Geoderma Regional 14 (2018) e00172

Contents lists available at ScienceDirect

Geoderma Regional

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

Carbon and nitrogen in the topsoils of Inceptisols and Mollisols under native sage scrub and non-native grasslands in southern California

Tal Caspi [a], Leo Estrada [b], Anna V. Dowling [b], Erin Su [b], Maxim Leshchinskiy [b], André R.O. Cavalcanti [b], Edward J. Crane III [b], Colin R. Robins [a], Wallace M. Meyer III [b,*]

[a] W.M. Keck Science Department, Claremont McKenna, Pitzer, Scripps Colleges, 925 N. Mills Avenue, Claremont, CA 91711, USA
[b] Department of Biology, Pomona College, 175 W. 6th St., Claremont, CA 91711, USA

A R T I C L E I N F O

Article history:
Received 29 October 2017
Received in revised form 2 May 2018
Accepted 4 May 2018
Available online xxxx

Keywords:
Soil organic carbon
Soil microbes
Fungi:bacteria ratio
Shrubland
Invasive grass
Soil density

A B S T R A C T

Understanding how invasive plants influence terrestrial carbon (C) and nitrogen (N) budgets is important in the context of global climate change. In southern California, type-conversion, a process in which native California sage scrub is type-converted to non-native grassland, is thought to negatively impact total C and N storage in surface soil horizons. To better understand the extent to which type-conversion influences regional nutrient storage, we examined C and N concentration (%) and quantity (g/m^2), key soil properties, and microbial abundances and assemblages in sage scrub and non-native grassland habitats at three sites that represent varying environmental conditions. Type-conversion decreased soil C concentration, but did not influence C quantity. Differences between these two metrics were driven by a higher aggregate soil density in the non-native grassland habitat compared to the sage scrub habitat at one site. Contrary to previous studies, we found that type-conversion did not impact total N storage, even in a site previously found to have increased soil N quantities under sage scrub. Sage scrub habitats contained more active fungi, and differences in microbial assemblages were found between habitat types. Despite the vast number of microbial OTUs, habitats harbored unique communities of microbial taxa with some species consistently more abundant in one habitat type across sites. Our results demonstrate that type-conversion negatively impacts topsoil C concentrations, but accurate modeling of nutrient stocks requires consideration of the links between vegetation structure, soil properties such as soil density, and microbial communities that vary significantly across small spatial scales. Collectively, we demonstrate that invasive grasses alter microbial communities and reduce soil C storage capacity in the region.

1. Introduction

Determining how non-native species influence nutrient storage is crucial to our understanding of global carbon (C) and nitrogen (N) cycling (Bradley et al., 2006; Houghton, 2007; Ostle and Ward, 2012; Pinno and Wilson, 2011). In many systems, invasive grasses are dominant competitors that play important roles in nutrient storage dynamics by modifying abiotic and biotic factors and altering the natural disturbance regimes (D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998). Such alterations may have profound effects on ecosystem processes because changes in plant composition can also influence microbial communities, which are drivers of biogeochemical cycling (Jackson et al., 2002; Jobbágy and Jackson, 2000; Wardle, 2006; Wurst et al., 2012). While many studies have examined how grass invasion influences nutrient storage, conflicting outcomes indicate that impacts are dependent on ecological context (Pinno and Wilson, 2011). Thus, for many regions, our knowledge of how invasion by grasses affects terrestrial C and N budgets is limited.

Effects of invasion on nutrient storage in the California sage scrub ecosystem (hereafter sage scrub), a native low-elevation habitat in southern California dominated by drought deciduous shrubs, is still rudimentary (but see, Wheeler et al., 2016; Wolkovich et al., 2010). Sage scrub is undergoing largescale replacement by non-native grass species, a process known as type conversion (Cox et al., 2014; Talluto and Suding, 2008). Estimates indicate that sage scrub has declined by nearly 50% since the 1930s largely due to type-conversion (Riordan and Rundel, 2014; Rundel, 2007; Talluto and Suding, 2008). Reductions in fire return intervals are facilitated by grass invasion leading to a positive feedback with shorter fire return intervals as grass establishment enhances fire ignition probabilities(D'Antonio and Vitousek, 1992; Kimball et al., 2014; Talluto and Suding, 2008). Increased N deposition contributes by facilitating growth of non-native grasses and increasing their competitive ability (Kimball et al., 2014; Talluto and Suding, 2008). Together, these factors facilitate largescale type-conversion of sage scrub, resulting in long-lasting alterations in the region's

