less grassland and more intact CSS vegetation in the surrounding area (within the 2250 m neighborhood of the sample plot). Although our analysis does not account for intensity and type of surrounding land use during the last ~80 years, we still identify present day factors associated with conversion and recovery. This indicates natural recovery is dependent on seed sources from the surrounding neighborhood, whether CSS or exotic grass. Restoration ecologists typically make up for seed limitation by planting seeds (Cox and Allen, 2008), but our analyses indicate that artificial restoration of an area with >11 kg N ha^{-1} yr^{-1} will eventually revert to exotic grassland even under normal fire regimes, especially if exotic grassland dominates the neighborhood.

Analyses of vegetation change typically identify multiple drivers, among which N deposition has figured strongly in European studies (Payne et al., 2011; Verheyen et al., 2012) and was a strong driver in our study. We omitted grazing as a landscape-scale driver. The earliest attempts to find an explanation for CSS conversion to exotic grasses focused on the effects of grazing (Burcham, 1957). However, much of the observed conversion of CSS occurred more recently than the grazing hypothesis would support, since most extensive grazing ended early in the 1900s in western Riverside County (Robinson and Risher, 1993). Subsequent explanations have settled on fire (Minnich and Dezzani, 1998; Talluto and Suding, 2008; Fleming et al., 2009), urbanization, fragmentation, and "disturbance" corridors (Zink et al., 1995), or the competitive characteristics of the exotic grasses themselves (Eliason and Allen, 1997; Fleming et al., 2009). Type conversion in our study occurred in areas with high N deposition, suggesting a relationship between elevated N and exotic grass productivity. In support of this observation, experimental field N fertilization resulted in increased exotic grass productivity at the expense of native species (Kimball et al., 2014).

Our analysis excluded sites with recent fire (since 2003), and therefore does not analyze the effect of frequent fire on CSS conversion or recovery. Frequent fire is well known to increase the abundance of exotic grasses in CSS (Allen et al., 2000; Talluto and Suding, 2008; Fleming et al., 2009; Kimball et al., 2014), but we explored the conversion and recovery of CSS in areas for which the fire return interval was approximately normal, or 30–40 years (Keeley et al., 2005b). We find that even under appropriate fire return intervals, CSS may convert to exotic grassland, and our analysis identifies possible drivers. HilleRisLambers et al. (2010) found that such drivers would likely be required for conversion to exotic grasses to persist, at least for the native annuals common to CSS, rather than be inherent characteristics of the exotic grasses themselves. We support this conclusion, and find that for most locations in Riverside County with normal fire intervals, CSS is most at risk when nitrogen deposition is high.

The prominence of geographic factors in our models also agrees with the previous literature. At a larger scale, a geographic component to CSS loss was noted by Taylor (2005), who observed that more CSS is lost in inland than coastal associations. This may be related to water stress, as inland stands of CSS tend to experience higher summer temperatures (Westman, 1981). Experimental drought increased CSS shrub mortality and annual grass dominance even in a coastal association (Kimball et al., 2014). Likewise, Talluto and Suding (2008) found that local-scale topography is important; grass abundance was higher on more northern-facing slopes, especially with high fire frequency. Our analysis showed an increased probability of conversion on west but not north-facing slopes. This may be because we only included sites that had not burned recently. We also calculated greater conversion to grass on shallow rather than steep west-facing slopes. This may be because grasses tend to perform better in deeper soils near valley bottoms than rocky hillsides (Wood et al., 2006). Also, valley bottoms were converted to agriculture prior to the 1930 VTM survey (VTM, 2006), and adjacent shallow slopes may have experienced invasion from fallow croplands, as suggested by our analysis that showed importance of adjacent vegetation type.

Studies on CSS conversion may overestimate historic exotic annual grassland that may have been native annual forblands, a vegetation type that has only recently been recognized (Minnich, 2008). Uncertainty in the amount of CSS remaining (estimated as 10%–40%) may derive in part from areas that were mapped as potential CSS by Küchler (USBR, 1996) but that may actually have been annual forblands, and converted to exotic annual grassland before modern botanical surveys. Because of the potential occurrence of native annual forblands (Minnich, 2008), some areas classified as grassland in the VTM map may actually have been native forbs. The 1930's VTM mapping crew would have classified any forb–grass mix as annual grassland, as there is no further classification of this vegetation type (VTM, 2006). This would tend to produce more exotic grassland that stayed exotic grassland. We hypothesize that exotic grassland can convert to CSS, but if CSS was never in that location because it was originally forbland, then we have overestimated the potential for CSS recovery. Conversely, points that were originally CSS and converted to annual grassland would have been accurately classified in the 1930s.

