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Carbon and nitrogen storage in California sage scrub and non-native grassland habitats

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ABSTRACT

Human activity has altered global carbon and nitrogen cycles, leading to changes in global temperatures and plant communities. Because atmospheric carbon (C) and nitrogen (N) concentrations are affected by storage in terrestrial vegetation and soil, it is critical to understand how conversions from native to non-native vegetation may alter the C and N storage potential of terrestrial landscapes. In this study, we compared C and N storage in native California sage scrub, non-native grassland, and recovering California sage scrub habitats in the spring and fall by determining the C and N content in aboveground biomass, litter, and surface soil. Significantly more C and N were stored in intact and recovering California sage scrub than in grassland habitats. Intact and recovering sage scrub did not differ significantly in C or N storage. Our results highlight that preserving and restoring California sage scrub habitat not only provides habitat for native biodiversity, but also increases carbon and nitrogen storage potential even without restoration to intact sage scrub.

1. Introduction

Carbon dioxide and N_2O concentrations are increasing in the atmosphere, leading to increases in global temperatures and changes in the hydrological cycle (Ciais et al., 2013). Terrestrial vegetation is a volatile carbon and nitrogen sink which is heavily influenced by human activity through habitat conversions including the introduction of non-native species and alteration of vegetation (Aber and Melillo, 2001). The impacts of these changes on nutrient storage cannot be well explained without first determining how different terrestrial habitat types store carbon (C) and nitrogen (N). As such, studies that examine storage in different habitats are critical to our understanding of global C and N cycling and how habitat modifications influence storage (Bradley et al., 2006; Hobbs and Mooney, 1986; Jackson et al., 2002; Knapp et al., 2008; Wolkovich et al., 2010).

The California sage scrub ecosystem (hereafter sage scrub) is native to areas of Southern and Baja California on lower elevation hillslopes (Rundel, 2007). It is characterized primarily by drought-deciduous shrubs such as *Artemisia californica* Less. (coastal sagebrush), with a few evergreen shrubs in some stands (Mooney, 1977; Rundel and Gustafson, 2005). The drought deciduous species are largely dormant in the hot, dry summer months and resume growth in the winter and spring, following the rainy season (Mooney, 1977). The California sage scrub ecosystem is listed as endangered (85–98% lost) by the USGS (Noss et al., 1995), and as critically endangered by the World Wildlife Fund (Olson et al., 2015). More than thirty years ago, Westman (1981) estimated that the then extant stands of sage scrub reflected less than 10% of their original distribution. Replacement by non-native species following disturbances (primarily fire and high levels of N deposition) and human development currently threaten remaining sage scrub (Cox et al., 2014; Mooney, 1977; Riordan and Rundel, 2014).

In Southern California, much of the remaining native sage scrub habitat has been replaced or invaded by non-native grass species (Cox et al., 2014; Jackson et al., 2002; Wolkovich et al., 2010). Grass-dominated communities differ in structure from native sage scrub, which likely affects their nutrient storage potential. While sage scrub contains woody shrubs, non-native grasslands in Southern California are primarily composed of introduced European annual

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grasses, which affect the above and belowground biomass as well as the litter composition in these communities (Schlesinger, 1997). For example, woody litter takes significantly longer than leafy litter to decompose and to release stored nutrients back into the soil and atmosphere (Aber and Melillo, 2001). Additionally, vegetation functional type has been found to significantly influence soil C concentration, including surface soil horizons as well as deeper horizons where C is less likely to be quickly released into the atmosphere (Jobbágy and Jackson, 2000).

While the C storage profile for sage scrub has been measured (Gray and Schlesinger, 1981), the differences in C storage between sage scrub and non-native grasslands are not yet well quantified and are sometimes contrary to expectations. There have been studies both of shrubs invading grasslands (Hobbs and Mooney, 1986; Jackson et al., 2002; Knapp et al., 2008) and of grasses invading shrublands (Bradley et al., 2006; Wolkovich et al., 2010), which present conflicting interpretations of the effects of changing from one habitat type to the other on C storage. Two recent studies on C storage in California shrubland and grassland habitats are contradictory, with Wolkovich et al. (2010) finding increased storage in coastal sage scrub systems invaded by grasses and Bradley et al. (2006) finding decreased storage in cheatgrass-invaded native California shrublands. Due to the inevitable complexity of nature and differences in study priorities, many studies on grass versus shrub dynamics contain confounding factors such as fire (Bradley et al., 2006), limited consideration of plant species (Wolkovich et al., 2010), and short establishment of habitat types (Knapp et al., 2008), which make it difficult to compare true C storage differences between sage scrub and type-converted grassland habitats.

