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Livestock species rather than grazing intensity shape plant guild proportions in interaction with multiple environmental drivers in grassland from the Pyrenees

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Abstract

Questions:

1. Does grazing management shape the proportion of plant guilds (grasses, legumes, forbs and sedges) in mountain grasslands?
2. Which properties of grazing management have the greatest effect on the proportion of plant guilds: grazer diversity/identity or grazing intensity?
3. Are the effects of grazing management on guild proportion modified by other environmental variables that explain plant guild distribution at broad spatial scales?

Location: Mountains in the Pyrenees.

Methods: We modelled the proportion of grasses, legumes, forbs and sedges using data from the PASTUS database ($n=96$), which contains a wide range of environmental and management conditions due to the high variety of environmental conditions in mountain grasslands in the Pyrenees. We used a machine-learning algorithm to find those variables that best explained the proportions of each plant guild. We focussed on the differences between the levels of grazing intensity and the grazing species included in the model, and on detecting interactions between grazing variables and climate, topography and soil conditions.

Results: The proportion of forbs and grasses strongly depended on the grazing livestock species at broad spatial scales. Only soil pH showed a higher overall explanatory power on guild distribution. In general, forbs were favoured in cattle- and grasses in sheep-grazed grasslands, the latter also being favoured on acidic soils, while forbs were favoured in more alkaline soil conditions. However, the effects of those factors (grazing species and soil pH) were modulated through interactions with several other environmental variables, including soil Mg, K and P, and terrain slope. In contrast, grazing intensity was a minor driver of guild distribution.

Conclusions: Our results provide information about the relationship between plant functional diversity, indicated by the different plant guild proportions, and grazing management in the Pyrenean grasslands. This information could be useful for developing hypotheses for future experimental studies and for designing policies to improve the management of mountain grasslands.

KEYWORDS

boosted-regression trees, gbm, mountain grasslands, natural grasslands, plant functional types, vegetation composition

1 | INTRODUCTION

Mountain grasslands are ecosystems of high cultural and socio-ecological value in Europe (Silva et al., 2008). They have been traditionally shaped by the presence of grazer animals that modified the landscape during centuries of traditional grazing practices (Sanjuán et al., 2018; García-Ruiz et al., 2020). In these ecosystems, the animals, mostly cattle and sheep, extensively graze in the field during spring–summer, while the animals are stabled during the winter. Over the last few decades, however, traditional management practices have changed. In the particular case of the Pyrenees, there has been a profound socio-economic transformation since the second half of the 20th century. Valley bottoms and fertile lands have been generally intensified and transformed to grow forage crops to feed stabled animals; while less productive and less accessible grasslands have been abandoned (García-Ruiz & Lasanta-Martínez, 1993). That decline in the total number of livestock directly grazing in the field has also been accompanied by a significant change in the livestock population. Cattle herds have increased in size, while sheep herds have drastically declined (García-Ruiz & Martínez, 1990).

All these changes in grazing intensity and the grazing species may lead to an increase in woody encroachment of mountain grasslands (Gelabert et al., 2021) and an upward advance of the tree line (Ameztegui et al., 2016); as well as changes in the herbaceous vegetation diversity and composition. Generally, low and moderate grazing intensity has been related with enhanced plant diversity (Wang & Tang, 2019). Also, some studies have suggested that mixed cattle–sheep grazing (Liu et al., 2015) and cattle grazing may increase plant diversity (Sebastià et al., 2008; Cutter et al., 2022), both compared to sheep-grazed pastures. This has been related to the distinct intake preferences, since sheep are more selective than cattle (Cuchillo-Hilario et al., 2017) and exert a higher pressure on some species. However, sheep may also promote the presence of some rare high-value conservation species, and may palliate plant species loss due to grasslands fragmentation, since they are more efficient plant dispersers than cattle (Sebastià et al., 2008; Rodríguez et al., 2018).

Livestock management is therefore a key tool to modulate plant diversity and composition (Sebastià et al., 2011), which in turn is a keystone driver of productivity (Connolly et al., 2009; Brophy et al., 2017), forage quality (Sturludottir et al., 2014; Villalba et al., 2019; Schaub et al., 2020), soil carbon storage (Rodríguez et al., 2021), soil fertility and functionality (Debouk et al., 2020) and greenhouse gas fluxes (Ibañez et al., 2020, 2021; Pauné i Fabrè, 2021). Management decisions will therefore influence simultaneously several ecosystem services and functions. Some authors have described management interactions with several multiscale filters to drive plant richness, for instance, interactions between

livestock management and ecosystem fragmentation (Rodríguez et al., 2018); or interactions between grazing intensity and environmental conditions (Herrero-Jáuregui & Oesterheld, 2018). However, the studies addressing those management–environment interactions on the vegetation, have mainly focussed on those effects on taxonomic plant diversity (species richness), even though taxonomic plant diversity may not be fully accounting for the different ecosystem services and functions.