4.1. Conclusions

Multivariate analyses of drivers of vegetation change have shown that nitrogen may be one of several variables, as was shown in European forests (Verheyen et al., 2012). Our analysis shows that the amount and type of vegetation in the surrounding landscape plays a role in the recovery of CSS. Managers of CSS preserves may be best served by working to protect CSS patches existing in the most resilient locations. We suggest that conservation and restoration efforts are best applied to those areas where success is most likely: areas with nitrogen deposition <11 kg N ha^{-1} $\mathrm{yr}^{-1}$and steeper slopes with ample CSS in the neighborhood. There was no significant threshold value of N for recovery, but the percentage of land in the local area dominated by CSS was important in determining recovery. Since N deposition drives the loss of CSS, actively restored sites would revert to exotic grass under high deposition. Large-scale, comprehensive plans that address both nitrogen deposition and regional abundances of exotic grasses may be the best option for conserving this unique vegetation type.

Managing N deposition rates may provide the greatest hope for conserving CCS. The modeled N deposition in the study area varies from 5.3 to 23.8 kg N ha^{-1} yr^{-1} (Fenn et al., 2010). Our analyses suggest that permanent vegetation type conversion to exotic grassland can be reduced if N deposition is ≤ 11 kg N ha^{-1} yr^{-1}under normal fire regimes. However, fire frequency may increase under elevated exotic grass biomass; fire risk increased with elevated N deposition in desert scrub at a threshold of 3 kg N ha^{-1} yr^{-1} up to a stabilization point (where increased N no longer elevated fire risk) of 9 kg N ha^{-1} yr^{-1} Rao et al. (2010). While the current analysis in CSS does not enable us to set minimum N deposition values for increased fire risk, we have refined the CL for conversion to exotic grass and supported a previous CL that used species loss criteria (Fenn et al., 2010). Regulatory policy based on CL has been implemented in Europe and Canada and is gaining momentum in the United States (Pardo et al., 2011; Porter et al., 2005; Blett et al., 2014) and may provide further protection for vegetation sensitive to N deposition.

Acknowledgments

We thank Christopher Clark for reviewing the manuscript, Darrel Jenerette for advice, and Jeff Tracey for help with R coding. This research was supported by National Science Foundation grant DEB 04-21530 and the Center for Conservation Biology, UC Riverside.

Table A.1
Steps involved in developing datasets to model conversion of coastal sage scrub to exotic grassland and recovery of exotic grassland and agriculture to coastal sage scrub. Included are sample sizes of initial, interim and final modeling datasets.

Steps used in selecting sample plots for conversion and restoration modeling datasets	Conversion dataset sample sizes	Recovery dataset sample sizes
We developed a grid of 250 × 250 m sample plots characterizing environmental conditions across the 460,400 ha study area	73,663	73,663
We used the combined USGS and FRAP fire history GIS layer to delete sample plots burned after 2003, since these sites would have insufficient time to recover to coastal sage scrub.	68,117	68,117
We selected sample plots that were coastal sage scrub in the 1930 Wieslander Vegetation Type Map and were coastal sage scrub or exotic grassland in the 2002 California Department of Fish and Game vegetation map for western Riverside County.	7029	
We selected sample plots that were exotic grassland or agriculture in the 1930 Wieslander Vegetation Type Map (VTM) and were coastal sage scrub or exotic grassland in the 2002 California Department of Fish and Game vegetation map.		3774
We reduced spatial autocorrelation for each dataset by systematically selecting one sample plot per 16 km^2 area represented by a single 4000 m cell for climate and nitrogen values. The sample plot closest to the center of each cell was selected and retained only if it was further than 1000 m from any other sample plot in the same dataset.	212	231
We used Google Earth to view sample plots and update vegetation, land use and fire history through 2009. We deleted sample plots showing signs of recent fire or that were converted to agriculture or development.	176	184
The California Department of Fish and Game vegetation map categorizes shrub vegetation as having $\geq$10% shrub cover. Sample plots identified as coastal sage scrub may be highly invaded with exotic cover dominant over shrub cover. We used features of the vegetation map categorizing shrub density and exotic cover to ensure comparisons were between relatively intact coastal sage scrub and exotic grassland. We first reviewed the percentage of coastal sage scrub and exotic grassland cover within the 250 m sample plot and deleted plots identified as coastal sage scrub but where the percent cover of exotic grassland exceeded that of coastal sage scrub and vice versa. We then deleted coastal sage scrub sample plots where the majority of scrub had a shrub cover less than 25% and exotic cover exceeded 25%.	91	96
Adequacy of values for time since most recent fire calculated from our compiled USGS and FRAP data was checked against the fire history interpreted from a time-series of aerial imagery.	87	90
Sample plot locations were compared against 1938 aerial photographs to confirm VTM cover type. Plots with the incorrect historic cover type were deleted and the 1st, 2nd, or 3rd closest neighbor sample plot was substituted if it met other selection criteria.	77	76
Single predictor logistic regression models were run for each environmental variable and the residuals evaluated for normality. Extreme outlier sample plots having Pearson Residuals $\geq$3.0 or $\leq$-3.0 were then excluded from the modeling.	76	75

Appendix

See Table A.1.