* Corresponding author.
E-mail address: wallace.meyer@pomona.edu (W.M. Meyer).

https://doi.org/10.1016/j.geodrs.2018.e00172
2352-0094/

vegetation community and structure (Mooney and Zavaleta, 2016; Rundel, 2007). Such changes can impact C and N cycling of the ecosystem in a number of pools (Ehrenfeld, 2003; Wheeler et al., 2016).

Soil is a major terrestrial pool of C, storing two to three times more C than aboveground biomass or litter components (Houghton, 2007; Wheeler et al., 2016). Total soil C is sensitive to both abiotic and biotic factors such as topography, soil texture, and plant species composition (Batjes, 2014; Jobbágy and Jackson, 2000; Pouyat et al., 2006; Wheeler et al., 2016). Less total N is stored in the soil than C, but soil N is equally important because fluxes between pools of N are largely controlled by soil microorganisms (Fowler et al., 2013; Ward, 2012). Surface soil horizons, which are typically generalized for sampling and discussion in the ecological literature as the top 10 cm of the A horizon or mineral soil profile, contain more microbial biomass than deeper soil horizons (Fierer et al., 2003; Lavahun et al., 1996) and are especially volatile with regard to C and N storage. Carbon and N in surface soil horizons are primarily controlled by soil mineralogy and organic matter inputs from plant growth, and balanced by respiration of the soil microbial community (Houghton, 2007). Bacterially-dominated soils promote rapid nutrient turnover and low nutrient storage (Manning, 2012; Wardle, 2002), whereas soils with higher abundances of fungi enhance soil C accumulation, because fungi use C more efficiently (Allison et al., 2005; Manning, 2012; Wardle, 2002). In addition, different habitats can harbor unique assemblages of microbial taxa with distinct functional characteristics (Fierer et al., 2012; Sigüenza et al., 2006). As such, it is essential to consider the complex links between vegetation structure, the microbial community, and soil C and N cycling when examining the effects of invasive grasses on sage scrub communities.

To better understand the impact of type-conversion on southern California surface soils, we examined differences in total C and total N storage in sage scrub and non-native grasslands at three representative sites across the region. While soils contain many key nutrients (P, S, Ca, Mg, Na, K, etc.), we use the term nutrient to refer exclusively to soil C and N. Sampling soil from both habitat types at each site, we (1) assessed the concentration and quantity of C and N stored in the uppermost mineral soil horizon (A horizon) and (2) tested whether microbial abundance and assemblages differed between habitat types. We also collected data on key soil properties in each habitat at each site to preliminarily examine how those properties may influence nutrient storage and assess differences in soil types. We hypothesized that sage scrub stores more total soil C and N than non-native grasslands. We also predicted that sage scrub soils would have increased fungal abundance and a higher fungi:bacteria ratio. By comparing total C, total N, and soil microbial assemblages between sage scrub and non-native grasslands at multiple sites spanning various environmental gradients, we demonstrate how type-conversion influences nutrient storage in the region and offer insight into the role of microbes in this key ecosystem process.

