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Research Paper

Effects of grazing abandonment on soil multifunctionality: The role of plant functional traits

B. Peco[a,*], E. Navarro[a], C.P. Carmona[b], N.G. Medina[c], M.J. Marques[d]

[a] Departamento de Ecología, Universidad Autónoma de Madrid, Spain
[b] Institute of Ecology and Earth Sciences, University of Tartu, Estonia
[c] Department of Botany, University of South Bohemia, Czech Republic
[d] Departamento de Geología y Geoquímica, Universidad Autónoma de Madrid, Spain

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ABSTRACT

Extensive livestock grazing is a global land use activity that has numerous social, cultural, and environmental benefits. Many marginal zones grazed for centuries are now suffering from abandonment, which has been found to be interrelated with species and functional diversity loss, and has potential consequences for the provision of ecosystem services such as soil fertility and soil carbon storage. We sampled soil and plant species abundance in a total of 64 plots (5 × 5 m), in wet and dry habitats under different grazing regimes (from moderate grazing to grazing abandonment for at least 30 years) in Central Spain. We tested the influence of grazing intensity and water availability on different variables related to soil fertility and also on soil carbon storage. In addition, Community weighted mean and Rao quadratic entropy were calculated for two effect traits (specific leaf area and plant height), in order to assess the ultimate effects of these functional attributes on multifunctionality (i.e., the provision of several simultaneous ecosystem functions). We found that grazing abandonment generally produces a reduction in soil organic matter, total nitrogen, available potassium and phosphorus, aggregate stability and soil carbon storage. In addition, grazing abandonment had a negative effect on soil texture with loss of fine particles (clay and silt) and water holding capacity, but only in dry habitats and in longer-term abandoned situation. In general, soil multifunctionality was higher in wet than dry habitats, decreased with grazing abandonment in both habitats. Soil multifunctionality was indirectly mediated by the functional structure of size and leaf traits of the local plant communities, but our results suggested that macroscale grazing effects, i.e. translocation of nutrients by grazers among habitats via dung and urine deposition, might be important mechanisms that influence soil multifunctionality at the local level. Agri-environmental policies should be aware of the risk of widespread grazing abandonment and take advantage of the benefits of low-intensity grazing regimes for ecosystem services such as soil fertility and stability, and soil carbon storage.

1. Introduction

Land use change, one of the major drivers of global change, is causing widespread changes in biodiversity, with consequences for ecosystem process and the services they provide to humans (Chapin, 2013). Extensive livestock systems provide a major contribution to world biodiversity. These are one of Europe's most threatened anthropogenic ecosystems as a result of a dual processes of intensification in the more productive and populated areas, and abandonment in marginal zones (Jepsen et al., 2015). While the effects of grazing abandonment on vegetation have been closely monitored (Carmona et al., 2015, 2012; Castro et al., 2010; Peco et al., 2005), relatively few studies have focused on the consequences of grazing abandonment for soil structure and function (Marriott et al., 2010; Peco et al., 2012, 2006; Stark et al., 2015), and ecosystem services such as soil fertility (Peco et al., 2012) and soil carbon storage (Guo and Gifford, 2002). Large herbivores have direct effects on nutrient cycling in ecosystems worldwide (Bardgett and Wardle, 2003). Herbivory also affects soil physical properties through trampling, compacting the soil and thus reducing its capacity to hold water and to supply oxygen to plant roots (Steffens et al., 2008). Herbivores may also influence nutrient cycling indirectly through changes to plant species composition and richness and plant functional structure. However, studies on nutrient cycling have generally ignored indirect effects (Valencia et al., 2015).

The effects of grazing on nutrient cycling depend on primary productivity. In productive habitats, urine and dung input increases labile

* Corresponding author.
E-mail address: begonna.peco@uam.es (B. Peco).

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organic matter and nitrogen (N) inputs to soil (Bardgett and Wardle, 2003; Harrison and Bardgett, 2008). Furthermore, increasing grazing intensity below the overgrazing threshold has been associated with higher microbial biomass-carbon and heterotrophic microorganisms (Prieto et al., 2011). Grazing also increases root/shoot ratio, root exudation, possibly primary production, and thus the availability of belowground labile organic substrates (Bardgett and Wardle, 2003). The main mechanisms behind this acceleration of nutrient cycling are increased soil temperature and temperature fluctuations, increased water-holding capacity by means of the input of organic matter with livestock faeces, and increased forage quality with greater tissue N concentration (Odriozola et al., 2014). On the other hand, negative effects of herbivory on soil biota and rates of nutrient cycling have been documented in unproductive ecosystems where browsing is more frequent than grazing (Harrison and Bardgett, 2008). These negative effects have been related to the dominance of defended plants that produce recalcitrant litter (Ritchie et al., 1998), or when excessive stocking densities affect soil physical properties, leading to lower microbial activity and increased nutrient loss through erosion (Steffens et al., 2008; Soliveres et al., 2014).

Livestock (particularly cattle) trampling can also modify physical attributes such as bulk density and soil penetration resistance and breaks up soil aggregates (Wen et al., 2016). Compacted soil is generally less fertile due to its lower aeration and water holding capacity (Bonneau and Souchier, 1982) which affects the presence/absence of different species, depending on the ease of rooting, nutrient uptake and root breathability (Marriott et al., 2010).

