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What are the relative roles of abiotic and grazing management factors on plant community distribution in landscapes? How are livestock type and stocking rate related to changes in vegetation structure and composition?

Sub-alpine grasslands in the central and eastern Pyrenees.

Multivariate analysis and variance partitioning methods were used to evaluate the relative roles of environmental factors in structuring vegetation composition and diversity patterns in three surveys on differently managed grasslands.

Vegetation composition within a region was affected by environmental factors hierarchically, changing first according to abiotic factors and then to grazing management. At landscape scales, abiotic factors explained two-fold more variation in vegetation composition than grazing factors. Within landscape units, cattle grazing increased vegetation heterogeneity at landscape and patch scales, while sheep grazing favoured the presence of a specific set of species with high conservation value. Species composition was highly responsive to management variables compared to diversity components.

The combination of sheep and cattle grazing at various stocking rates is an effective tool to preserve the diversity of plant species and communities within a region with a long tradition of livestock management, through the scaling up of effects by local processes occurring in patches at smaller scales.

Abiotic factor; Cattle grazing; Grazer type; Grazing intensity; Landscape; Livestock management; Plant community; Plant diversity; Sheep grazing; Stocking rate.

IS = Specific quality index; LU = Livestock unit; PV = Pastoral value.

Tutin et al. (1964-1980); Bolòs et al. (1993).

Biodiversity conservation – preserving species, ecological communities and landscape variety – is an urgent task for our society (Balmford et al. 2005). Compared to other community types, traditionally managed European grasslands have a rich flora with a particular suite of species (Pärtel et al. 1996). Various studies have addressed the consequences of changes in land-use and management on various vegetation attributes (e.g. Wilson et al 2003; de Bello et al. 2006). Management can be used as a tool for multifunctional planning, including conservation and agricultural use (Austrheim & Eriksson 2001), but there is still uncertainty. A better understanding of vegetation responses to environmental factors and tighter links between ecological theory, applied research and practical applications are necessary.

Changes in management can modify both abiotic and biotic environmental factors, therefore providing a suitable setting to test and develop ecological hypotheses on vegetation-environment relationships. In particular, the relative effect of management and abiotic factors on vegetation structure still needs to be better understood for generalization beyond specific locations. Community assembly processes are shaped by interactions between abiotic and biotic factors acting at different spatial scales. At a particular site, a hierarchy of environmental filters, from abiotic to biotic, has been proposed to act at decreasing spatial scales (Keddy 1992). Sebastià (2004) found that topography and soils predicted, with some accuracy, grassland community distribution in the landscape in a wide survey of sub-alpine grasslands on limestone in the eastern Pyrenees. In addition to abiotic factors, biotic disturbance by grazing is expected to play a role in how plant species assemble into communities in grasslands, and how the assembled communities are found in landscapes within a region. Therefore, to define the most appropriate management practices for diversity conservation in traditionally grazed grasslands,

it is necessary to understand to what extent abiotic and grazing management affect vegetation.

Changes in grazing management are known to dramatically modify vegetation structure (Bullock et al. 2001), affecting vegetation spatial heterogeneity (Adler et al. 2001) and influencing biodiversity and ecosystem processes (Collins et al. 1998). Grazing has been found to promote species diversity (de Bello et al. 2007) and modify functional type composition (de Bello et al. 2005) in pastures along climatic gradients in the north-east of the Iberian Peninsula. In addition, changes in plant species composition in response to environmental changes are expected to feed back and affect the grassland value as a feeding source for livestock (Sebastià 2007).

Although much research has been conducted on the effects of grazing pressure and abandonment on vegetation patterns (Milchunas & Lauenroth 1993; Biondini et al. 1998; Frank 2005; Altesor et al. 2006; de Bello et al. 2006), less is known about the sensitivity of grazed ecosystems to other grazing variables, such as herbivore guild (Hulme 1996) and size (Bakker et al. 2006). In this study, we aim to assess the role of grazing intensity and grazer type as structuring factors in sub-alpine grasslands in the Pyrenees and to investigate how livestock grazing interacts with abiotic variables and contributes to shaping grassland structural patterns in terms of (a) species diversity, vegetation composition and associated herbage quantity and quality within the community and (b) community distribution in the landscape. Specifically, we address two questions: 1. What is the relative role of livestock management in structuring vegetation in comparison to abiotic factors? 2. How strongly does vegetation respond to changes in grazing variables such as grazer type and grazing intensity?

We carried out three surveys on sub-alpine grasslands in the Pyrenees. We evaluated the relative roles of abiotic environmental heterogeneity and grazing in structuring plant species composition at landscape scales through a regional survey (S1) under a range of environmental conditions. Then, to separate the roles of livestock type and stocking rate at finer spatial scales, we focused on the effect of grazer type on otherwise homogeneous areas in the second survey (S2) and, finally, analysed vegetation responses along grazing intensity gradients in environmentally similar sheep-grazed areas in the third survey (S3). The response variables analysed were plant species composition, diversity (richness and evenness) and herbage quantity and quality, if applicable.

