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Woody shrubs increase soil microbial functions and multifunctionality in a tropical semi-arid grazing ecosystem

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A B S T R A C T

Woody encroachment is of global concern in arid and semiarid regions around the world. Due to reduction in grass (forage), woody encroachment is viewed as ecosystem disservice and degradation, even though this may not reduce ecosystem functions. Often, management perceptions of degradation remain inadequately informed by knowledge of ecosystem processes. We compared 11 biotic variables related to soil and microbial functions under shrubs against paired-adjacent grassland:- carbon, nitrogen, C:N ratio, organic matter, plant-available N, N-mineralization rate, microbial biomass C and N, basal respiration, and metabolic-quotient. We summarized these as a multifunction-index. We also measured five soil physico-chemical covariates:- pH, conductivity, bulk density, texture and water holding capacity. These 11 biotic variables were 15–48% higher under shrubs than under grass; multifunction-index was also higher (by 366%). After accounting for spatial autocorrelation and background differences in physico-chemical covariates (redundancy analysis), altered ecosystem functions were attributable to shrubs. Overall, shrubs can enhance ecosystem functions, and maintain important ecological processes through concomitant changes in soil physico-chemical properties. While shrubs should not be equated to ecological degradation, they present a challenging triage of ecosystem service, disservice, and function for grasslands. Management strategies could benefit from targeting patterns of nutrient re-distribution under shrubs.

1. Introduction

Arid and semiarid grasslands and savannas cover nearly 40% of the earth's terrestrial surface (over 52 million km^2). These rangeland ecosystems provide nearly one-third of terrestrial net primary productivity, are potential carbon sinks, house important biodiversity, support majority of the world's livestock production, and sustain livelihoods of about a billion humans (MEA, 2005; Yahdjian et al., 2015). Over the past decades, open grasslands and savannas have experienced encroachment by shrubs, and increased woody cover now affects grasslands in all continents (Eldridge et al., 2011; Naito and Cairns, 2011; van Auken, 2000). Woody encroachment is linked to a number of interrelated factors, including CO_2 fertilization, increased N-deposition, fire suppression, intensified grazing, and altered precipitation regimes (Archer, 1995; Eldridge et al., 2011; Naito and Cairns, 2011; van Auken, 2000). Woody shrub proliferation is predicted to continue at the annual rate of up to 2% of area yr^{-1} in some ecoregions (Barger et al., 2011).

Since woody shrubs displace grasses, they reduce foraging opportunities for herbivores, particularly grazers. This loss in ecosystem service can have severe consequences for human livelihoods that depend on livestock production (Anadón et al., 2014). If grazing pressures become concentrated on remnant grassy patches, it can lead to degradation via overgrazing. Understandably, due to reduced grazing services, woody encroachment is equated with ecosystem disservice and ecological degradation (Anadón et al., 2014; Briggs et al., 2005; Eldridge et al., 2011; López-Díaz et al., 2015). Current estimates consider 10-20% of global drylands as degraded, with consequences for nearly 250 million people in the developing world (Maestre et al., 2016b). Yet, it is debatable whether woody encroachment actually drives loss of ecosystem function. On the contrary, it may effectively enhance primary production, with positive effects on soil nutrients and hydrology (Eldridge et al., 2011; Eldridge and Soliveres, 2014; Liao and Boutton, 2008; Maestre et al., 2016a; Wilcox and Huang, 2010). Shrubs are frequently associated with fertility islands under their canopies (Allington and Valone, 2014; Schlesinger et al., 1996), and the effect can even propagate beyond their canopy and increase soil functions in adjacent open spaces (Eldridge et al., 2013; Hibbard et al., 2001). However, effects of shrubs on a number of other ecosystem functions, particularly those mediated by soil microbial processes, remain

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relatively unclear. Integrated effects, or multifunctionality (Hector and Bagchi, 2007; Maestre et al., 2012; Quero et al., 2013; Wagg et al., 2014), and simultaneous change in multiple ecosystem responses also remain unresolved. Thus, management decisions on degradation are often taken with incomplete knowledge about ecological functions and processes. Such areas become susceptible to landuse conversion, which jeopardizes ecosystem functions they may otherwise offer, and the biodiversity they may support. Such opportunity costs seldom feature in discussions that are dominated primarily by perceptions of ecological degradation. This narrow viewpoint about degradation does not consider restoration as an option, and take advantage of any positive effects that shrubs may have on ecosystem processes (Hibbard et al., 2001; Maestre et al., 2003). Redistribution of soil nutrients, and their localization under shrubs as fertility islands (Allington and Valone, 2014; Schlesinger et al., 1996) can maintain ecological processes that are of high relevance for restoration efforts (Alday et al., 2014; Suding et al., 2004).

Ecosystems are often valued for their ability to provide multiple services and to maintain a series of functions simultaneously, i.e., multifunctionality (Bennett et al., 2009; Hector and Bagchi, 2007; Smith et al., 2013). However, maximizing one aspect can lead to decline among others – reflecting inherent tradeoffs in how these functions are sustained and how the resultant services are provisioned (Bennett et al., 2009). So, all functions and services need not be positively related to one another (Byrnes et al., 2014). Most of our understanding of effects of shrub encroachment is based on measurements of individual ecosystem attributes, while assessments of multifunctionality are rare (Eldridge et al., 2011; Maestre et al., 2016b). In general, while shrubs can increase biomass production, they may reduce forage availability, while also influencing other ecosystem processes such as nutrient cycling, hydrology, etc. An important management concern is to reconcile loss of forage production (a service) with gain in other functions, and include potential tradeoffs in landuse decisions (Bennett et al., 2009). Another concern is implementation of appropriate restoration strategies, particularly by taking advantage of any positive effects of shrubs (Alday et al., 2014; Hibbard et al., 2001).