Plant functional diversity refers to those components of biodiversity that affect ecosystem functions (Tilman, 2001). Plant guilds are a good proxy of that functional diversity, since they are classified according to resource use and acquisition strategies (Tilman et al., 1997; Symstad, 2000; Lavorel et al., 2007; Sebastià, 2007; Vandvik et al., 2022). Grassland plant species are often classified as grasses, non-legume forbs (hereafter ‘forbs’) and legume forbs (hereafter ‘legumes’), a classification that is based on nitrogen and light (and therefore CO₂) acquisition and use. Thus, the study of plant guilds provides an opportunity to address mechanistic links between vegetation and ecosystem functions, as for instance is the role of legumes as drivers of soil organic carbon storage (Rodríguez et al., 2021), and of soil nitrogen (Debouk et al., 2020), among others.

We perform, in this study, an assessment of how livestock management, including grazing intensity and grazing species, and environmental variables, including climate, microtopography and soil fertility, may shape plant functional guilds in grasslands of the Pyrenees. To that effect, we take advantage of the high variety of environmental heterogeneity in the Pyrenees, and specifically ask the following questions: (i) Does grazing management shape the proportion of plant guilds (grasses, legumes, forbs and sedges) in mountain grasslands? (ii) Which properties of grazing management have the greatest effect on the proportion of plant guilds: grazer diversity/identity or grazing intensity? (iii) Are the effects of grazing management on guild proportion modified by other environmental variables that explain plant guild distribution at broad spatial scales?

2 | METHODS

2.1 | The PASTUS database

The data set used in this study was extracted from the PASTUS Database (<https://ecofun.ctfc.cat/index.php/pastus/>), compiled by the Laboratory of Functional Ecology and Global Change (ECOFUN) of the Forest Sciences Centre of Catalonia (CTFC) and the University of Lleida (UdL). These data were already used in previous published articles to test other hypotheses (Rodríguez et al., 2018, 2020, 2021). The data are comprised of 96 grassland patches distributed across the Pyrenees (Appendix S1), including topographical, climate,

soil, herbage and management variables. The setup of the PASTUS Database is summarized in Appendix S2. The sampled area encompasses a wide range of temperate (mean annual temperature range: 1–9.9°C) and precipitation conditions (mean annual precipitation range: 964–1586 mm), depending on altitude and geographical location, from Mediterranean to continental and Boreo-Alpine environments (de Lamo & Sebastià, 2006; Rodríguez et al., 2018, 2020). The majority of the plant species in the grasslands are perennial (Sebastià, 2004), and both plants and environments are highly heterogeneous (Rodríguez et al., 2018). Most of the grasslands are grazed mainly in the summer season.

2.2 | Sampling design

The sampling design in the database was stratified random sampling, where samples were selected at random within strata. This process was undertaken using the ArcMap 10 software (ESRI, Redlands, CA, USA). The following maps formed the basis for randomization: the map of habitats of Catalonia 1:50,000 (Carreras & Diego, 2006) for the eastern and central sectors of the Pyrenees; the map of habitats of Madres-Coronat 1:10,000 (Penin, 1997) for the northeastern sector; and the land-use map of Navarre 1:25,000 (Gobierno de Navarra, 2003) for the western sector. Four variables were initially considered for sampling stratification within each sector: altitude (<1800; 1800–2300; >2300 m), slope (0–20; 20–30; >30°), macrotopography (mountain top/south-facing slope; valley bottom/north-facing slope) and grazer type (sheep; cattle; mixed). Accordingly, we determined a set of homogeneous grassland patches by crossing the stratification variable layers. Grassland patches were then listed by type and arranged within each list randomly to determine sampling priority. At least one to two replicates of each patch type, defined by the stratification variables, were sampled. We obtained a database of more than 200 grassland sites, from which we used 96 in this work (which had the available information of plant guild biomass proportion).

In each sampled grassland patch, a 10 m × 10 m plot was systematically placed in the middle of each homogeneous grassland patch including a particular plant community. We collected soil and vegetation samples and assessed environmental variables within each 100-m² plot (see Rodríguez et al., 2018; Rodríguez et al., 2020; Rodríguez et al., 2021, for additional details about sampling design). Local environmental variables were assessed inside the 100-m² plots.

2.3 | Climate, topographical and grazing drivers

All the variables included in this study are listed in Appendix S3. Climate variables were determined from Worldclim 2.0 (Fick & Hijmans, 2017). Based on previous work addressing the effects of climate on Pyrenean vegetation (Rodríguez et al., 2018), we selected mean annual temperature (MAT), mean summer temperature (MST),

the Temperature Seasonality Index of Sebastià (TSIS; Rodríguez et al., 2020), mean annual precipitation (MAP) and mean summer precipitation (MSP) as the climate variables to be included in our plant guild models.

Topographical variables included slope and macrotopography. Slope was determined in the field by clinometer. Macrotopography included two positions: exposed (south- and east-facing slopes, mountain tops) and protected (north- and west-facing slopes, valley bottoms).

