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Understanding herbivore-plant-soil feedbacks to improve grazing management on Mediterranean mountain grasslands

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ABSTRACT

The surface of many European mountain grasslands is decreasing due to global change and extensive grazing stands out as a key tool for their conservation. Sound knowledge of grassland ecosystem functioning and its feedback processes is required to implement sustainable grazing management. This study aimed to understand the effect of different grazing intensities on herbivore-plant-soil feedbacks in Mediterranean mountain grasslands. We estimated spatial distribution of sheep grazing intensity using GPS technology in order to assess the effect of grazing pressure on vegetation and soil properties measured throughout the study area. Our results showed that grazing intensity ranged from 0.06 to 2.85 livestock units / ha, corresponding to a gradient of pasture utilisation rates varying from 2.38% to 45.60% of annual productivity from pasture. Increasing grazing pressure was associated with smaller relative cover and species richness of non-leguminous forbs, while the opposite trends were observed for graminoids. Forage had a greater concentration of N and smaller C:N ratio in more heavily grazed areas. Increasing grazing intensity was also associated with higher values of total soil N, NO_3^-, NH_4^+, soil organic carbon, microbial biomass C and activity of β-glucosidase. Higher litter quality was the main factor explaining greater content of soil organic matter, which favoured both soil microbes and plant productivity. Grazing induced changes in the plant community triggered positive hervibore-plant-soil feedbacks, as they ultimately improved forage quality and productivity, which significantly influenced the pasture preference of free-ranging domestic grazers. Our work showed that grazing management aiming pasture utilisation rates of around 45% is critical in sustaining positive herbivore-plant-soil feedbacks and preserving or enhancing the whole ecosystem functioning in the Mediterranean mountain grasslands studied.

1. Introduction

Conservation of grassland ecosystems is important for preserving the ecosystem services they provide, such as food production, biodiversity conservation or sequestration of CO_2 (Hopkins, 2009). Preserving these ecological systems is particularly challenging in European mountain regions due to socio-economic changes, which lead to land abandonment and modification of traditional grassland management, and together with global warming promote the encroachment of thermophilic and woody plants (Alados et al., 2014; Gartzia et al., 2016; Komac et al., 2013; MacDonald et al., 2000). In this context, adequate grazing management may be an important tool for grassland conservation and restoration (Komac et al., 2013; Lagendijk et al., 2017; Pykälä, 2003), especially when considering that domestic grazers are the only component of the pastoral system that can be readily managed on many summer mountain ranges (Komac et al., 2014).

Grazing is frequently associated with desirable changes in plant biodiversity, plant community composition and net aerial primary productivity of grasslands (Altesor et al., 2005; Komac et al., 2014; Nunes et al., 2019; Pykälä, 2003). Grazing may also increase forage quality by delaying ecological succession and keeping a low dead:live biomass ratio (Casasús et al., 2007; Milchunas et al., 1995; Pavlů et al., 2006; Wardle et al., 2004). However, excessive grazing pressure may lead to grassland degradation in terms of diversity, vegetation

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productivity and nutrient content (Aguiar et al., 1996; Austrheim et al., 2008; Komac et al., 2014; Škornik et al., 2010). Furthermore, grazing can modify soil properties such as bulk density (Abdalla et al., 2018; Pueyo et al., 2013), water infiltration (Pueyo et al., 2013), nutrient availability through facilitating nutrient cycling (Abdalla et al., 2018; Bardgett and Wardle, 2003; Medina-Roldán et al., 2012), soil temperature and microbial activity (Aldezabal et al., 2015; Bardgett and Wardle, 2003).

Knowing the functioning of pastoral ecosystems is critical to implementing sustainable grazing management. Good knowledge of plant-soil feedback processes and the effect of herbivory on these processes is required to understand the functioning of terrestrial ecosystems (Bardgett and Wardle, 2003). A feedback is a string of interactions that ends up affecting the conditions that originally caused the process. A feedback is said to be positive when the result of the process makes the process increase in magnitude, generating a cascade effect in a certain direction (Ehrenfeld et al., 2005). There are several studies focused on the impact of herbivores on plant-soil feedbacks (e.g. Chen et al., 2017; Medina-Roldán et al., 2012; Veen et al., 2014). They address the question of how diverse grazing intensities imposed in the study area (or grazing presence/absence) affect different plant-soil feedbacks. However, little has been done to advance understanding of how these modified plant-soil feedback patterns may impact on freely moving herbivores. It is known that pasture quality and productivity determines the selection patterns of grazers (Durant et al., 2004; Laca et al., 2010; Treydte et al., 2013). Therefore, it would make sense considering herbivore-plant-soil feedback processes, because the changes in the plant community and associated soil environment caused by herbivores will ultimately affect the behaviour and productivity of free-ranging grazers.

Global positioning systems (GPS) have increasingly been used during the last 2 decades for tracking movements of free-ranging animals (e.g. Liu et al., 2018; Turner et al., 2000). This technology has multiple applications for grazing management, such as assessment of habitat use (Putfarken et al., 2008) or animal activity (Augustine and Derner, 2013). GPS technology has also been used to estimate grazing pressure (Akasbi et al., 2012).

The main goal of this study was to improve knowledge on herbivore-plant-soil feedbacks in order to gain information on grazing management in Mediterranean mountain grasslands. Specific objectives of this research included (1) analysing the main effects of increasing grazing intensity on the plant-soil feedbacks of the studied grasslands; (2) understanding how these changes in plant-soil feedbacks may affect the grazing behaviour of free-ranging domestic grazers; (3) identifying the main feedback mechanisms operating in the study area, based on a complex conceptual-hypothetical model that includes previously described interactions within the herbivore-plant-soil system (Fig. 1).

