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Forum

An integrated perspective to explain nitrogen mineralization in grazed ecosystems

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ABSTRACT

Large herbivores are key drivers of nutrient cycling in ecosystems worldwide, and hence they have an important influence on the productivity and species composition in plant communities. Classical theories describe that large herbivores can accelerate or decelerate nitrogen (N) mineralization by altering the quality and quantity of resource input (e.g. dung, urine, plant litter) into the soil food web. However, in many situations the impact of herbivores on N mineralization cannot be explained by changes in resource quality and quantity.

In this paper, we aim to reconcile observations of herbivores on N mineralization that were previously regarded as contradictory. We conceptually integrate alternative pathways via which herbivores can alter N mineralization. We illustrate our new integrated perspective by using herbivore-induced soil compaction and subsequent changes in soil moisture and soil aeration as an example.

We show that the net effect of herbivores on mineralization depends on the balance between herbivore-induced changes in soil physical properties and changes in the quality and quantity of resource input into the soil food web. For example, soil compaction by herbivores can limit oxygen or water availability in wet and dry soils respectively, particularly those with a fine texture. This can result in a reduction in N mineralization regardless of changes in resource quality or quantity. In such systems the plant community will shift towards species that are adapted to waterlogging (anoxia) or drought, respectively. In contrast, soils with intermediate moisture levels are less sensitive to compaction. In these soils, N mineralization rates are primarily associated with changes in resource quality and quantity.

We conclude that our integrated perspective will help us to better understand when herbivores accelerate or decelerate soil nutrient cycling and improve our understanding of the functioning of grazed ecosystems.

Introduction

Large vertebrate herbivores are key determinants of plant community composition, productivity and the functioning of many ecosystems worldwide (Olff and Ritchie, 1998; Knapp et al., 1999; Bardgett and Wardle, 2003; Cromsigt and Kuijper, 2011). One of the major pathways through which large herbivores affect the plant community is via their influence on nutrient cycling and soil nutrient availability (Fig. 1, McNaughton, 1984; Georgiadis et al., 1989; Hobbs, 1996; Frank et al., 2000; Bardgett and Wardle, 2003). Herbivores can either speed up or slow down rates of nitrogen (N) mineralization (Hobbs, 1996; Bardgett and Wardle, 2003). Classical theories that explain the impact of large herbivores on N cycling primarily focus on herbivore-induced changes in the quality and quantity of resources that are returned to the soil food web, i.e. dung, urine and plant litter (Fig. 1; McNaughton, 1984; McNaughton et al., 1997b; Bardgett and Wardle, 2003; Pastor et al., 2006). Herbivores speed up N mineralization through the deposition of dung and urine and by promotion of fast growing species and high quality (palatable) regrowth (with a low C/N-ratio), hence enhancing litter quality. In contrast, they slow down N

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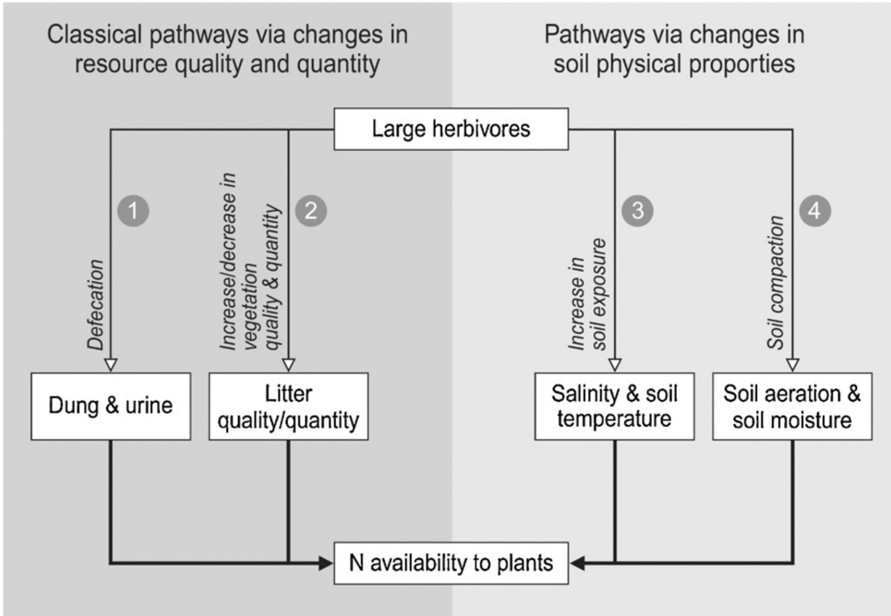

