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Soil nitrogen cycling is resilient to invasive annuals following restoration of coastal sage scrub

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ABSTRACT

Southern California coastal sage scrub (CSS) is highly invaded by Mediterranean annual grasses and undergoing extensive restoration efforts. Exotic plant invasion alters ecosystem structure and function through plant-soil feedbacks that can be detrimental to native plants. Assessments of CSS restoration have focused on aboveground plant communities, while belowground effects have received less attention. We examined CSS soil resilience following restoration of native CSS species using ecosystem property divergence in restorations from an invaded state as a measure of exotic plant impacts. We hypothesized that exotic annual plants compete with native species for nutrients and change nutrient cycling, and exotic plant removal and native plant restoration would allow soil recovery under native plant-soil inputs. Nitrogen (N) cycling was resilient but not resistant to vegetation changes. Exotic annual plants increased N mineralization and nitrification but did not affect total soil carbon (C) and N and extractable phosphorus. Extractable N was reduced in invaded plots, and immediately increased following weeding. These changes suggest that exotic plants are directly competing with native plants for N. Impacts to N cycling were reversible after exotic plants were removed and native shrubs reestablished, which may have important implications for recovery of other ecosystems invaded by annual grasses.

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1. Introduction

Invasion of exotic species offers the opportunity to assess ecosystem resistance to invasion-caused impacts, and resilience of the system once invasives are removed. Resistant ecosystems would remain unaltered by an invading species such that soil nutrient pools would remain unchanged. Ecosystems that are not resistant to invasion may still be resilient following restoration (Lake, 2013; Westman, 1978). Exotic plants have traits that can alter native ecosystem processes, including different quality, quantity and timing of litter deposition; root exudates; phenology; and microbial associations (Christian and Wilson, 1999; Ehrenfeld, 2003; Klironomos, 2002; Yoshida and Allen, 2004). Exotic plants can alter plant-soil feedbacks to facilitate their persistence by fostering a microbial community or soil nutrients that hinder natives, facilitates exotics, or both (Batten et al., 2008; Ehrenfeld, 2003; Hawkes et al., 2006; Klironomos, 2002; Kourtev et al., 2002; Kulmatiski et al., 2008). Exotic plants can directly impact natives through competition for space, light, water and soil nutrients (D'Antonio et al., 1998; Ehrenfeld, 2003; Eliason and Allen, 1997). Comparison of short- and long-term restorations in invaded and restored lands can be used to identify soil characteristics that are more sensitive to invasion (Callaway and Ridenour, 2004). For instance, removal of exotics could increase availability of mobile and faster-cycling nutrients, such as nitrate, within a single growing season, while longer term impacts might include changes in slower cycling organic N and carbon (Schlesinger, 1997; Scott and Morgan, 2012; van der Putten et al., 2007). If removal of the invading species leads to recovery of natural soil resource levels, then soils are believed to be resilient to the initial impact of the invading, exotic species.

Coastal sage scrub (CSS) is a semi-deciduous, Mediterranean-type shrubland distributed from coastal, central California to northern Baja California, Mexico. Most of the remaining CSS that has not been converted to urban or agricultural uses has been invaded by Mediterranean annual grasses and forbs. It is one of the most endangered ecosystems in the United States (Klopatek et al., 1979; Rubinoff, 2001; Westman and Oleary, 1986), making it a priority ecosystem for preservation and restoration. Regional, uninvaded CSS references are becoming increasingly rare, so much so, that many Southern California CSS restoration projects lack a

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