Finally, grazing also changes the floristic composition of plant communities through different mechanisms that affect the colonization-extinction dynamics of species (Olff and Ritchie, 1998), acting as a filter in the assembly of plant communities. Plants adopt two main strategies (avoidance and tolerance) to deal with grazing (az et al., 2007a,b; az et al., 2007a,b; Rota et al., 2017). Grazing-avoidant plants reduce their accessibility and/or palatability with traits such as short stature, rosette growth forms and small and/or tough leaves with small specific leaf area (SLA). On the other hand, grazing-tolerant plants usually have traits such as large SLA or high leaf N concentration to permit fast regrowth after defoliation. The SLA response to grazing seems to be dependent on productivity. In a productivity/water availability gradient, we should expect grazing-tolerant plant strategies to only appear when there is a sufficient availability of resources (Cingolani et al., 2005), given that these traits imply less efficient resource conservation. However, the effect of grazing on plant communities depends not only on ecosystem's productivity but also on its herbivory history (Díaz et al., 2007b).

Grazing abandonment in annual-dominated Mediterranean grasslands with a long history of grazing has been related to an increase in community plant height, seed weight, leaf dry weight, late flowering, perennial species, leaf dry matter content and low SLA, and a decrease in annual species and prostrate or rosette growth forms (Castro et al., 2010; Peco et al., 2012, 2006). However, the patterns of plant trait response to grazing abandonment are heavily dependent on habitat productivity and interannual variations in rainfall (Carmona et al., 2015). Grazing abandonment in these systems has also been related to a decrease in soil organic matter and soil fertility and fine soil particles (Farris et al., 2010; Peco et al., 2006, 2012). However, little attention has been paid to the potential role of grazing abandonment in ecosystem multifunctionality, defined as the provision of simultaneous multiple services (Valencia et al., 2015) through cascading effects in changing community functional structure.

A response-effect framework based on functional plant traits has been proposed to analyse the direct and indirect effects of drivers of global change such as grazing abandonment on ecosystem functioning (Lavorel and Garnier, 2002). Indirect effects occur through changes in community functional structure. Within this framework, response traits are those which change due to the effects of grazing on plant communities, while effect traits are those that can influence ecosystem processes. The same trait can be both a response and an effect trait. Grazing can, for example, promote species with a high SLA, and this trait can be positively related to decomposition rate (Garnier et al., 2004), which in turn affects nutrient availability in the soil. Furthermore, changes in community functional structure promote effects on multifunctionality via two non-exclusive mechanisms, the mass-ratio hypothesis (Grime, 1998) and the niche complementarity hypothesis. The mass-ratio hypothesis states that traits of the dominant species largely determine the effects of plant communities on ecosystem functioning. This hypothesis can be tested by analysing changes in the community weighted mean (CWM, reviewed in de Bello et al., 2010). However, grazing can also alter the distribution of traits values in the communities (functional diversity, FD), with high values of FD indicating high complementarity in resources use and therefore improved ecosystem functioning (Díaz et al., 2007a).

The overall aim of this paper is to assess the impact of grazing abandonment in comparison with moderate extensive grazing on annual-dominated Mediterranean grasslands. In particular, we evaluate (1) the effects of grazing abandonment on soil parameters related to soil fertility (soil texture and structure, nutrient content and microbial activity) and carbon storage (organic matter content and bulk density); (2) the relative importance of direct and indirect effects of abandonment on soil multifunctionality by means of structural equation models; and (3) the relative contribution of mass ratio (reflected by CWM) and niche complementarity (reflected by FD) on the indirect effects on ecosystem multifunctionality for two traits, SLA and plant height, which represent two key dimensions of plant functions (Diaz et al., 2016). Plant height regulates the responses to resource availability and disturbance, and can be interpreted as an indicator of successional status and response to grazing (Díaz et al., 2007b). SLA ($mm^2\ mg^{-1}$) is an indicator of resource-use strategies, with low SLA values associated with long-lived leaves, low relative growth rates and long-term residence times of nutrients (Westoby et al., 2002). We hypothesized that grazing abandonment of extensive pastures reduces soil organic matter, with negative consequences for other properties related to soil fertility and soil carbon storage. We also hypothesized the presence of taller plants with lower SLA values than in grazed pastures, which would reinforce the negative effects on nutrient cycling. Finally, we hypothesized that both mass-ratio and niche complementarity will be important to explain soil multifunctionality.

2. Material and methods

2.1. Study area

The study area was on the southern flank of Sierra de Guadarrama, 35 km north of Madrid, Spain (40°42′N, 3°39′W; at 860 m). The climate is Mediterranean with hot and dry summers (13° C annual mean) and peak rainfall in spring and autumn, with major fluctuations around the annual mean (540 mm). The relief generally consisted of gentle slopes (< 5%) with superficially acid soils (Dystric Cambisols pH = 5.3 ± 0.24) and occasional rocky outcrops above a gneiss substrate. In the open woodland vegetation, the predominant arboreal species were *Quercus ilex* subsp. *ballota* L. and *Juniperus oxycedrus* L., with approx. 40 trees/ha, while the grassland understorey contained a high percentage of annual species.

The study area has been grazed extensively for centuries by sheep. The gradual abandonment over the last 100 years in many parts of this area has been accompanied by changes to traditional grazing patterns and the replacement of sheep with free-grazing cattle and horses. This has generated a mosaic of zones with differing degree of grazing abandonment (Peco et al., 2005). In the grazed areas, the average stocking density is 0.5 LU ha^{-1} and herbivores consume about 80% of the grassland biomass production which is c.a. 350 g m^{-2} $year^{-1}$ of dry weight (unpublished data). Woody species (*Lavandula stoechas* subsp

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