We hypothesised that (1) grazing intensity around the recommended pasture utilisation rate for humid grasslands would promote diverse grasslands with a greater proportion of species of high pastoral value, because it would prevent the colonisation of unpalatable and nutrient-poor plant species associated with later stages in the ecological succession of sub-alpine grasslands. (2) This properly-grazed, diverse ecosystem would be more productive because nutrient cycling would benefit from nutrient-rich plant material and labile organic matter from animal excreta. In addition, the higher diversity expected in grazed pastures should promote more efficient use of resources, due to niche complementarity among plant species. (3) As a result of the previous hypotheses, high grazing intensity (without reaching overgrazing) would be part of positive feedback processes on the herbivore-plant-soil system, because the changes caused by the livestock on the vegetation and soil of grasslands will benefit more productive and nutritious pastures that will be preferred by free-ranging grazers.

2. Methods and materials

2.1. Study area

The study was carried out within the natural protected area Parque Natural de Sierra y Cañones de Guara, located on a mountain ridge limiting the southern section of the Spanish Central Pyrenees. The study area extends over 358.42 ha, with the centre located at 42.3045° N, 0.1749° W. This region has a Mediterranean climate with an oceanic influence. Mean annual precipitation and temperature are 944 mm and 8.6 °C, respectively. Mean annual maximum and minimum temperatures are 12.8 °C and 4.3 °C, respectively (Cuadrat et al., 2007). The

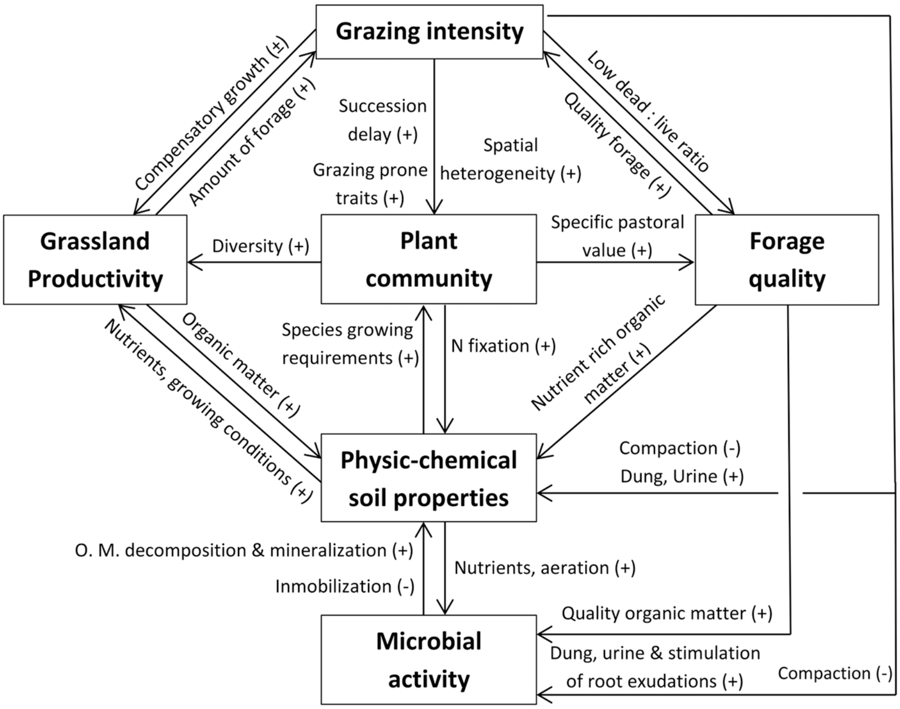

Fig. 1. Conceptual model showing the functioning of Mediterranean mountain grasslands based on interactions within the herbivore-plant-soil system described on previous research. The direction of the interactions is that expected in grasslands which are not overgrazed. (+) = positive interaction, (-) = negative interaction, (±) = interaction may be positive or negative. (Abdalla et al., 2018; Altesor et al., 2005; Bardgett and Wardle, 2003; Butterbach-Bahl et al., 2011; Chen et al., 2017; Ehrenfeld et al., 2005; Hector, 1999; Laca et al., 2010; Magdoff and Van Es, 2009; Milchunas et al., 1995; Oesterheld and McNaughton, 1991; Pavlů et al., 2006; Peco et al., 2005; Pueyo et al., 2013; Tilman et al., 2001; Treydte et al., 2013).

grasslands under study stood between 1200 and 1500 m a.s.l. and are included within the priority habitat category 6210 “Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia)” (European Commission, 2013). The studied sub-alpine grasslands were created as consequence of a long history of agro-pastoral practices in the area, which transformed the original forested ecosystem creating a mosaic of open spaces among forested/ shrubby areas (Riedel, 2007). The slope of all the studied areas was negligible. Extensive grazing by Rasa Aragonesa sheep flocks averaging 506 adult ewes is common in the area. However, breeding intensification practices, depopulation trends and poor communication with remote areas are leading to the abandonment of remote pastures, which are progressively colonised by woody plant species associated with later stages of ecological succession, causing grassland degradation (Bernués et al., 2005; Riedel, 2007).

2.2. Grazing pressure estimation

The study area was grazed by a local flock of 700 Rasa Aragonesa sheep during 90 non-consecutive days between mid-July and early November 2017, following tradition. The movement of the free ranging herd was recorded using a GPS device (SPOT trace https://www.findmespot.com/es-es/products-services/spot-trace) attached to the collar of one sheep, which recorded the position of the animal every hour. The local shepherd selected an old sheep with well-known leadership to carry out the GPS, because its movements would be followed by the majority (or, at least, many individuals) of the flock. It was considered that the animal was grazing when the average speed from the previous point was greater than 1 m/min and smaller than 20 m/min (Putfarken et al., 2008). As we were only interested in the location of the animal when it was grazing, the rest of the animal locations were discarded. The resulting sheep movement database was used along with the following formula (Eq. 1), modified from Akasbi et al. (2012), to estimate the spatial variations of grazing intensity using ArcGIS 10.4.1 (ESRI, 2016):

$$G.I. = \frac{No.\ animals * Point\ density * Recording\ interval * Livestock\ conversion\ factor}{Total\ number\ of\ sheep\ locations} \tag{1}$$

Where *G.I.* is the number of livestock units/ha estimated for each 10 m size pixel; *No. animals* is 700 sheep; *Point density* is the number of sheep locations/ha estimated for each 10 m size pixel using the kernel density tool in ArcGIS; *Recording interval* is number of hours between two consecutive GPS fixes, i.e. 1 h; *Livestock conversion factor* is 0.125 livestock units/animal, i.e. the average livestock unit value officially assigned to an adult sheep in Spain (MARM, 2010).