While several studies have investigated differences in C storage between these habitat types, N storage in sage scrub and type-converted grassland has been less thoroughly researched. Type conversion is likely to influence N storage, but interactions between high N deposition and conversion make storage predictions difficult. High rates of N deposition often facilitate conversion of sage scrub to non-native grassland and slow the recovery of shrubs after fire or invasion (Cox et al., 2014; Fenn et al., 2003; Kimball et al., 2014), and California shrublands experience rates of N dry deposition as high as 29 kg N ha^{-1} y^{-1} (Bytnerowicz and Fenn, 1996). High N has also been shown to reduce plant species richness and promote non-native species over natives in shrublands and grasslands (Clark and Tilman, 2008; Huenneke et al., 1990; Kimball et al., 2014). While increased N addition can also increase primary production, it is unclear how changes in plant diversity and functional types associated with high N deposition may interact with increased primary productivity to influence N storage potential in these habitat types in Southern California. Determining current N storage potential of Southern California shrubland and grassland systems would provide estimates of N storage in different habitat types against which to measure future change and monitor the N saturation of these systems.

Here we report on a study to address a knowledge gap in the current understanding of C and N biogeochemical cycles in intact sage scrub, recovering sage scrub, and non-native grassland ecosystems, the three primary non-urban/suburban habitat types in the greater Los Angeles basin. We compared these habitats by measuring and modeling the amount of C and N stored in three major terrestrial components: aboveground biomass, litter, and soil. The fourth major component, belowground biomass, was excluded from this analysis due to difficulty of sampling or modeling C and N concentrations, particularly in the fall after the senescence and death of annual grasses. We hypothesized that intact sage scrub would store more C and N than non-native grassland, but due to the contradictory findings of previous studies, had no strong predictions about whether intact or recovering sage scrub would have higher C and N storage. The results of this comparison between habitat types are needed to evaluate how type conversion from sage scrub to non-native grassland impacts C and N storage and whether preserving or restoring native sage scrub habitat areas has a C and N storage benefit.

2. Materials and methods

2.1. Study system

This study was conducted at the Robert J. Bernard Biological Field Station (hereafter, field station) in Claremont, CA, on the eastern edge of Los Angeles County (Appendix A, Fig. A1). The climate in Claremont is xeric (Mediterranean) and has been specifically classified as the Intermediate Valley type, with average temperatures between 32 °C in the summer and 4 °C in the winter with most precipitation occurring in the winter (Bailey, 1966). There were three primary habitat types within the field station: intact sage scrub, non-native grassland, and a transitional habitat where sage scrub shrubs had begun to recolonize a non-native grassland area. Sage scrub habitat at the field station was defined by the dominance of shrub species including *Artemisia californica*, *Eriodictyon crassifolium* Benth. (thickleaf yerba santa), and *Eriogonum fasciculatum* Benth. (Eastern Mojave buckwheat). Other shrub species in the field station sage scrub habitat included *Salvia apiana* Jeps. (white sage), *Rhus integrifolia* (Nutt.) W.H. Brewer & S. Watson (lemonade sumac), *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (Pacific poison oak), *Lepidospartum squamatum* (A. Gray) A. Gray (California broomsage), *Ericameria pinifolia* (A. Gray) H.M. Hall (pinebush), *Malosma laurina* (Nutt.) Nutt. ex Abrams (laural sumac), *Sambucus nigra* L. (black elderberry), and *Ribes aureum* Pursh (golden current). The field station grassland habitat was by definition dominated by non-native annual *Bromus* spp. Also common in this grassland were patches of *Croton setigerus* Hook. (dove weed), which were more prevalent in the fall prior to the sprouting of the grasses. The transitional habitat contained plant species from both the sage scrub and grassland communities in roughly even proportions. As shown by aerial photographs and satellite imagery, none of the studied habitat areas had experienced a fire for at least 40 years previous to this study, and each had been established as the current habitat type for at least as long (Hamlett, 2012).

Soil morphology and taxonomy were described as part of this study following the protocols of Schoenenberger et al. (2002, 2012) and Soil Survey Staff (2014), using small, 1 m^3 test pits (see Appendix A for soil profile descriptions and laboratory characterization data). Soils were similar among the three communities sampled in this study and were best characterized as mixed, sandy-skeletal Humic Haploxerepts, which are simple, young, weakly developed soils with thin (~10–15 cm) surface horizons. Parent material consisted of alluvial sands and gravels derived from granitic and metamorphic rocks in the San Gabriel Mountains.

2.2. Sample collection and processing

To determine total carbon and nitrogen storage in these three habitats, we sampled aboveground biomass, litter, and soil in each habitat in the fall (Oct–Dec 2012), when plants were dormant, and again in the spring (Apr–May 2013), when new growth had emerged. In each of the three habitats, we computer-generated random points to select eight and six 2 × 2 m plots in the fall and spring respectively. Upon visiting the sites we intentionally avoided sites with trees, poison oak, and highly disturbed areas such as paths. Because we avoided trees such as *Sambucus nigra* in the sage scrub habitat, our estimations of aboveground biomass in