Regarding grazing management variables, detailed surveys were carried out among farmers, shepherds and land managers, to complete the initial general information used in the sampling design. We used these surveys to determine grazing intensity by estimating livestock stocking density measured as livestock units ha⁻¹ (LU ha⁻¹). We treated it as a semiquantitative variable with three categories (Sebastià et al., 2008): low (1, <0.2 LU ha⁻¹), moderate (2, 0.2–0.4 LU ha⁻¹) and high-moderate (3, up to 0.4 LU ha⁻¹); a few samples corresponded to abandoned grasslands (0 LU ha⁻¹). We considered that 1 LU was equivalent to one cow and a calve, equivalent to seven sheep (Government of Catalonia, 2011, 2014).

2.4 | Soil environmental factors

In each plot, one soil core was extracted with a 5 cm × 5 cm probe at 0–20 cm soil depth. To determine bulk density, we air-dried and weighed the soil samples: we then sieved each sample to 2 mm to separate stones and gravels from the fine earth fraction. Textural classes in the top 10-cm soil layer were determined by the Bouyoucos method (1936), and soil pH in the top 10-cm soil layer was measured in water (Solly et al., 2014).

Total nitrogen (0–20 cm), and soil extractable cations (0–10 cm) were measured on air-dried samples (Schöning et al., 2013; Solly et al., 2014). Total nitrogen contents of the fine earth were determined by an elemental auto-analyser (Carlo-Erba NA-1500). The soil cations measured were extractable phosphorus (soil P), magnesium (soil Mg) and potassium (soil K). Available phosphorus was extracted by the Olsen method (Olsen et al., 1954). Soil Mg and K were extracted by ammonium acetate (Simard, 1993) and measured by flame-atomic absorption spectroscopy (AAS) (David, 1960).

2.5 | Plant guild proportions

Plots of 10 m × 10 m were established in the middle of homogeneous grassland patches holding a given plant community (Canals & Sebastià, 2000; Sebastià, 2004). Above-ground biomass was estimated from herbage harvested in four 50 cm × 50 cm quadrats placed in a 2 m × 2 m subplot within the 10 m × 10 m plot. Plant guild biomass was determined in one of the four quadrats per plot by hand separation. Four guilds were sorted: C3 grasses (Gramineae), sedges

(Cyperaceae), legumes (Fabaceae) and non-legume forbs (the latter including some subshrubs), following Sebastià (2007). Guild biomass was then oven-dried at 60°C to constant weight.

2.6 | Data analysis

2.6.1 | Boosted-regression trees (BRT)

We used boosted-regression trees to model the biomass proportions of the four plant guilds (grasses, forbs, legumes and sedges) according to the climate, topography, soil and management explanatory variables. The BRT approach is an automatic technique that combines insights from traditional statistical modelling and machine-learning traditions (Elith et al., 2008). BRT uses two algorithms: regression trees and boosting. Regression trees are from the decision tree group of models, and boosting builds and combines a collection of models (Elith et al., 2008). We chose this method because BRT can handle multiple variables better than other techniques such as general linear models, and can detect automatically curvilinear relationships and interactions, ignoring non-informative ones. Additionally, this approach had performed appropriately when previously using the PASTUS database (Rodríguez et al., 2020). We used the *gbm* (Greenwell et al., 2020) and *dismo* (Hijmans et al., 2022) R packages, which provide several functions to fit these models.

We fitted four BRT models, each one using one of the plant guilds as response variable and the environmental variables in Appendix S3 as explanatory variables. BRT has several parameters that need to be set before the modelling (Elith et al., 2008). We configured the models to assume a Gaussian distribution of the error. As legume and sedge biomass proportions did not follow a normal distribution, we did a log-transformation to make their distributions closer to normal (Appendix S4). The remaining parameters were optimized using a modified version of the method used in Pistón et al. (2019), detailed in Appendix S5–S7.

2.6.2 | Fitting the final model set

Once the model parameters were set, we fitted 50 BRT models for each plant guild, considering the average of their outcomes as the final results. We accounted the goodness of fit of the models by the average R^2 of the regression between the model predictions and the real values, using both the model predictions and 10-fold cross-validation. The importance of each explanatory variable was estimated as the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Elith et al., 2008). The relative influence (or contribution) of each variable is scaled so that the sum adds to 100, with higher numbers indicating stronger influence on the response. We represented the single effects of the explanatory variables using partial dependence plots, which show the effect of a variable on the

response after accounting for the average value of the rest of the variables in the model (Friedman, 2001; Elith et al., 2008). For detecting interactions between plant guild drivers, we used the interaction importance index provided by the function “*gbm.interactions*” from the *dismo* package (Elith et al., 2008). We represented the most important interactions by partial dependence plots.

3 | RESULTS

Models of grass, forb and legume biomass proportions had acceptable goodness of fit values (cross-validated R^2 values of 0.27, 0.38 and 0.38 respectively; Table 1), whereas the model of sedge proportions presented a poor goodness of fit (cross-validated R^2 values of 0.06; Table 1), and hence was discarded from our study.