Autocorrelation of the dataset was tested following the procedure suggested by Perotto-Baldivieso et al. (2012). The Pearson test revealed very weak correlation between successive sheep positions ($r = 0.128$, $P = 0.056$), thus we considered the selected time interval between GPS fixes to be adequate for using the Kernel density estimator.

2.3. Experimental design

On April 2017, 8 square sampling plots of 40 m x 40 m were distributed across the study site in order to represent a gradient from very low to approximately the highest grazing intensity in the area. The location of the plots was based on previous knowledge of the study area and advice from local shepherds. Each sampling plot consisted of 5 independent 1 m x 1 m quadrats located in the corners and the centre or the plot, where soil, vegetation and excrement surveys were performed. In addition, three 1 m x 0.2 m vegetation samples were harvested within each of the 8 sampling plots in order to analyse pasture nutrients. Vegetation and soil surveys were carried out in early July, at the peak of vegetation growth. The number of excrements in every quadrat was counted at the end of the grazing season. The central quadrat was fenced off in July 2017 to prevent grazing and obtain an accurate measure of grassland annual productivity in undisturbed conditions on July 2018.

2.4. Vegetation cover and productivity surveys

The canopy cover of every species within the 1 m^2 quadrats was included in one of the cover categories defined by Daubenmire (1959). A wooden frame and ropes were used to divide the 1 m^2 quadrat into 100 squares in order to facilitate visual estimation of the canopy cover of the plant species. Three random measures were taken with a semi-rigid measuring tape in order to estimate the average height of each species occurring within a sampling quadrat. Plant species were classified into the following functional groups: graminoids, legumes, herbs (non-leguminous forbs), and woody plants.

The annual productivity in pasture from each 40 m x 40 m sampling plot was estimated as the dry matter produced within the fenced-off quadrats at the peak of vegetation growth after one year of grazing exclusion. Vegetation samples of 1 m × 0.2 m were cut with mechanical scissors at ground level within the enclosures. Pasture samples were oven-dried at 60 ^{o}C for three days and weighed on a precision scale. As productivity was only measured on fenced off quadrats, the weighted height of all the species occurring within a quadrat was used as a productivity proxy for statistical analyses (Eq. 2), because it had a significantly strong correlation with productivity within the fenced off quadrats ($r = 0.855$, $P < 0.05$):

$$Weighted\ \ height = \sum \left(\frac{species\ \ cover_i}{total\ \ cover} * \ \ species\ \ height_i \right) \tag{2}$$

Where *species cover$_i$* is the midpoint of the cover class for the species *i* within a given quadrat; *total cover* is the sum of the cover class midpoints of every species found in the quadrat; and *species height$_i$* is the average height of species *i* in the quadrat.

2.5. Pasture nutrient estimation

A total of 24 pasture samples of 1 m × 0.2 m were cut using mechanical scissors (three pasture samples within each 40 m × 40 m sampling plot). These samples were more than 20 m apart from each other. They were oven-dried at 60 °C for 3 days and ground for analysis. Total N and C content were measured using a Variomax CN elemental analyser. The fibre composition analysis was carried out following the procedure proposed by Van Soest et al. (1991). Potential digestibility was estimated from the results of the fibre analysis using the equation defined by Van Soest (1994).

2.6. Soil surveys and laboratory analyses

Four soil cores 5 cm in height and diameter were collected within every 1 m x 1 m quadrat in order to quantify several physical-chemical and biological soil properties. Two of the cores were used to estimate soil bulk density (Grossman and Reinsch, 2002). The soil from the other two cores was passed through a 2 mm sieve. A fraction of each soil sample was stored at 4 °C and the rest was oven-dried at 60 °C for three days. Fresh soil was used to estimate microbial biomass C as proposed by Vance et al. (1987), $N\text{-}NO_3^-$ as described by Kaneko et al. (2010), $N\text{-}NH_4^+$ by using the salicylate method (Kempers and Zweers, 1986), and activity rate of the C-liberating enzyme β-glucosidase and the P-liberating enzyme phosphatase as proposed by Tabatabai (1994). Dry soil was used to quantify total soil N with a Variomax CN elemental analyser, the content of soil organic carbon (SOC) as proposed by (Heanes, 1984), and the soil available P (Bray and Kurtz, 1945).

2.7. Statistical analyses

Non-metric multidimensional scaling (NMDS) of the Bray-Curtis dissimilarity metrics and permutational (9999 permutations) multivariate analysis of variance (perMANOVA) with the *"Adonis"* function in the *vegan* package in R (Oksanen et al., 2019) were used to assess the effect of grazing on plant species composition. To this end, quadrats were grouped in three categories of grazing intensity: high, containing the 33% of quadrats with higher grazing intensity; low, containing the 33% of quadrats with lower grazing intensity; medium, containing the rest of the quadrats. The Kruskal-Wallis test and the post-hoc Mann-Whitney *U* test were used to identify changes in species cover between the three groups of grazing intensity. Every species was given a value from 0 to 5 corresponding to its specific quality index (Is), which is based on productivity, palatability and nutritional value (Ascaso and Ferrer, 1993; Daget and Poissonet, 1971). Plant species were reclassified into three categories of pasture quality: low, when *Is* is equal to 0 or 1; medium, when *Is* equals 2 or 3; high, when *Is* equals 4 or 5 (Table B1-Appendix B).

