



# Herbivores suppress soil microbes to influence carbon sequestration in the grazing ecosystem of the Trans-Himalaya



Sumanta Bagchi\*, Shamik Roy, Alakananda Maitra, Rubanpreet S. Sran

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

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## ABSTRACT

Understanding factors that regulate carbon (C) pools is of high importance for offsetting greenhouse-gas emissions. Soils represent a vast C pool, whose size and stability are strongly influenced by land-use. Grazing, by native herbivores and livestock, is the predominant land-use across over 40% of the terrestrial surface and influences over  $10^9$  Mg of soil-C annually in the world's dry regions. The interactions between plants, grazers, and soil microbes, is of critical importance for this soil-C pool. However, soil microbial responses to grazing, and associated feedbacks, remain poorly understood. Grazing management policies are unable to adequately accommodate key interactions that are important for effective ecosystem stewardship. After 10-yr of experimental herbivore-exclusion in the semiarid Trans-Himalayan ecosystem, we measured grazer effects on soil microbial abundance in  $n=30$  herbivore enclosures, each paired with an adjacent control plot using substrate-induced respiration, microbial-carbon, and microbial-nitrogen (SIR, MBC, MBN). We found that grazing reduced soil microbial biomass by 13–16%, over the course of the vegetation growing season. But, the strength and direction of grazer effects varied through time at different points in the growing season. Grazing also shifted fungal:bacterial ratio towards dominance by fungi which were more tolerant of periodic dry-down and seasonal fluctuations in soil moisture than bacteria. So, grazer influence on microbial abundance and community composition may collectively play crucial roles in net soil-C dynamics. But, this effect is constrained by environmental factors, such as moisture availability. The projected climatic trend in the Trans-Himalaya is towards progressively wetter conditions, and this may counter grazer effect on microbes, alter microbial communities, and ultimately impact potential soil-C storage. So, accounting for projected changes in precipitation, in addition to managing stocking density of herbivores, may also be crucial for these large soil-C pools.

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## 1. Introduction

Under ongoing and projected climate change, it is increasingly becoming important to identify and manage carbon (C) pools as C-sinks. Soils are the most important C-pool in the terrestrial realm; globally they store more C than the atmosphere (Chapin et al., 2009). As grazing ecosystems represent over 40% of the terrestrial realm, understanding and managing the impacts of herbivores becomes important for the size and stability of the soil-C pool (Bagchi and Ritchie, 2010a; Conant et al., 2002; Lal, 2004; Li et al., 2013; McSherry and Ritchie, 2013; Reid et al., 2004; Wang et al., 2014; Wen et al., 2013). Large mammalian herbivores (native

grazers, and livestock), can exert both direct and indirect influence on soil-C (Conant et al., 2002; Derner et al., 2006; Derner and Schuman, 2007; Ganjegunte et al., 2005). Grazer effects on soil-C arise from a number of different inter-related pathways. These are conceptualized into three types (Cherif and Loreau, 2013; Hamilton and Frank, 2001; Hobbs, 1996): Type I – where grazing alters total plant production; Type II – where grazing alters the cycling of a limiting nutrient; Type III – where grazing induces plant physiological responses which further alter material and energy flow (e.g., root exudation). Their direct influence, on quantity of C-input to soil, is exerted by consuming plants and diverting C away from soils and toward secondary production, while releasing  $\text{CO}_2$  and  $\text{CH}_4$  in the process, and also altering vegetation composition. Their indirect influence, on quality of C-input to soil, determine how soil microbes respond to grazing, and represent feedbacks between producers, consumers and

\* Corresponding author.

E-mail address: [sbagchi@ces.iisc.ernet.in](mailto:sbagchi@ces.iisc.ernet.in) (S. Bagchi).

decomposers (Cherif and Loreau, 2013). Although this latter effect, mediated via feedbacks (Crowther et al., 2015; Jastrow et al., 2007; Yue et al., 2015), is likely very important, it remains relatively poorly understood. Key questions persist over the influence of herbivores on soil microbes, whether this interaction has implications for the size and stability of soil-C pools, and what underlying mechanisms could be involved (Tanentzap and Coomes, 2012).

Microbial responses to grazers is known to be highly variable, with positive, negative and neutral effects in different ecosystems (Tanentzap and Coomes, 2012). Since the different feedbacks involving microbes and grazers seldom act in the same direction, this gives rise to pluralistic results in different ecosystems (Cherif and Loreau, 2013). Grazer effects on soil-C generally shift from positive to negative with increasing precipitation in clayey soil, but this trend is reversed for sandy soils (McSherry and Ritchie, 2013); making grazing management very important for many arid and semi-arid regions. Existing theory posits that net effect of grazers on microbes can be explained by the balance between direct and indirect effects (Cherif and Loreau, 2013; Sankaran and Augustine, 2004), i.e., quantity of C-input vs. quality of C-input. While grazers reduce the quantity of C-input to soil through secondary production and respiration, they also alter the quality of C-input to soil by converting plant material to dung and urine and by altering species composition; this can change the fraction of labile substrates relative to more recalcitrant forms (Frank and Groffman, 1998). Simultaneous changes in quantity and quality can alter plant nutrient availability, plant production, and also grazing (Bagchi and Ritchie, 2010b; Cherif and Loreau, 2013; Ritchie et al., 1998; Wen et al., 2013). So, if the direct effect of grazing dominates, then reduction in quantity of C-input to soil will manifest as negative effects on soil microbes. Alternatively, if the indirect effect of grazing dominates, then improvement in quality of C-input to soil will manifest as a positive effect on soil microbes. Relative strengths of these pathways would also likely influence abundance of key microbial groups: bacteria and fungi, due to physiological differences between prokaryotes and eukaryotes (Barnard et al., 2013; Jastrow et al., 2007; Six et al., 2006; Strickland and Rousk, 2010; Waring et al., 2013). The net effect of grazing will arise from the balance between these two pathways, and will determine whether grazing increases or decreases soil microbial abundance, and ultimately influence the size and stability of soil-C pools.