Understanding the effect on integrated functioning of ecosystems requires an approach that focuses on multiple variables, and assess how shrub encroachment affects multiple functions simultaneously, i.e., multifunctionality (Hector and Bagchi, 2007; Maestre et al., 2016a; Quero et al., 2013). Now, nearly all terrestrial ecosystem functions are ultimately mediated by microbial processes in soil (Falkowski et al., 2008). Inter-related parameters such as soil C and N, pH, conductivity, microbial biomass, microbial respiration and microbial metabolic quotient (respiration to biomass ratio, qCO_2), N-mineralization (conversion of organic N to inorganic forms for re-uptake by plants), collectively represent the status of soil functions. These are useful indicators of ecosystem responses to stress and disturbances (Liao and Boutton, 2008; Tian et al., 2008; Wardle, 1993).

Here, we assess whether shrub encroachment is associated with differences in the soil physico-chemical environment and microbe-mediated soil functions. For example, meta-analyses have revealed that woody encroachment is associated with lowering of soil pH, but increase in soil C and N (Eldridge et al., 2011). So, the response in inter-related soil microbial functions, and multifunctionality, may not be independent of changes occurring simultaneously in soil physico-chemical aspects. We addressed this hypothesis in a semiarid tropical rangeland in peninsular India.

Semiarid rangeland ecosystems cover about 1 million km^2 area across India, where degradation due to woody encroachment is a major concern. Studies estimate that about a third of India's land area is degraded to various extents, of which about 8×10^6 ha are deemed degraded due to vegetation change, particularly in the arid and semiarid regions (Ajai et al., 2009; Reddy, 2003). Unfortunately, drylands and rangelands in India are characterized as "wastelands", and are frequently earmarked for landuse conversion, particularly tree plantations (Anonymous, 2010; Baka, 2014; Fleischman, 2014; Ratnam et al., 2016; Singh and Bagchi, 2013). Similar aversion to rangelands as legitimate ecosystems is fairly deep-rooted and widespread in many regions (Parr et al., 2014; Ratnam et al., 2016). For example, $9 \times 10^6\,km^2$ of rangelands, worldwide, were recently classified as degraded lands, and were recommended for forest plantations (Veldman et al., 2015). Currently, a number of well-meaning initiatives promote greening of rangelands through tree plantation (Das, 2010; Parr et al., 2014; Ratnam et al., 2016). For example, India has pledged to restore 13×10^6 ha of degraded land through forest plantation by 2020 under the Bonn Challenge (plus, an additional 8×10^6 ha by 2030). New legislations, such as the CAMPA Act of 2016 (Compensatory Afforestation Management and Planning Authority), also promote tree plantation in areas that are presumed to be degraded. But, these well-meaning efforts can lead to trees being planted in rangelands, especially once they are earmarked as degraded or "wastelands" (Anonymous, 2010; Das, 2010; Parr et al., 2014; Ratnam et al., 2016). One can incur substantial loss of ecosystem function and biodiversity if millions of hectares of rangelands are perceived to be degraded, and converted to other landuse (Baka, 2014; Das, 2010; Parr et al., 2014; Veldman et al., 2015).

2. Materials and methods

2.1. Study area

We studied alterations in soil due to woody encroachment in a semiarid rangeland in Karnataka state in peninsular India (14° N, 76° E), approx. 150 km northwest of Bangalore city (see photographic plates, Fig. S1, Supplementary Material). This region receives annual rainfall ranging between 400 and 500 mm yr^{-1}. Vegetation in the study area consists of three common native shrubs (*Acacia ferruginea*, *Albizia amara*, and *Dodonaea viscosa*, which can grow to 1-2 m in height) interspersed between grasses (*Aristida* spp., *Arundinella* spp., *Themeda* spp., *Heteropogon* spp., *Ischaemum* spp., *Isachne* spp., *Eleusine* spp., and *Chrysopogon* spp.). Few other woody species also occur (*Acacia leucophloea*, *Prosopis juliflora*), but are relatively rare and are often restricted to riverine patches where they can grow to 2-3 m in height. The region is primarily used by goat and sheep, alongside a few cattle and blackbuck (an endemic and endangered antelope, *Antilope cervicapra*). For the last few decades, livestock husbandry is the major landuse in the region, alongside rain-fed and irrigated farming in certain pockets. During informal discussions, local herders opined that shrub cover has expanded in this region largely in the last 4-5 decades. In general, shrub encroachment across drylands of India has been a general concern since the 1950s-1960s (Singh and Joshi, 1979), similar to few other regions (Archer, 1989; Hudak and Wessman, 1998; Laliberte et al., 2004). The goat and sheep were seen to browse on the shrubs; foliar N-content of *Albizia* and *Acacia* in summer is between 2.2% and 2.7% (C:N ratio between 17 and 20). These values are favorable compared to typical C_4 grasses in summer (N-content 1–1.5%, C:N ratio > 30, Coppock et al., 1983).

2.2. Sampling and analysis

We compared soil functions under the shrub canopy and in a paired-adjacent location in open grassland 5 m away from the canopy, each located within replicated 10 m × 10 m quadrats. We sampled soil with a 5 cm diameter and 20 cm depth soil corer at n = 34 paired locations spread across 6 km^2. Samples were air-dried and transported to the laboratory for analysis. Here, we oven dried the soil samples at 40 °C and sieved them to remove all visible roots, stones and pebbles, using a 1.5 mm mesh. We estimated 10 inter-related variables related to microbial and biotic functions:- total soil C, soil N, soil organic matter (SOM), ammonium and nitrate concentration, potential N-mineralization (N-min), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), soil basal respiration (BR), and soil metabolic quotient