References

Allen, E.B., Eliason, S.A., Marquez, V.J., Schultz, G.P., Storms, N.K., Stylinski, C.D., Zink, T.A., Allen, M.F., 2000. What are the limits to restoration of coastal sage scrub in southern California?. In: Keeley, J.E., Keeley, M.B., Fotheringham, C.J. (Eds.), 2nd Interface Between Ecology and Land Development in California. U.S. Geological Survey, Sacramento, CA, USA, pp. 253–262.

Allen, E.B., Padgett, P.E., Bytnerowicz, A., Minnich, R.A., 1998. Nitrogen deposition effects on coastal sage vegetation of southern California, In: Bytnerowicz A., Arbaugh M.J., Schilling S. (Tech coords.), Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems. Riverside CA Feb 1996. Albany, CA: USDA Forest Service, Pacific Southwest Research Station, Gen. Tech. Rep. PSW-GTR-166, pp. 131–140.

Allen, E.B., Sirulnik, A.G., Egerton-Warburton, L., Kee, S.N., Byntnerowicz, A., Padgett, P.E., Temple, P.J., Bytnerowicz, A., Padgett, P.E., Temple, P.J., Fenn, M.E., Poth, M.A., Meixner, T., 2005. Air pollution and vegetation change in Southern California coastal sage scrub: a comparison with chaparral and coniferous forest, in: Kus, B.E., Beyers, J.L., (Tech coords.), Planning for Biodiversity: Bringing Research and Management Together. Albany, CA: USDA Forest Service, Pacific Southwest Research Station, Gen. Tech. Rep. PSW-GTR-195, pp. 79–95.

Blett, T.F., Lynch, J.A., Pardo, L.H., Huber, C., Haeuber, R., Pouyat, R., 2014. FOCUS: A pilot study for national-scale critical loads development in the United States. Environ. Science Policy 38, 225–236.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bostamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59.

Borgmann, K.L., Rodewald, A.D., 2006. Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. Restor. Ecol. 13, 334–340.

Bowler, P.A., 2000. Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. Environ. Manage. 26, S85–S86. supp.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677–688.

Brooks, M.L., Pyke, D.A., 2001. Invasive plants and fire in the deserts of North America, in: Galley, K.E.M., Wilson, T.P., (Eds.), Proceedings of the Invasive Species Workshop: The Role of Fire in the Spread and Control of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Tall Timbers Research Station, Tallahassee, FL. Miscellaneous Publication No. 11, pp. 1–14.

Burcham, L.T., 1957. California rangeland: An historico-ecological study of the range resource of California. Division of Forestry, Department of Natural Resources, Sacramento, CA.

Burnham, K.P., Anderson, D.R., 2002. Model selection and inference: a practical information-theoretic approach, second ed. Springer-Verlag, New York.

Callaway, R.M., Davis, F.W., 1993. Vegetation dynamics, fire and the physical environment in coastal central California. Ecol. 74, 1567–1578.

CDF (California Department of Forestry), 2008. Fire Perimeters. Available online http://frap.cdf.ca.gov/projects/fire_data/fire_perimeters/ (accessed 12.06.08).

Cione, N.K., Padgett, P.E., Allen, E.B., 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. Restor. Ecol. 10, 376–384.

Clark, C.M., Morefield, P.E., Gilliam, F.S., Pardo, L.H., 2013. Estimated losses of plant biodiversity in the United States from historical N deposition (1985–2010). Ecology 94, 1441–1448.

CNPS (California Native Plant Society), 2001. Inventory of rare and endangered plants of California (sixth edition). California Native Plant Society, Sacramento CA.

Cox, R.D., Allen, E.B., 2008. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. Plant Ecol. 198, 37–46.

D'Antonio, C.M., Chambers, J.C., Loh, R., Tunison, J.T., 2009. Applying ecological concepts to the management of widespread grass invasions. In: Inderjit, R.L. (Ed.), Management of Invasive Weeds. Springer, Netherlands, pp. 123–149.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.