3.1 | Relative importance of variables

Soil pH was the most relevant explanatory variable in the models for grasses, forbs and legumes (Figure 1). Soil Mg, grazing species, slope and soil K were the other variables selected for the grass and forb proportion models. Additionally, MAT, TSIS and P10 were included in the forb proportions model. MAT, soil Mg and slope were the variables selected in the legume proportions model.

3.2 | Grazing management effects on plant guild proportions

Grazing species was an important driver of both forb and grass biomass proportions according to our models. By contrast, grazing intensity did not enter in any model (Figure 1). However, the overall effect of the grazing species variable on forb and grass biomass proportions was modified according to multiple interactions with other environmental variables (Figure 2). Overall, the effect of livestock type on forb and grass proportion was different for each: forbs were favoured in cattle-grazed grasslands, and grasses under sheep-grazed regimes; whereas mixed livestock assemblages showed intermediate values of both forbs and grasses (Figure 2). In the following, we describe the most important interactions between grazing species and other environmental variables according to the importance

TABLE 1 Average R^2 of the correlation between each plant guild biomass proportion and the predicted values of the corresponding model; and the corresponding ten-fold cross-validated R^2

Plant guild model	R^2	Cross-validated R^2
Grasses	0.64 ± 0.04	0.27 ± 0.05
Forbs	0.79 ± 0.03	0.38 ± 0.05
Legumes	0.65 ± 0.03	0.38 ± 0.05
Sedges	0.5 ± 0.03	0.06 ± 0.03

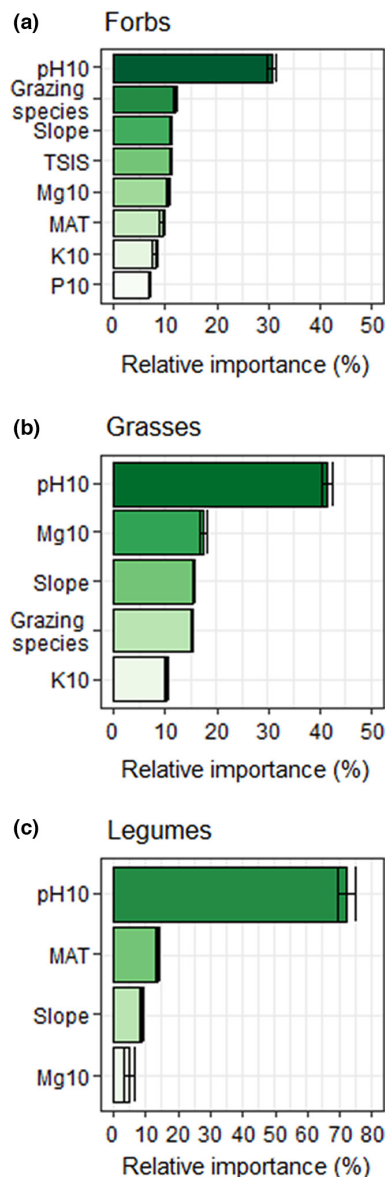


FIGURE 1 Mean variable importance \pm standard deviation of the explanatory variables in the (a) forb, (b) grass and (c) legume biomass proportion models

of the environmental variables involved (Figure 1) and the interaction importance index (Appendix S8). These were of similar importance to interactions involving other environmental variables.

Firstly, under the three grazing regimes (cattle grazing, sheep grazing and mixed grazing), increasing soil pH favoured forbs and suppressed grass biomass proportions. Furthermore, at low soil pH values, mixed grazed grasslands showed forb and grass proportions similar to sheep-grazed ones, whereas, at high soil pH values, mixed grazed grasslands had forb and grass proportions similar to cattle-grazing regimes (Figures 3a and 4a). Secondly, forb biomass proportions increased with soil Mg, and the opposite was observed for grass biomass proportions. However, forb proportions increased with soil Mg more under sheep than under cattle grazing, and vice versa for grass proportions (Figures 3b and 4b). Thirdly, under cattle and mixed grazing regimes, forb proportions declined, but grass proportion increased with soil K. Nevertheless, this relationship was

negligible in sheep-grazed grasslands (Figures 3c and 4c). Fourthly, forbs tended to decrease with the increase of soil P, but this decline was higher under cattle than under sheep grazing (Figure 3d). Finally, slope showed a negative relationship with forb proportions and a positive one with grass proportions, but under cattle regimes these changes only appeared at very steep slopes whereas under sheep regimes they were more gradual (Figures 3e and 4d).

3.3 | Other effects influencing plant guilds

Our models detected multiple interactions among environmental factors driving plant biomass proportions, many of them not involving grazing variables (Appendix S8). Interestingly, the relationship between forb, grass and legume proportions with the most important variable in their corresponding models, i.e., soil pH, was modulated by other environmental variables, like MAT or terrain slope. We illustrate some of these results in Appendix S9.