Fig. 1. Overview of the influence of large herbivores on the nitrogen (N) cycle in grasslands. This diagram depicts four main pathways via which herbivores can affect soil N mineralization. Prevailing theories mainly focus on pathways 1 and 2 via which herbivores alter the quality of resources entering the soil food web, i.e. by excreting dung and urine and by changing plant quality and quantity. Pathways 3 and 4 operate through soil physical properties. Pathway 3 describes the effects of herbivores on the exposure of bare soil, thereby increasing soil temperature or soil salinity (e.g. Gornall et al., 2009; Buckeridge and Jefferies, 2007). Pathway 4 represents effect of large herbivore trampling via soil compaction on soil moisture and soil aeration, which consequently affects N mineralization (discussed in this article).

mineralization rates when promoting low-quality plant species (with a high C/N ratio), hence decreasing litter quality (Hobbs, 1996; Ritchie et al., 1998). The acceleration of N mineralization rates through nutrient deposition and stimulation of plant growth is the basis of the grazing optimization hypothesis (McNaughton, 1979) which may apply under a restricted set of conditions (De Mazancourt et al., 1998).

Although changes in the quality of resource input into the soil food web can explain the impact of large herbivores on N cycling in a number of ecosystems (McNaughton, 1984; Pastor et al., 1993; Ritchie et al., 1998; Wardle et al., 2002; Harrison and Bardgett, 2004; Persson et al., 2005), they cannot explain contrasting effects of large herbivores on N mineralization in many other situations (e.g. Biondini et al., 1998; van Wijnen et al., 1999; Kiehl et al., 2001; Bakker et al., 2004; Su et al., 2004; Pei et al., 2008; Wang et al., 2010; Shan et al., 2011; Gass and Binkley, 2011). For example, in some systems plant quality increased under grazing, but mineralization rates were reduced (Chaneton and Lavado, 1996; van Wijnen et al., 1999; Kiehl et al., 2001). Even in a large-scale comparison across different sites herbivore effects on soil N cycling could not be understood from changes in plant quality (Bakker et al., 2006, 2009). Therefore, there is a need to explore additional mechanisms that can explain herbivore-induced changes in N cycling (Gass and Binkley, 2011).

In the current theories on large herbivores and N mineralization (McNaughton et al., 1997a; Bardgett and Wardle, 2003), impacts that run via soil physical conditions received little attention (Gass and Binkley, 2011). However, large herbivores can be major drivers of changes in soil physical conditions, for example, of soil moisture and oxygen contents and soil temperature (Fig. 2). This can in turn have important consequences for N mineralization rates (Hamza and Anderson, 2005). Therefore, in this paper we explore whether integrating herbivore-induced changes in soil physical conditions into current theories on N cycling in grazed systems will help us to understand when herbivores speed up or slow down N mineralization. We aim to reconcile contrasting observations into a novel perspective, to be able to understand the impact of herbivores on N mineralization across a wide range of ecosystems.

We start by proposing the key drivers of soil N mineralization, i.e. resource quality and quantity and soil physical conditions, that should be integrated into theories on N mineralization in grazed ecosystems. Then we use trampling-induced soil compaction as an example to illustrate in detail how herbivores can alter N mineralization via changing soil physical conditions and how an integrated perspective can help us to understand the impact of herbivores on N

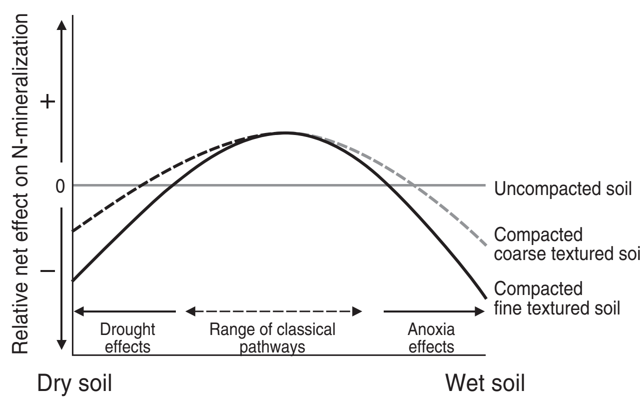

Fig. 2. Hypothetical changes in N mineralization as a result of herbivore trampling in soils with different textures. All effects are scaled relative to an uncompacted soil (dotted straight line). On a relatively fine-textured soil (clay: solid line) herbivore compaction may lead to soil anoxia (wet end of the gradient) and strongly reduced water infiltration (dry end of the gradient), both affecting net N mineralization negatively. These effects may outweigh the positive effects on N mineralization via litter quality and quantity. At intermediate moisture availability, effects that operate via increased plant quality, plant quantity, dung and urine) result in a positive effect of large herbivores on N mineralization. On a relatively coarse textured soil (sand: striped line), herbivore trampling induced effects on N mineralization are less pronounced, and may therefore be outweighed by effects through excreta, litter quantity and quality. Grey part of striped line indicates the range in which no studies were found.