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

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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

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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,