4 | DISCUSSION

Our models provided evidence that grazing management, in particular grazing species, can partially explain plant guild patterns in Pyrenean grasslands. Grazing species was one of the most important variables in grass and forb proportion models. Overall, grasses increased their average predominance under sheep grazing, whereas cattle grazing was associated with a higher (but not dominant) presence of forbs. Mixed grazing presented intermediate values between sheep and cattle regimes. Moreover, we found that the overall patterns of the relationship between forb and grass biomass proportions and grazing species varied depending on several soil properties (pH, K, P and Mg content) and terrain slope.

4.1 | Overall effects of grazing management

Our results showed how plant guilds vary under different grazing regimes at the regional scale. We identified that grazing species can be an equally important driver of both grass and forb biomass proportion patterns as other environmental drivers (Figure 1), surpassed in importance only by soil pH. In addition, our results show how the interaction with several of those other drivers can modify the effects of livestock grazing species.

Our models showed how the presence of sheep grazing in the Pyrenean grasslands favoured the dominance of grasses in terms of biomass proportion, and that this shift was mostly at the expense of forbs (Figure 2). This result is consistent with the literature (van der Plas et al., 2016), since sheep are described as more selective in their feeding than cattle, preferring the more palatable plants and thus favouring the predominance of unpalatable grasses (Rook et al., 2004; Sebastià et al., 2008). Additionally, shepherds often move sheep to specific sites with more nutritious plants (Sebastià et al., 2008). Hence, sheep can produce a strong homogenizing effect on plant

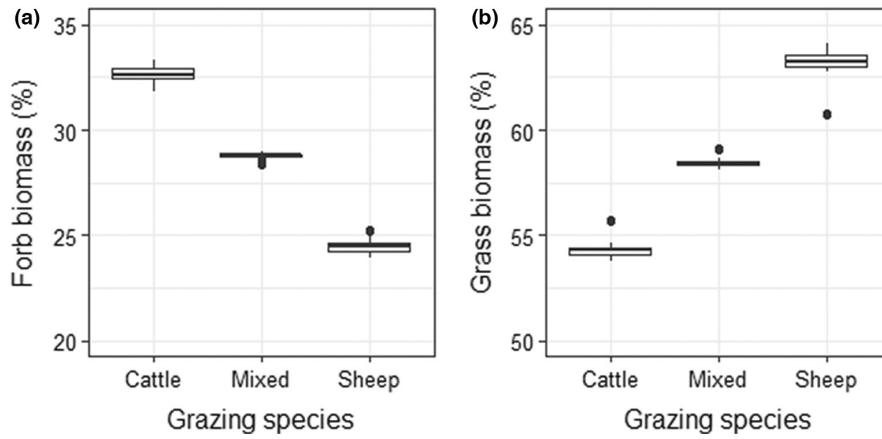


FIGURE 2 Partial dependence plots of (a) forb and (b) grass biomass proportions under cattle, mixed and sheep grazing. Boxplots represent the obtained values from the 50 fitted models. Boxes represent 50% of the observations, whereas points represent outliers as values surpassing $1.5 \times \text{IQR}$ interquartile range, IQR being the difference between the third and the first quartiles