Linear mixed-effects models (LMM) were used to study the effect of grazing intensity on the physical-chemical and microbiological soil properties, vegetation diversity (species richness and Shannon index) and the structure of the pasture (relative cover of each functional group) with the *nlme* package in R (Pinheiro et al., 2020). The sampling plots of 40 m x 40 m were used as a random factor in the LMM analyses. Models *with* and *without* grazing intensity as an explanatory fixed-factor were compared using the likelihood ratio test in order to find whether the level of grazing pressure significantly affected the variables of interest.

According to the conceptual model (Fig. 1) there is a direct positive feedback process between pasture nutrient content and grazing intensity when the grassland is not overgrazed, thus it would be difficult to define whether a given variable is the cause or effect in an LMM. A similar issue occurred when assessing the relationship between grazing and grassland productivity. For this reason we ran Spearman correlation tests instead with the *"rcorr"* function in the *Hmisc* package in R (Harrell and Dupont, 2020) to analyse the relationship between grazing and both pasture productivity and quality.

Structural equation models (SEM) were used in order to assess ecosystem functioning and feedback processes in the grasslands under study with the *"sem"* function in the *lavaan* package in R (Rosseel et al., 2019). Non-significant weak interactions between variables were progressively removed from the hypothetical model in order to generate a more parsimonious model. Grazing intensity was used as the variable to represent the degree of perturbation caused by grazers. We assumed that this variable accounted for the effect of excrement depositions, as LMM showed a significant positive relationship between grazing intensity and the number of excrements ($X^2_{(1)} = 4.267$, $P = 0.039$). SOC (i.e. the carbon component of soil organic matter) was used as an indicator of soil physical-chemical properties, because organic matter is directly or indirectly linked to many of these (Magdoff and Van Es, 2009). Microbial biomass C was chosen as an indicator of soil microbiological activity. Species richness of forbs was selected as the variable for characterising the diversity and structure of the grassland. Weighted height was used as a proxy for pasture productivity. C:N ratio of plants was used as an indicator of forage quality, as it is a good indicator of the ease with which vegetation decomposes (Nicolardot et al., 2001) and it was strongly correlated with plant N ($r = -0.978$, $P < 0.001$).

As the samples for plant nutrient analyses were gathered outside the 1 m × 1 m quadrats where soil and vegetation cover sampling was carried out, the value of pasture C:N ratio corresponding to each quadrat was simulated using the "boot" function within the *boot* package in R (Canty and Ripley, 2019). The value assigned to each quadrat was the average of 500 random combinations of the C:N ratio measured for the three pasture samples taken within the 40 m × 40 m sampling plot in which the 1 m × 1 m quadrat is located. All statistical analyses were carried out in R version 3.4.2 (R Core Team, 2017).

3. Results

3.1. Grazing pressure

The grazing intensity calculated with the GPS data for the locations of the sampling plots ranged from 0.06 to 2.83 livestock units/ha, whereas the maximum estimated for the study area was 2.85 livestock units/ha. When comparing these grazing intensities against grassland productivity, we estimated that the flock of sheep consumed between 2.38% and 45.60% of the annual forage dry biomass production in the sampling plots during the grazing season (Appendix A). The average grazing intensity estimated for all the quadrats included in the same category of grazing intensity was: high, 2.06 livestock units/ha; medium, 0.67 livestock units/ha; low, 0.12 livestock units/ha.

3.2. Effects of grazing on grassland biodiversity and community structure

The NMDS showed significant differences in plant composition, depending upon grazing intensity ($F_{2,\ 44} = 1.673$, $P < 0.001$, stress = 0.159). High grazing intensity showed a different composition from medium and low grazing pressure that appeared to overlap (Fig. 2). The Kruskal-Wallis and Mann-Whitney *U* tests revealed that, among the plant species presenting significant changes in cover at different grazing intensities, the majority of the species of medium to excellent specific quality index showed an increase in cover in high grazing intensity quadrats. On the contrary, most of the species in the lower specific quality index categories showed a significant decrease in cover under high grazing intensity (Fig. B1-Appendix B). The total cover of all species included in the high pasture quality category was greater in high, rather than low, grazing intensity. A similar trend was observed in the total cover of all the species within the medium pasture quality category, while the opposite tendency was detected in the total cover of all the species included in the low quality pasture category (Fig. B2-Appendix B).

The LMM analyses and the likelihood ratio tests revealed that

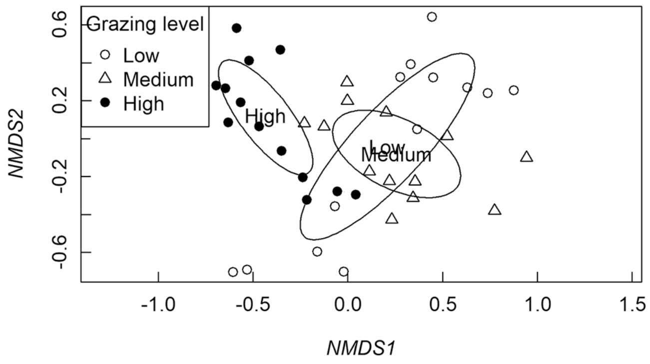

Fig. 2. Non-metric multidimensional scaling (NMDS) of the Bray-Curtis dissimilarity metrics (n = 40; $F_{2,\ 44} = 1.673$, $P < 0.001$, stress = 0.159). High: 33% of 1 m^2 quadrats with higher grazing intensity (n = 14); Low: 33% of 1 m^2 quadrats with lower grazing intensity (n = 13); Medium: the other 33% of quadrats (n = 13).