Stoichiometry of litter and dung can regulate microbial responses to C-input and ultimately control soil-C (Cherif and Loreau, 2013). It is known that microbes can utilize the labile fraction of soil-C in 5–10 weeks, whereas it takes longer (20–50 weeks) to utilize the more recalcitrant forms (Frank and Groffman, 1998). So, distinguishing the relative roles of change in quantity and change in quality of C-input requires repeated sampling of microbial responses through time to account for this 4–5 fold difference in residence times. As previous studies have often depended on one-time sampling, usually during peak growing season, the purported feedbacks between producers, consumers, and decomposers remain inadequately resolved. Here we address this hypothesis over quantity and quality of C-input using a long-term herbivore-exclusion experiment (Bagchi and Ritchie, 2010a, b), by measuring changes in microbial biomass at regular intervals throughout the vegetation growing season in the Trans-Himalayan ecosystem of northern India. The specific questions addressed were: (1) do grazers suppress or enhance microbial biomass, and whether this varies across the growing season, and (2) how does grazing influence two key microbial groups, namely, bacteria and fungi. From these two inter-related aspects, one can draw inference over potential implications for the size and stability of soil-C pools (Derner and Schuman, 2007; Schuman et al., 2002).

## 2. Materials and methods

### 2.1. Experimental design

The Trans-Himalayas represent a vast high-altitude grazing ecosystem in Central Asia covering India (Spiti, Ladakh), China (Tibet) and Nepal (Mustang). Here, plant productivity is low. However, due to cold climate and arid conditions, the potential for soil-C sequestration is likely high (Bagchi and Ritchie, 2010a; Graham et al., 2012; Nikrad et al., 2016; Vincent, 2010). In 2005, we initiated a long-term study on grazing in Spiti region of northern India (32°N, 78°E). Twenty-four herbivore exclosures, each 100 m<sup>2</sup> (10 m × 10 m) and with a paired adjacent control plot, were established in 2005; another six exclosures were added in 2006. Elevation ranged between 4300 and 4500 m asl. Vegetation is a characterized by sedges (Cyperaceae) and grasses (Poaceae), with a few forbs and shrubs (mainly Fabaceae, Polygonaceae, Asteraceae, Chenopodiaceae). These rangelands are grazed by native herbivores (bharal, *Pseudois nayaur*; ibex, *Capra sibirica*; domesticated form of yak, *Bos grunniens*) and various non-native livestock (cattle, yak-cattle hybrids, donkey, horse, sheep, goat).

Here, grazers remove 55–68% of aboveground plant production during the growing season, and return about half of it as dung (Bagchi and Ritchie, 2010a). This prevailing grazing intensity falls in the range where grazing effects on soil-C can shift from positive to negative (McSherry and Ritchie, 2013; Zhang et al., 2015). This raises important concerns over degradation, which may call for pragmatic management interventions (Bagchi et al., 2012; Bagchi and Ritchie, 2010a). At the same time, C:N ratio of plant litter is between 55 and 60, and C:N ratio of dung is between 20 and 33 (Bagchi and Ritchie, 2011, 2010b). So, as expected (Cherif and Loreau, 2013; Frank and Groffman, 1998; Sankaran and Augustine, 2004), herbivores reduce quantity of C-input to soil, but improve the quality of C-input. Soils are slightly alkaline (pH between 7.6 and 8.0) and of sandy-loam texture. Average soil-C ranges between 1.5 and 2.0%, and soil-N between 0.1 and 0.2% (Bagchi et al., 2012; Bagchi and Ritchie, 2011, 2010a,b).

This ecosystem is highly seasonal. Vegetation growing season is short (May–August); temperatures drop below –30 °C during the winters (Fig. 1). Precipitation occurs as snow (100–200 cm, November–March) and rain (150–300 mm, July–August, Bagchi and Ritchie, 2010b). So, soil microbial abundance is expected to reflect these alternating wet/dry and cold/warm periods (Barnard et al., 2013; Sawicka et al., 2010).

### 2.2. Sampling

In 2015, after c. 10 years of herbivore exclusion, we sampled soil with a 2.5 cm diameter and 20 cm depth corer five times at monthly intervals, to cover the entire growing season from prior to green-up till after senescence (Fig. 1, early-May to early-October), from the grazed and ungrazed plots. Soil microbial activity between November and April (i.e., the period not included in our study) is expected to be much less than during the growing season. Previous studies, in similar ecosystems, have found that microbial respiration is negligible when temperatures are below 5 °C, and increases sharply after 10 °C (e.g., Frank et al., 2002). So, any grazer impacts during the dormant period (Fig. 1) may have only a minor role in overall patterns. Plant rooting depth rarely exceeds 20 cm here, and the upper layers are most important for net soil-C dynamics (Bagchi and Ritchie, 2010a; Yue et al., 2015). Soils were sun-dried, then oven-dried at 40 °C, and transported for laboratory analysis. From monthly samples, we estimated soil microbial abundance with two methods: (1) substrate-induced respiration (SIR, Anderson and Domsch, 1978; Robertson et al., 1999), and (2) microbial biomass as carbon and nitrogen using

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