2. Methods

2.1. Study site

The sage scrub ecosystem is broadly characterized by a Mediterranean climate consisting of warm, dry summers and cooler, moist winters while also experiencing a gradient of increasing continentality moving from the coast inland (Mooney and Zavaleta, 2016). Within sage scrub, the climate gradient strongly influences the distribution of individual plant species (Riordan and Rundel, 2014; Rundel, 2007). Even though mean annual precipitation (MAP) and mean annual temperature (MAT) values can be nearly identical across the gradient, vegetation at the coast is buffered from climatic extremes, experiencing reduced temperature fluctuations and reduced drought stress compared to inland sites (Mooney and Zavaleta, 2016; Rundel, 2007). Work in the region by Bauer (1936) indicates that areas within 5 km from the coast experience double the humidity of more inland, higher-elevation sites. Along the coast to inland gradient, these climatic differences, topographic variation (primarily slope angle and aspect), and different soil types all contribute to and/or reflect distinct floristic assemblages responsible for the known “patchwork” or “mosaic” composition of the sage scrub community (Rundel, 2007). Most notably, evergreen shrubs, e.g., *Rhus integrifolia* and *Malosma laurina*, are more abundant at coastal sites, while drought deciduous shrubs like *Artemisia californica* and drought-tolerant species such as *Salvia apiana* become more frequent at inland sites (Rundel, 2007).

To better understand how type-conversion influences regional nutrient storage, we collected samples at three sites that span this coast to inland gradient in both Los Angeles and San Bernardino counties. The coastal site was in the Santa Monica Mountains (34.035948°, −118.804160°; MAP = 461 mm; MAT = 17 °C) while the most interior site was in the Crafton Hills Conservancy (34.037760°, −117.121647°; MAP = 324 mm; MAT = 18 °C), 155 km east (PRISM Climate Group, 2018). An intermediate site was the Robert J. Bernard Biological Field Station (hereafter Bernard Field Station; 34.109047°, −117.710374°; MAP = 514 mm; MAT = 18 °C), located 101 km east of the Santa Monica Mountains and 55 km west of Crafton Hills (see Fig. 1) (PRISM Climate Group, 2018). The Santa Monica Mountains site was only 2 km from the coast, whereas the Bernard Field Station and Crafton Hills sites were 55 km and 82 km from the coast, respectively, with the nearest coastline most often south of the study sites. Sites contained both sage scrub and type-converted grassland in close proximity (within 300 m) of one another to minimize the impacts of confounding variables such as variations in soil characteristics and microclimate within a site. Additionally, we chose sites in “protected areas” where differences in habitats were not associated with different contemporary land management practices such as grazing or disking for fire mitigation. Sage scrub was defined as areas dominated by native drought-deciduous and evergreen woody shrubs, most commonly *Artemisia californica*, and containing <10% cover by visual estimate of non-native species. Invasive grasslands were defined as containing <5% cover of native shrubs and were dominated instead by non-native European annual grasses *Bromus* spp. at inland sites. In addition to *Bromus* spp., the coastal site was co-dominated by *Brassica* spp., *Silybum marianum*, and *Centaurea melitensis*, highlighting the diversity of invasive annuals that can be abundant in disturbed areas in southern California.

Soils within these three sites exhibit a range of soil-landform characteristics representative of the sage scrub habitat diversity in southern California, and thus also differ in taxonomy. Soils at the coastal site are largely mapped by Soil Survey as Mollisols (Malibu or Boades series) formed in sandstone or shale parent materials (Soil Survey Staff, 2017). These soils are reported to have higher (e.g., 20–48%) clay content and CEC (~15 $cmol_c$/kg) than the inland sites where soils are much simpler, younger, and less developed Inceptisols and Entisols formed in alluvium (Bernard Field Station) and granitic residuum (Crafton Hills) with lower reported clay contents (8–20%) and CEC values (10–13 $cmol_c$/kg) (Soil Survey Staff, 2017). Soil Survey map units at Crafton Hills also include a clay-rich Alfisol (Ramona series) (Soil Survey Staff, 2017). Soil surveys are a useful first approximation, but their coarse 1:24,000 scale necessitates sampling at a finer-scale, especially in detailed studies of C and N. For instance, profile descriptions and sample analyses by Wheeler et al. (2016) found that the Bernard Field Station soils do not match and were more developed than any of the series suggested by existing survey units. Whatever the range in soil properties, comparisons between distinct soils are still warranted and even vital for regional study of type-conversion impacts on soil C and N storage under sage scrub, because sage scrub habitats span many distinct slope angles and parent materials. Moreover, Wheeler et al. (2016) found that soils were morphologically similar across the Bernard Field Station, and field observations for this study at the other