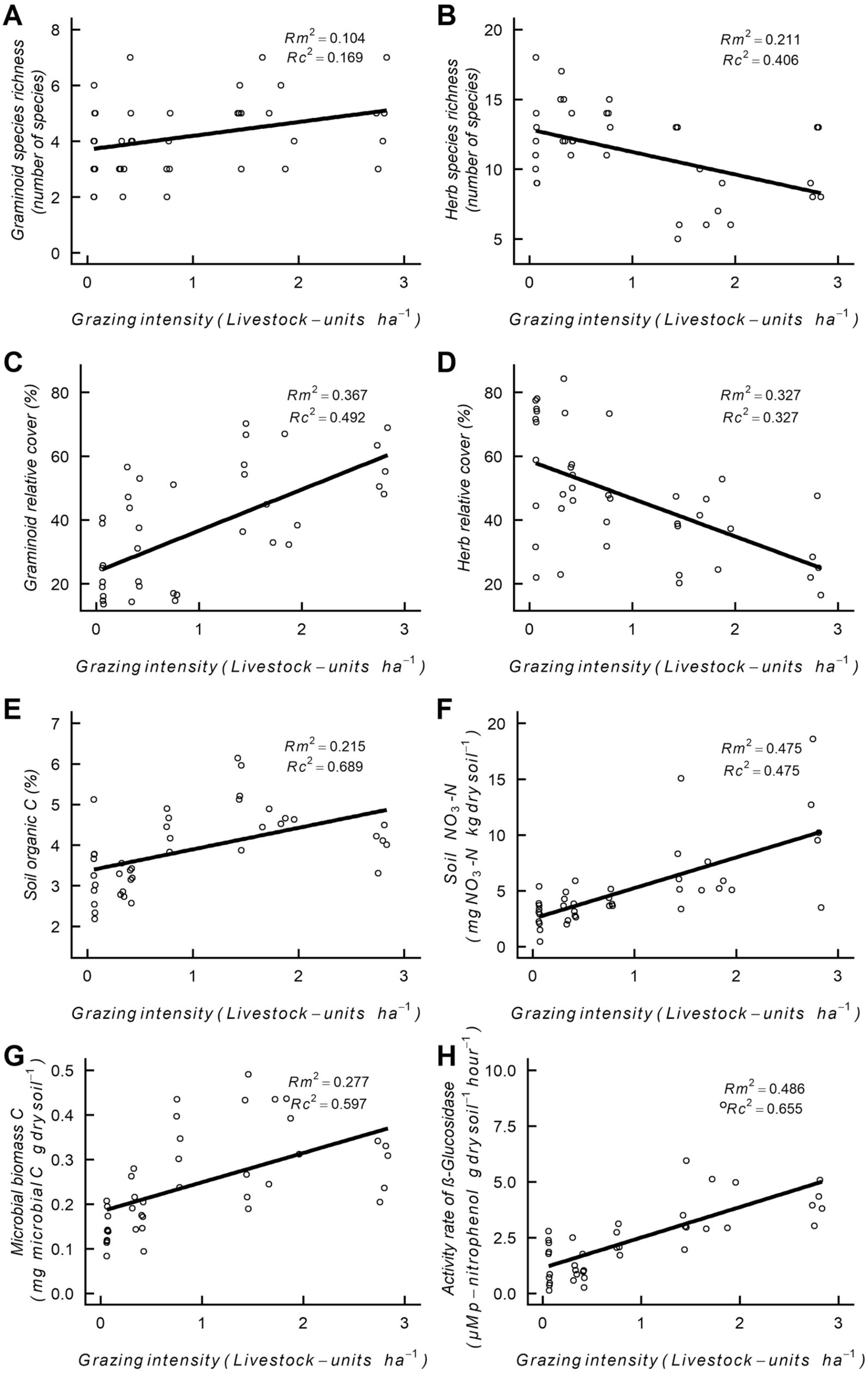

Fig. 3. LMM showing the effects of grazing intensity on vegetation composition and soil properties of the Mediterranean mountain grasslands studied (n = 40): (A) Species richness of graminoids in 1 m^2 quadrats at increasing grazing intensity; (B) Species richness of herbs in 1 m^2 quadrat as a function of grazing intensity; (C) Effect of grazing intensity on the relative cover of graminoids; (D) Effect of grazing intensity on the relative cover of herbs; (E) % of soil organic carbon at increasing grazing intensity; (F) Variation of N from NO_3^- at different grazing intensities; (G) Soil microbial biomass C at increasing grazing intensity; (H) rate of enzymatic activity of β-Glucosidase as at different grazing intensities. Rm^2 = marginal R^2 (i.e. percentage of the dependent variable explained by the fixed factors of the LMM). Rc^2 = conditional R^2 (i.e. percentage of the dependent variable explained by the LMM, including both fixed and random factors). Significance of the effects can be found in the results section (Subsections 3.2 and 3.4).

increasing grazing intensity affected the species richness of the 1 m^2 quadrats negatively ($X^2_{(1)} = 4.084$, $P = 0.043$), but had a negligible effect on the Shannon diversity index. When looking at the functional groups, the analyses showed that lower grazing intensities were related to a higher herb relative cover ($X^2_{(1)} = 13.212$, $P < 0.001$) and number of species ($X^2_{(1)} = 5.110$, $P = 0.024$) within the quadrats (Fig. 3). On the contrary, increasing grazing intensity favoured greater graminoid relative cover ($X^2_{(1)} = 8.950$, $P = 0.003$) and species richness ($X^2_{(1)} = 3.642$, $P = 0.056$). Neither the species richness nor the relative cover of legumes and woody plants were significantly affected by the level of grazing.