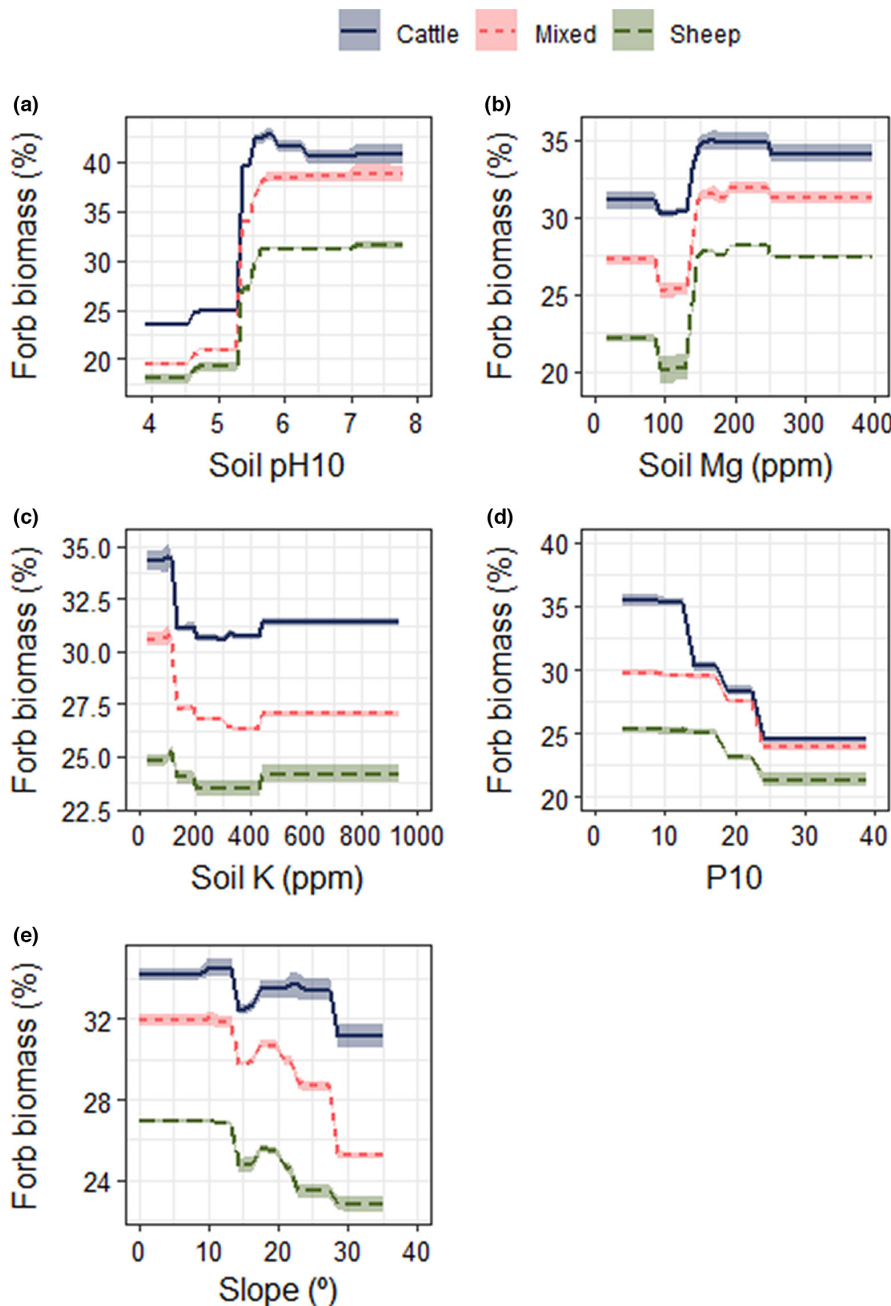
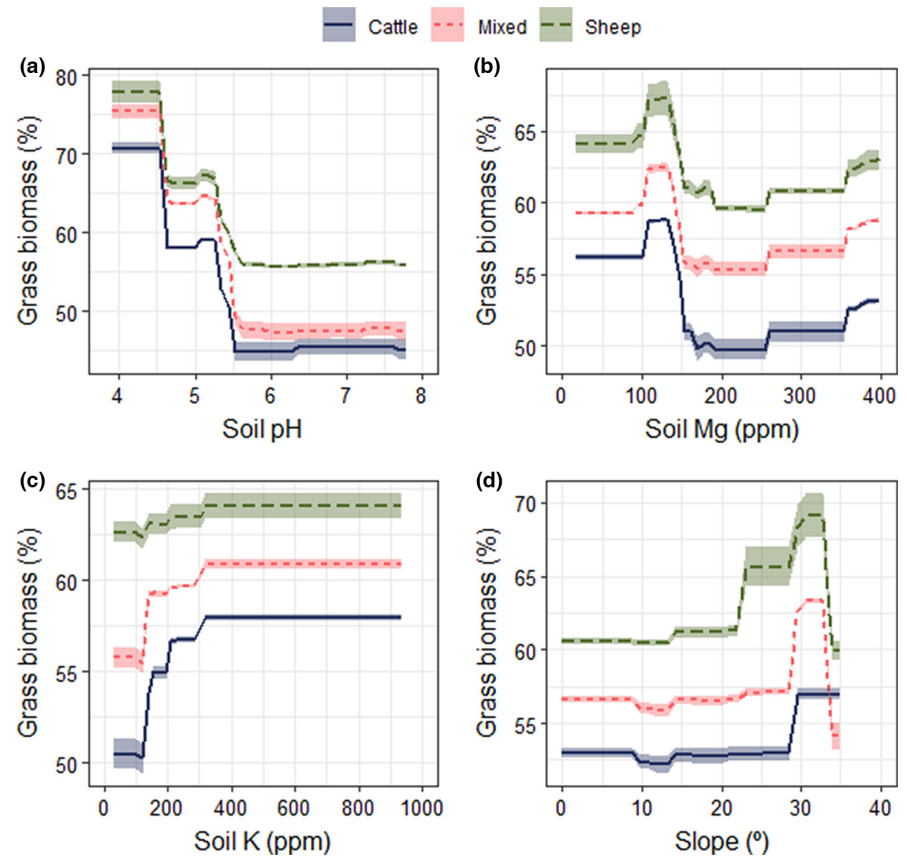


FIGURE 3 Partial dependence plots depicting the relationships of forb biomass proportion with (a) soil pH, (b) soil Mg, (c) soil K, (d) soil P, and (e) slope under cattle, mixed and sheep grazing. Lines represent the averages of the 50 fitted models, whereas the shaded areas represent their standard deviations

FIGURE 4 Partial dependence plots depicting the relationships of grass biomass proportion with (a) soil pH, (b) soil Mg, (c) soil K, and (d) slope under cattle, mixed and sheep grazing. Lines represent the averages of the 50 fitted models, whereas the shaded areas represent their standard deviations



communities (de Bello et al., 2006; Sebastià et al., 2008, 2011), whereas cattle are less selective, allowing a greater diversity of plant species on the landscape and regional levels (Sebastià et al., 2011). According to previous studies, overall sheep prefer forbs over grasses due to their higher palatability (Sebastià et al., 2008; Dumont et al., 2011; Chang et al., 2018).