DeSimone, S., 1995. California's coastal sage scrub. Fremontia 23 (4), 3–8.

Eliason, S.A., Allen, E.B., 1997. Exotic grass competition in suppressing native shrubland re-establishment. Restor. Ecol. 5, 245–255.

ESRI. 2009. ArcGIS 9.3.1 Geographic Information System. Environmental Systems Research Institute Inc., Redlands, CA, USA.

Evens, J.M., Klein, A.N., 2006. A new model for conservation planning: vegetation mapping in Western Riverside County. Fremontia 34, 11–18.

Fenn, M.E., Allen, E.B., Weiss, S.B., Jovan, S., Geiser, L.H., Tonnesen, G.S., Johnson, R.F., Rao, L.E., Gimeno, B.S., Yuan, F., Meixner, T., Bytnerowicz, A., 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. J. Environ. Manage. 91, 2404–2423.

Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P., 2003. Ecological effects of nitrogen deposition in the Western United States. BioScience 53, 404–420.

Fleming, G.M., Diffendorfer, J.E., Zedler, P.H., 2009. The relative importance of disturbance and exotic-plant abundance in California coastal sage scrub. Ecol. Appl. 19, 2210–2227.

Fox, M.D., 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. In: Di Castri, F., Hansen, A.J., Debussche, M. (Eds.), Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic, Dordrecht, The Netherlands, pp. 179–200.

Freudenberger, D.O., Fish, B.E., Keeley, J.E., 1987. Distribution and stability of grasslands in the Los Angeles Basin. Bull. South Calif. Acad. Sci. 86, 13–26.

HilleRisLambers, J., Yelenik, S.G., Colman, B.P., Levine, J.M., 2010. California annual grass invaders: the drivers or passengers of change? J. Ecol. 98, 1147–1156.

Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., 2006. Establishment of non-native plant species after wildfires, effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. Int. J. Wildland Fire 15, 271–281.

Keeley, J.E., Baer-Keeley, M., Fotheringham, C.J., 2005a. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecol. Appl. 15, 2109–2125.

Keeley, J.E., Fotheringham, C.J., Baer-Keeley, M., 2005b. Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. Ecol. Appl. 15, 1515–1534.

Kimball, S., Goulden, M.L., Suding, K.N., Parker, S., 2014. Altered water and nitrogen input shifts succession in a southern California coastal sage community. Ecol. Appl. 24, 1390–1404.

Klein, A., Evens, J., 2005. Vegetation alliances of Western Riverside County, California. Final report prepared for the California Department of Fish and Game Habitat Conservation Division, Contract Number: P0185404.

Klopatek, J.M., Oson, R.J., Emerson, C.J., Jones, J.L., 1979. Land use conflicts with natural vegetation in the United States. Environ. Conserv. 6, 191–199.

Lenz, T.I., Moyle-Croft, J.L., Facelli, J.M., 2003. Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. Austral. Ecol. 28, 23–32.

Minnich, R.A., 2008. California's Fading Wildflowers. University of California Press, Berkeley, California.

Minnich, R.A., Dezzani, R.J., 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. Western Birds 29, 366–391.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Noss, R.F., Laroei, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. US National Biological Service, Washington, DC. Available at: http://biology.usgs.gov/pubs/ecosys.htm, accessed 25 Apr. 2012 (accessed May 2012).

O'Leary, J., 1995. Coastal sage scrub: threats and current status. Fremontia 23, 27–31.

OSU (Oregon State University), 2006. PRISM digital temperature and precipitation data. Available online at: http://www.prism.oregonstate.edu/ (accessed March 2006).

Padgett, P.E., Allen, E.B., Bytnerowicz, A., Minnich, R.A., 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. Atmos. Environ. 33, 769–781.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., Baron, J., Bobbink, R., Bowman, W.D., Clark, C., Emmett, B., Gilliam, F.S., Greaver, T., Hall, S.J., Lilleskov, E.A., Liu, L., Lynch, J., Nadelhoffer, K., Perakis, S., Robin-Abbott, M.J., Stoddard, J., Weathers, K., Dennis, R.L., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21, 3049–3082.

Payne, R.J., Stevens, C.J., Dise, N.B., Gowing, D.J., Pilkington, M.G., Phoenix, G.K., Emmett, B.A., Ashmore, M.R., 2011. Impacts of atmospheric pollution on the plant communities of British acid grasslands. Environ. Pollut. 159, 2602–2608.

Porter, E., Blett, T., Potter, D.U., Huber, C., 2005. Protecting resources on federal lands: Implications of critical loads for atmospheric deposition of nitrogen and sulfur. Bioscience 55, 603–612.