3.3. Grazing intensity vs. pasture nutrient content and productivity

Grazing intensity had a moderate positive correlation with dry biomass and N content of the pasture. On the contrary, it had a moderate negative relationship with the C:N ratio of the vegetation (Table 1). Grazing intensity had a weak, marginally-significant positive relationship with neutral detergent fibre. There was no significant correlation between grazing intensity and other variables related to pasture digestibility (i.e. acid detergent fibre and potential digestibility).

3.4. Grazing intensity and soil properties

Increasing grazing intensity positively affected the amount of total soil N ($X^2_{(1)} = 3.906$, $P = 0.048$), soil inorganic N from NO_3^- ($X^2_{(1)} = 15.794$, $P < 0.001$) and NH_4^+ ($X^2_{(1)} = 6.397$, $P = 0.011$), soil organic C ($X^2_{(1)} = 3.364$, $P = 0.067$), soil microbial biomass C ($X^2_{(1)} = 5.140$, $P = 0.023$), and the activity rate of β-glucosidase ($X^2_{(1)} = 10.725$, $P = 0.001$) (Fig. 3). The soil bulk density slightly decreased in areas of greater grazing pressure ($X^2_{(1)} = 2.272$, $P = 0.099$). The amount of available P in soil and the activity rate of phosphatase were not significantly affected by the amount of grazing.

3.5. Herbivore-plant-soil-feedbacks

The results of the analysis using SEM, showing the main herbivore-plant-soil feedbacks operating on the study area are presented on Fig. 4. The saturated model showed that many of the interactions followed the direction predicted in the conceptual model shown in Fig. 1, though few of them were significant. The results of this model are not presented, as it was over-fitted due to the high number of interactions in relation to the number of observations. The parsimonious model indicated that grazing affected the plant composition of the grassland. These changes in the plant community had a positive effect on the vegetation nutrient content. This improvement in vegetation nutrient properties had a positive effect on soil nutrient cycling and soil microbial activity, which also had a positive effect on grassland productivity. Finally, the model illustrated that both higher grassland productivity and plant nutrient content are two important factors defining the site preference of grazers. In summary, the parsimonious model displayed two positive feedback mechanisms because the changes in grassland plant composition caused by grazing had positive (direct or indirect) effects on vegetation nutrient quality and productivity, which are at the same time beneficial for grazers.

Table 1
Spearman correlation tests between grazing intensity and pasture nutritious traits. NDF = neutral detergent fibre; ADF = acid detergent fibre; n = 24.

	r	P-value
Dry biomass	0.690	<0.001
% N	0.551	0.005
% NDF	0.367	0.078
% ADF	0.142	0.509
Potential digestibility	-0.025	0.907
C:N	-0.586	0.003

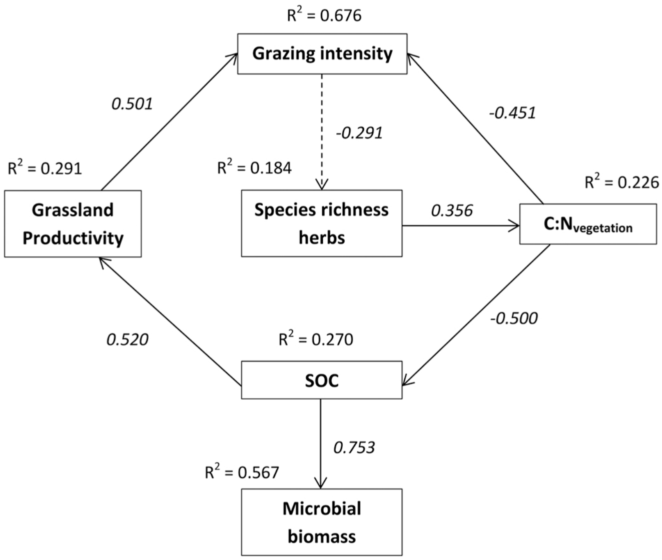

Fig. 4. Structural equation model showing herbivore-plant-soil feedbacks in the Mediterranean mountain grasslands studied (n = 40, X^2 =14.813, df = 8, $P = 0.063$, RMSE = 0.159). Grassland productivity is estimated with the proxy “weighted height”. SOC = soil organic carbon. Solid lines represent significant interactions ($P < 0.05$) and dashed lines represent marginally significant interactions ($P < 0.1$). Figures in italicface correspond to standardised path coefficients.

4. Discussion

This study analysed the effect of grazing on plant community and soil properties in Mediterranean mountain grasslands. Augmenting grazing pressure had positive effects on plant nutritive quality and soil properties, and enhanced soil nutrient cycling and grassland productivity. Therefore the results of this study showed positive feedback mechanisms in the herbivore-plant-soil system that may have important implications for grassland management and conservation.

In this research we observed that increasing grazing pressure close to the 50% pasture utilisation rate recommended for humid grasslands by Galt et al. (2000) was positively related with several vegetation and soil properties in the Mediterranean mountain grasslands studied. Previous studies have associated different grazing intensities to positive or negative impacts on the plant community or soil properties (e.g. Abdalla et al., 2018; Austrheim et al., 2008; Chen et al., 2017; Wei et al., 2011), but our research also traced the main paths or mechanisms causing such changes in the ecosystem. The SEM showed that modifications in the plant community caused by grazing are the main drivers of the variations in pasture productivity, forage quality, and physical-chemical and microbiological soil properties (Fig. 4). Many authors mentioned the important role of grazer excrements on soil nutrient cycling as they provide labile organic matter to the soil (Aldezabal et al., 2015; Bardgett and Wardle, 2003; Mathews et al., 1994; Medina-Roldán et al., 2012). However, our results suggest that the proportion of easily decomposable vegetation in the ecosystem under study, which was associated with changes in the plant community caused by grazers, is a more relevant factor influencing the amount of organic matter incorporated into the soil. This could be explained by the fact that palatable nutrient-rich vegetation with little recalcitrant organic compounds would decompose easily and may also influence the nutrient content in the excreta (Bardgett and Wardle, 2003; Nicolardot et al., 2001; Van Soest, 1994). This agrees with previous research also suggesting that one of the main ways grazing affects ecosystem functioning is through changes in vegetation quality, biomass, and/or functional type composition (Aguiar et al., 1996; Austrheim et al., 2008; Bardgett and Wardle, 2003; Chuan et al., 2020).