In contrast to forbs and grasses, our results suggest that grazing species is of minor importance for legume biomass proportion, as this variable was not selected during the legume modelling process (Figure 1c). This is a surprising result as legumes tend to be selected by sheep (Nolan et al., 2001; Tóth et al., 2018). This result could be related to the small range of grazing intensity in our system ($0\text{--}0.3\text{LU ha}^{-1}$). For example, Tóth et al. (2018) found that legume cover was lower under sheep than under cattle grazing, but the grazing intensity of their system (steppes from East Hungary) ranged from 0.5 to 3LU ha^{-1} . Conversely, we could not fit a proper model for sedge proportions, maybe because this plant guild was normally scarce or absent in the grasslands from our dataset (Appendix S4).

Some studies carried out at local spatial scales (i.e., establishing different treatments in a single pasture) did not find important effects of grazing on plant guilds (Marinas & González, 2006; Fraser et al., 2013; Jerrentrup et al., 2015; Tardella & Catorci, 2020; but see Grant et al., 1996). This reinforces the finding of Sebastià et al. (2008), who demonstrated the scale-dependent relationship between grazing management and vegetation. Additionally, other factors such as diet overlap between cattle and sheep due to the plant species pool in a concrete site (Aldezabal, 2001; Jerrentrup

et al., 2015) or the spatial patterns of vegetation at site scale could explain the low effect of grazing on plant guilds in those works.

We did not find any effect of grazing intensity on plant guild biomass proportion. This result is consistent with that in the previous study of Tóth et al. (2018), which found that grazing species was a stronger driver of grassland plant communities than grazing intensity. Only plant species richness varied with grazing intensity in this last work, which was also found in Pyrenean grasslands (Sebastià et al., 2008; Rodríguez et al., 2018).

4.2 | Interactions between grazing management and other environmental variables

The novelty of our analysis was that we found that grazing species commonly interact with other important environmental drivers of plant communities to shape plant guild composition in Pyrenean grasslands. That is, the overall patterns concerning forb and grass proportions under the different grazing assemblages (described in the previous section) vary depending on environmental conditions (Díaz et al., 1999; Hayes & Holl, 2003; Irisarri et al., 2016).

Soil pH had a positive relationship with forb biomass proportion, but showed an opposite effect on grass proportion (Figures 3a and 4a), consistently with the different soil pH optimums of both groups (Palazzo & Duell, 1974; Mpokos et al., 2014; Wang et al., 2020). Nevertheless, the intensity of these patterns depended on grazing species (Figure 3a), and other environmental conditions (Appendix S9). Concerning grazing species, under acidic conditions

(pH < 5.5), grasses and forbs at mixed grazed sites had similar proportion to sheep-grazed grasslands (grass-dominated; [Figure 3a,b](#)). Conversely, at neutral or slightly alkaline sites (pH between 7 and 8) these plant guilds under mixed grazing regimes were in proportion similar to cattle-grazing regimes (forb-dominated; [Figures 3a and 4a](#)). Hence, the sole presence of the grazing species, which is an ecological filter for each group (i.e., sheep for forbs and cattle for grasses), alone or in mixed assemblages, would promote a decline in their biomass proportion if soil pH conditions are non-optimal for each guild (i.e., low soil pH for forbs and neutral–slightly high pH for grasses). On the other hand, when pH conditions are optimal for a plant guild, only a herd exclusively composed of its detrimental grazing species would decrease its proportion.

Forbs were favoured by high soil Mg, whereas the relative biomass of grasses was reduced ([Figures 3b and 4b](#)) consistently with the high Mg requirements of forbs (Bergmann, 1992; Schimmelpfennig et al., 2015). For each plant guild, the reduction of biomass proportion under unfavourable Mg conditions was more pronounced under the presence of the grazer type associated with the decline of that plant guild. Forb proportion decreased more at low soil Mg values under sheep than under cattle-grazed management; and grass proportion decreased more at high soil Mg values under cattle than under sheep management ([Figures 3b and 4b](#)).