Preston, K.L., Redak, R.A., Allen, M.F., Rotenberry, J.T., 2012. Changing distribution patterns of an endangered butterfly: Linking local extinction patterns and variable habitat relationships. Biol. Conserv. 152, 280–290.

Preston, K.L., Rotenberry, J.T., 2007. California State Department of Transportation and Center for Conservation Biology: WRC MSHCP niche model task order. Final Report. June 2007. Available online at: http://escholarship.org/uc/item/1ks2h81v (accessed May 2012).

Rao, L.E., Allen, E.B., Meixner, T., 2010. Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts. Ecol. Appl. 20, 1320–1335.

R Core Team. 2013. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org/.

Robinson, J.W., Risher, B.D., 1993. The San Jacintos. Big Santa Anita Historical Society, Arcadia, California.

Rubinoff, D., 2001. Evaluating the California gnatcatcher as an umbrella species for conservation of Southern California coastal sage scrub. Conserv. Biol. 15, 1374–1783.

Rundel, P.W., 2007. Sage scrub. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California, third ed. University of California Press, Berkeley, pp. 208–228.

SAS Institute,, 2013. The SAS System for Windows. Version 9.3, SAS Institute, Cary, North Carolina, USA.

Sawyer, J.O., Keeler-Wolf, T., 1995. A Manual of California Vegetation. California Native Plant Society, Sacramento, CA.

Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.A., 2013. Human population density explains alien species richness in protected areas. Biol. Conserv. 159, 137–147.

Stevens, C.J., Maskell, L.C., Smart, S.M., Caporn, S.J.M., Dise, N.B., Gowing, D.J.G., 2009. Identifying indicators of atmospheric nitrogen deposition impacts in acid grasslands. Biol. Conserv. 142, 2069–2075.

Stylinski, C.D., Allen, E.B, 1999. Lack of native species recovery following severe exotic disturbance in southern California shrublands. J. Appl. Ecol. 36, 544–554.

Tabachnick, B.G., Fidell, L.S., 2001. Using Multivariate Statistics, fourth ed. Harper Collins College Publishers, New York.

Talluto, M.V., Suding, K.N., 2008. Historical change in coastal sage scrub in southern California in relation to fire frequency and air pollution. Landscape Ecol. 23, 803–815.

Taylor, R.S. Jr., 2005. A new look at coastal sage scrub: What 70-Year-Old VTM plot data tell us about Southern California shrublands, in: Kus, B.E., Beyers, J.L., (Tech coords.), Planning for biodiversity: bringing research and management together. Albany, CA: USDA Forest Service, Pacific Southwest Research Station, Gen. Tech. Rep. PSW-GTR-195, pp. 57–77.

Tonnesen, G., Wang, Z., Omary, M., Chien, C.J., 2007. Assessment of nitrogen deposition: Modeling and habitat assessment. California Energy Commission, PIER Energy-Related Environmental Research, CEC-500-2005-032.

USBR (U S Bureau of Reclamation, Mid-Pacific Region, MPGIS Service), 1996. Digital representation of Küchler vegetation potential map for California: Natural Vegetation of California (1977) by A.W. Küchler. Original map was prepared in conjunction with the publication of Barbour, M.G., Major, J. (Eds.) 1977. Terrestrial Vegetation of California. California Native Plant Society, Sacramento.

USGS (United States Geological Survey), 2004. National Elevation Dataset, Digital Elevation Model. Available online at: http://data.geocomm.com/ (accessed March 2004).

USGS (United States Geological Survey), 2008. Burn Severity and Fire Perimeters. Available online at: http://www.mtbs.gov (accessed November 17–18, 2008).

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Romermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hedl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petrik, P., Pfadenhauer, J., Van Calster, H., Walther, G.R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. J. Ecol. 100, 352–365.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

VTM. 2006. Wieslander vegetation type mapping. College of Natural Resources, Geospatial Imaging and Informatics Facility, UC Berkeley. Available online at: http://vtm.berkeley.edu (accessed 13.11.06.

Weiss, S.B., 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conserv. Biol. 13, 1476–1486.

Westman, W.E., 1981. Factors influencing the distribution of species of coastal sage scrub. Ecology 62, 439–455.

Wieslander, A.E., 1935. A vegetation type map of California. Madroño 3, 140–144.

Wood, Y.A., Meixner, T., Shouse, P.J., Allen, E.B., 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated N-deposition. J. Environ. Qual. 35, 76–92.

Zink, T.A., Allen, M.F., Heindl-Tenhunen, B.I., Allen, E.B., 1995. The effect of a disturbance corridor on an ecological reserve. Restor. Ecol. 3, 304–311.