The plant community in areas under high grazing intensity was different from that found in areas of low and medium grazing intensity (Fig. 2). In addition, the species richness at 1 m^2 was negatively affected by grazing intensity in the study area. Although grazing is usually associated with increases in plant diversity (Altesor et al., 2005; Pavlů et al., 2007; Pykälä, 2003), heavy grazing can lead to a decrease in species richness (Škornik et al., 2010; Wei et al., 2011). Nevertheless, we do not consider the negative relationship between grazing pressure and species richness to be an indicator of excessive grazing in the study area. Grazing abandonment can favour the growth of less grazing-adapted species, low palatability species and woody plants (Aldezabal et al., 2015; Casasús et al., 2007; Medina-Roldán et al., 2012; Peco et al., 2005). Wardle et al. (2004) pointed that grazing in fertile, productive ecosystems tends to retard succession. Therefore, we believe that the zones under lower grazing pressure within our study area are in an intermediate situation in which grazing intensity is not enough to prevent the progressive colonisation of new species associated to later stages of ecological succession, while many species of the original grasslands are still on site. In agreement with this reasoning, Bernués et al. (2005) also found that grazing reduced the rate of woody plants encroachment in grasslands located in Sierra de Guara. Kahmen and Poschlod (2008) found that selective grazing, which is especially high at low grazing intensities (Nunes et al., 2019), benefited the spread of unpalatable species. This is supported by our results, which showed greater cover of several species with little pastoral value on areas of low grazing pressure (Fig. B1).

Higher grazing intensity was associated with greater graminoid species richness and relative cover, whereas the opposite was observed for herbs (Fig. 3). Some studies found forbs to benefit from grazing (Aldezabal et al., 2015; Altesor et al., 2005; Semmartin et al., 2004), while others detected a greater abundance of graminoids in grazed areas (Austrheim et al., 2008; Medina-Roldán et al., 2012). Peco et al. (2005) pointed out that the changes in the plant composition caused by grazing are difficult to compare between sites. It is a more common consensus that suitable levels of grazing in productive ecosystems (normally associated with humid regions) will favour smaller grazing-adapted species which usually have a greater pastoral value and high quality litter (Altesor et al., 2005; Pavlů et al., 2007; Semmartin et al., 2004; Wardle et al., 2004). Our results support these findings, as the cover of some species of medium to excellent specific quality index was significantly greater in areas under high grazing intensity (Fig. B1). Among these species are *Poa bulbosa*, *Phleum pratense* and *Trifolium repens*, which have also been found to benefit from grazing in other studies (Pavlů et al., 2007; Peco et al., 2005). These changes in plant composition caused a significant increase in the cover of species with medium to high pastural value in areas of high grazing intensity (Fig. B2). This explains the positive relationships between grazing pressure and nutritive properties of forage (Table 1). Lower dead:live biomass ratio associated with areas under high grazing intensity may also contribute to enhancing forage quality (Milchunas et al., 1995; Pavlů et al., 2006), but the SEM analysis indicated that this effect is not significant in the study site. In areas of greater grazing intensity (i.e. where the cover of medium and high quality pasture species increased) we found higher values of N content and smaller values of C:N ratio in vegetation. Rumen micro-organisms need N to digest forages. In addition, it is the main constituent of proteins forming muscles and organs (Butler et al., 1997). A high C:N ratio is associated with complex polymers such as lignin and polyphenols (Nicolardot et al., 2001), which are difficult to digest by ruminants (Van Soest, 1994). Despite the increase in the relative cover of graminoids with increasing grazing intensity, the results of the study did not display clear signs of reduced digestibility in these areas, because we only found a weak positive correlation between NDF and grazing pressure. Although both NDF and ADF reduce energy-use efficiency (Stergiadis et al., 2015), ADF is more frequently associated with reduced digestibility of forage and NDF to voluntary intake (Van Soest, 1994). Furthermore, we detected no significant changes in potential digestibility, which takes into account NDF, ADF and acid detergent lignin (ADL). On the other hand, Stergiadis et al. (2015) found quadratic relationships showing that increasing N concentration up to 35 and 33 g/ kg of forage dry matter enhanced digestibility of both N and organic matter in fresh grass cuts, respectively. As the N content of forage in the study area was below any of these thresholds, there could have been an increase in forage digestibility in more heavily grazed areas that was not revealed by Van Soest's equation of potential digestibility, which does not take into account forage N content. In support of our first hypothesis, we can assert that grazing pressure around a pasture utilisation rate of 40–45% was beneficial for biodiversity conservation of the Mediterranean mountain grassland studied and for improving its forage quality.

The structural equation model identified forage quality, which was positively influenced by changes in plant composition caused by increasing grazing pressure, as the main driver of nutrient cycling in the studied ecosystem (Fig. 4). It is commonly accepted that forage with a low C:N ratio promotes soil nutrient release (Semmartin et al., 2004). Chuan et al. (2020) found that grazing also favoured the growth of quality pasture and easily decomposable litter in relatively wet productive grasslands in Canada, boosting microbial activity and nutrient cycling. In agreement with other studies, increasing grazing intensity in the study site was related to higher content of soil total N (Wei et al., 2011), soil inorganic N (Chen et al., 2017), SOC (Wei et al., 2011; Zhang et al., 2018), soil microbial biomass C (Aldezabal et al., 2015; Zhang et al., 2018) and activity of β-glucosidase (Aldezabal et al., 2015; Chuan et al., 2020). Other studies observed that increasing grazing pressure was associated with decreasing levels of total N, activity of β-glucosidase, SOC, and microbial biomass C (Holt, 1997; Prieto et al., 2011). These works either mentioned overgrazing as the cause of these changes or showed results pointing in that direction (e.g. decreasing vegetation cover at higher grazing levels). Our study covered a range of grazing pressures from very low to approximately the maximum advisable intensity for this type of grassland (Galt et al., 2000), suggesting that the positive effects of increasing grazing pressure observed in our study area may change direction and / or magnitude if grazing intensity is not managed adequately.