Interestingly, the interaction between grazing species and soil K followed a different pattern. Under cattle and mixed grazing, forbs seemed to be favoured by low soil K conditions (<120ppm), while the biomass proportion of grasses was reduced ([Figures 3c and 4c](#)), suggesting that grasses have higher soil K requirements than forbs (Bezemer et al., 2006; Schimmelpfennig et al., 2015). Conversely, under sheep grazing, the modelled relationship between soil K and forb and grass proportions was almost neutral ([Figures 3c and 4c](#)). This indicates that the selective feeding behaviour of sheep is a stronger ecological filter than soil K content in these mountain grasslands.

Apart from soil pH, Mg and K, our results indicated that forbs probably had some competitive advantage in low soil P sites (Mládková et al., 2015 and references therein), increasing their biomass proportion ([Figure 3d](#)). This advantage of forbs would be tempered by the presence of sheep, as the highest increase of forb proportion at relatively low soil P was under cattle regimes, and the lowest in sheep-grazed sites, with mixed-managed grasslands in between.

Grazing species effects were also modulated by slope in the forb and grass biomass proportion models. Despite the high importance of topographical factors for plant composition (Sebastià, 2004; Marini et al., 2007; Wellstein et al., 2013; Niu et al., 2019) few studies have addressed the relationship between forbs and grasses with slope (but see Sanaei et al., 2018; Averett et al., 2022). Under cattle and mixed grazing, forb proportion seemed to be reduced in steep terrains, whereas grass biomass became more dominant. Grasses could be more competitive in the shallow and nutrient-poor soils typical of steep slopes (Sanaei et al., 2018), which also

present a more perpendicular radiation angle than plane sites (Bennie et al., 2008).

At sheep-grazed sites, these changes in guild composition began at lower slope values: forb proportion decreased above 13° and grass proportion increased above 23° ([Figures 3e and 4d](#)). This could be related to the higher adaptation of sheep to steeper slopes than cattle (McDaniel & Tiedeman, 1981; Díaz Falú et al., 2014; Larson et al., 2015), which suggests that conditions favour high grass proportions at steep slopes combined with sheep.

Interactions in ecology are a common and complex phenomenon (Darling & Côté, 2008; Dieleman et al., 2012), but they are often assumed, and not so frequently tested (Mantyka-pringle et al., 2012). The results presented in this manuscript are relevant since we found a number of interactions between grazing species and other environmental variables that shape forb and grass proportions at regional scales. These results can help formulating new hypotheses to test in experimental studies (Spiegelberger et al., 2012). Additionally, changes in grazing management in mountain grasslands are a manifestation of global change (Lasanta et al., 2017; Dibari et al., 2020), but are also a factor easy to manipulate, since it depends on human decisions (Komac et al., 2014; Muñoz-Ulecia et al., 2021). Consequently, they can contribute to the development of new management policies of grasslands in the Pyrenees, together with previous work that described the relationship of grazing management with plant diversity (Sebastià et al., 2008; Rodríguez et al., 2018) or ecosystem functions (Rodríguez et al., 2020, 2021).

5 | CONCLUSIONS

This study shows for the first time how grazing species may shape plant guild proportions at regional scales, while considering other environmental variables. Grazing intensity had no effect on plant guild proportion. However, grazing intensity is moderate on these grasslands, and different patterns could emerge at wider grazing intensity ranges. We found that grazing species has similar importance for forb and grass proportion as other environmental variables, including soil K, Mg, P and terrain slope, but was clearly surpassed by soil pH. Moreover, the highlight of this work is that we identified a number of interactions between grazing species and environmental variables that shape forb and grass proportions, including the modulation of soil pH patterns. These findings can contribute to the elaboration of new hypotheses to be tested in experimental studies as well as to the development of management practices and policies concerning mountain grasslands in the Pyrenees.

AUTHOR CONTRIBUTION

M.-Teresa Sebastià conceived of the research idea and collected the data. Antonio Rodríguez performed data modelling. Antonio Rodríguez and Mercedes Ibanez wrote the paper, with contributions from Cristina Chocarro and M.-Teresa Sebastià. All authors discussed the results and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

Data are not public as the PASTUS database is currently used for other research projects. Please contact one of the authors by e-mail for queries concerning the data used in this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Study area and sampling plot distribution.

Appendix S2. Scheme of the sampling procedure for building the PASTUS database.

Appendix S3. Variables considered in this study.

Appendix S4. Histograms and quantile plots of biomass proportions of (a) forbs, (b) grasses, (c) legumes, (d) log(legumes), (e) sedges, (f) log(sedges).

Appendix S5. Optimization of model parameters.

Appendix S6. Mean observed deviance of the BRT models fitted which each parameter combination (learning rate; minimum number of trees; bag fraction) for the (a) forb, (b) grass, (c) legume and (d) sedge models.

Appendix S7. Mean observed R^2 of the (a) forb, (b) grass, (c) legume and (d) sedge BRT models across the different tree complexity values.

Appendix S8. Interactions detected in the (a) forb; (b) grass and (c) legume BRT model.

Appendix S9. Partial dependence plots depicting the relationships of forb, grass and legume biomass proportions between soil pH and MAT (a, b) and soil pH and Slope (c–e).

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