Previously described positive effects from grazing, such as a higher concentration of available P (Wei et al., 2011) or greater activity rate of phosphatase (Aldezabal et al., 2015; Chuan et al., 2020) were not observed in this study. However, there is some controversy about the effect of grazing on available P. In agreement with our results, Chen et al. (2017) found no correlation between grazing intensity and available P, whereas Mathews et al. (1994) only found a significant positive relationship between grazing and extractable P in areas of very high dung density. Unexpectedly, higher grazing intensity tended to decrease soil bulk density in the study area. Grazing has very frequently been associated to soil compaction (Abdalla et al., 2018; Medina-Roldán et al., 2012; Prieto et al., 2011; Pueyo et al., 2013). Sheep trampling may cause less compaction than cattle trampling at a given stocking rate (Cournane et al., 2011). We think that the positive effects on soil structure caused by the higher amount of soil organic matter in areas under higher grazing intensity may overcome the compaction produced by the current intensity of sheep trampling.

Our results showed that organic matter in soil was the main factor determining microbial biomass C in the grasslands studied. Although factors like soil temperature and moisture may influence soil microbiological activity (Aldezabal et al., 2015; Olivera et al., 2014; Zhang et al., 2018), many authors highlighted the importance of organic matter for soil microorganisms and enzymatic activity, because it modifies the physical environment and is an important source of nutrients (e.g. Holt, 1997; Magdoff and Van Es, 2009; Olivera et al., 2014; Rice, 2005). High levels of microbial activity are related to good soil ecosystem functioning and are important to enhance nutrient release for plants, which has a positive impact on forage production (Aldezabal et al., 2015; Magdoff and Van Es, 2009). Regarding our second hypothesis, the results of this study showed that the enhanced soil nutrient cycling caused by changes in the plant community induced by grazing is positively related to aerial productivity. Indeed, the SEM indicated that soil organic carbon, which strongly correlated with total soil N ($r = 0.918$, $P < 0.001$), is the most significant factor determining aerial biomass productivity in the mountain grasslands under study. Previous research noticed that increasing levels of species and functional group richness are positively associated to aerial biomass production (Hector, 1999; Tilman et al., 2001, 1996). These authors stated that higher plant diversity implies a more efficient use of the system resources as different species occupy different ecosystem niches. However, our parsimonious SEM indicated that the relationship between biodiversity and vegetation productivity is not significant. These studies compared productivity between systems that range from monocultures to relatively diverse systems (e.g. up to 32 species in 4 m^2 plots). The difference in species richness observed between lightly grazed and heavily grazed areas in our study site was much smaller, thus the magnitude of the effect of plant diversity on aerial productivity should be much more subtle in this ecosystem than in the aforementioned studies. Grazing may induce higher relative growth rates in defoliated plants, which could partially or totally compensate for the biomass eaten by grazers. In addition, overcompensation can increase the yield to grazers, i.e. the sum of standing live biomass and tissue eaten by grazers (Oesterheld and McNaughton, 1991).

The results of the current study suggested that spatial patterns of grazing intensity of free-ranging sheep are driven by both pasture quality and productivity. Previous research suggested that grazer selective behaviour was influenced by pasture quality (Durant et al., 2004; Laca et al., 2010; Treydte et al., 2013), although larger animals tend to be less selective at finer spatial scales (Laca et al., 2010). The two main reasons behind this behaviour pattern could be that (1) large grazers tend to have a digestive system more adapted to extracting energy from high-fibre forage (Shipley, 1999); (2) there is a balance between the energy required to move around (the bigger the animal, the more energy needed for moving) and the benefits of selecting better quality food (Laca et al., 2010). In the current study, the effect magnitude of both pasture productivity and forage quality on grazing behaviour of free-ranging grazers was similar. This is likely to change in areas grazed by animals with different forage selectivity. The weight of vegetation productivity could increase in areas grazed by less selective herbivores such as cows. Further research on this topic would be advisable to understand how different types of domestic grazers affect herbivore-plant-soil feedbacks.

Nunes et al. (2019) suggested that pastures of high spatial homogeneity in terms of forage quality allow more efficient grazing behaviour. In the current study, the smaller cover of species of low pastoral value in areas under high grazing intensity created a more productive and spatially homogeneous pasture in terms of high-quality forage. This should be beneficial for both the average quality of fodder intake of low selective grazers, and the time use efficiency of more selective herbivores. Therefore, our results support the third hypothesis of the study, as grazing triggered positive herbivore-plant-soil feedbacks in the Mediterranean mountain grasslands studied.

5. Conclusions

This paper highlighted the importance of understanding herbivore-plant-soil feedback processes for the management and conservation of Mediterranean mountain grasslands. The results of this study suggested that grazing pressure management could be a useful tool for maintaining positive herbivore-plant-soil feedbacks in the studied ecosystem. Increasing grazing intensity up to a pasture utilisation rate of 45% was beneficial to improving or maintaining soil physical-chemical and microbiological properties, forage quality and productivity, and to prevent the encroachment of undesired plant species. The results from the study also suggested that managing grazing intensity for preserving productive and nutrient rich grasslands can also help to improve animal production. Further research is needed to find out whether the results of this study can be generalised to other Mediterranean mountain grasslands.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107833.

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