Location and sampling

In S1, we sampled sub-alpine grasslands on acidic and calcareous bedrock in five mountain ranges in Senet (2000-2250 m a.s.l., central Pyrenees; 3° 15'-18' E, 47° 11'-17' N). Vegetation composition and plant diversity were compared in sheep- and cattle-grazed areas, under a range of environmental abiotic conditions and grazing intensities. Grazing management was assessed through interviews with local experts and shepherds. Sampling was stratified, with samples distributed at random within strata. The stratification variables were: bedrock (calcareous / acidic), grazer type (cattle / sheep) and stocking rate (low: < 0.2 / moderate: 0.2-0.4 / high: > 0.4 at present, up to 0.8 livestock units/ha for historical rates). For each combination we randomly distributed up to three replicates per aspect (north/south facing) and slope interval (< 20° / > 20°). A total of 24 grasslands meeting the required conditions were sampled (some combinations could not be found). In each sampling area, we placed a 10 m × 10 m plot in the middle of the patch and recorded information on additional abiotic parameters, including altitude, macrotopography, microtopography and visual soil surface stoniness. Biomass was obtained at each plot by harvesting four 0.5 m × 0.5 m quadrats, equidistantly distributed on a 2 m × 2 m systematically sampled quadrat. Harvesting was done at the estimated peak of vegetation development (July). We separated above-ground dead matter and biomass by species and determined dry weight. Plant species richness was estimated by recording all separated species.

In S2, we studied sub-alpine mesic grasslands in the Cadí-Moixerò Natural Park (eastern Pyrenees), on limestone (1900-2100 m a.s.l.; 2° 54' E, 38° 10' N). Four different, separate grasslands were sampled, each located in sites split into cattle- and sheep-grazed areas but otherwise physiographically homogeneous. In all cases, an electrified fence crossed the grassland and separated sheep- from cattle-grazed areas. Sites were selected when homogeneous topographical characteristics were found at either side of the fence, and the grassland area was large enough to establish the sampling plots preventing a border effect. The sampled grasslands have been managed differently for at least 50 years. In the cattle-grazed area, ca. 300 cattle grazed during the growing season, from the end of June to the beginning of September. The sheep-grazed area was used by 2000-3000 sheep during the same period. Both areas had similar moderate stocking rates (0.2-0.4 LU/ha; LU = livestock unit). We established paired 3 m × 10 m plots on each side of the fence in each site and compared vegetation pair-wise. Within each of the eight 30 m² plots, a grid of 100 cm × 40 cm subplots was established. At each interception point, we recorded species presence/absence on a 2 mm

diameter pin according to the point-intercept technique. In total, we calculated species frequency over 100 points per plot.

In S3, we analysed the effect of grazing intensity (measured through livestock stocking rate) on vegetation. We sampled only sheep-grazed areas and compared the effect of grazing pressure, along a gradient from frequently grazed to abandoned, in the Alinyà valley (eastern Pyrenees; 1° 27' E 42° 12' N), on limestone. We interviewed local shepherds to identify areas: (a) abandoned for more than ten years, (b) grazed only a few times a year (ca. 0.15 LU/ha) and (c) grazed frequently during the year (ca. 0.35 LU/ha). We reduced heterogeneity in abiotic environmental conditions in this study by either keeping constant the range of variation of abiotic variables or introducing them as factors in the design. For each grazing intensity, 12 sites were selected through a randomized block design: three sheep grazing intensities × two aspects (south/north) × two replicates. Altitude varied by 120 m, and slope was fixed between 19° and 35°. In each site we sampled species frequency on a 10 m × 10 m plot divided into 100 1-m² quadrats. We recorded all the vascular species whose vertical projection was included in each of the 100-m² and the 1-m² plots (see de Bello et al. 2005, 2007 for further details).

In all three surveys, differences in management patterns arose arbitrarily. Vegetation was assessed at the time of expected peak development, in mid summer. Only livestock grazers were considered. Grazing was continuous during the summer growing season. Summer is the warmest and rainiest season in those mountain areas. Mean annual temperature in the study areas ranges between 5 °C and 6 °C and mean annual rainfall is over 1000 mm (Sebastià 2004). Grasslands were sampled at altitudes between 1900 and 2300 m a.s.l.
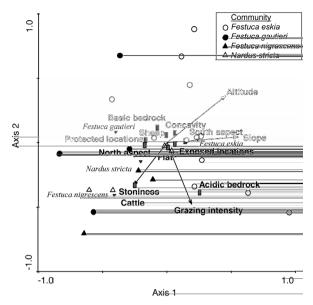
Data analysis

Plant community types and vegetation compositional patterns were analyzed by means of: (a) Detrended Correspondence Analysis (DCA) to investigate the main changes in vegetation composition, (b) cluster analysis on the variables generated by the sample scores on the main DCA axes to determine plant community types and vegetation groups and (c) the Bray-Curtis dissimilarity index to assess vegetation heterogeneity between and within grazing treatments (in S2).

To assess the effect of the considered environmental factors on vegetation composition, we applied ordination techniques (Canonical Correspondence Analysis, CCA) constrained by environmental variables (categorical, semi-quantitative and quantitative). In S1 we performed a variety of CCA to assess the relative effects of environmental variables on vegetation composition, introducing

variables in the model by forward selection according to *F*-ratios and *P*-values generated from randomization tests by 499 Monte Carlo permutations (see Lepš & Šmilauer 2003). Initially, we used two sets of explanatory variables: (a) abiotic variables: bedrock, altitude (recorded by altimeter), north and south aspects, slope, exposed and macrotopographically protected locations, concavities and microtopographical convexities, stoniness (> 30% visual surface stoniness vs < 30%) and (b) management variables: grazer type and grazing intensity. For partitioning analysis, all variables within each group were used as covariates in partial CCA (pCCA) to determine the relative effect of each group of variables in turn, and to separate the effect of the two management variables. In S2, we introduced only grazer type. In S3, we performed a CCA introducing all abiotic variables (altitude, slope, stoniness, aspect) and grazing intensity (semi-quantitative) as explanatory variables, and a pCCA introducing only grazing intensity, with all other factors as covariates.

We analysed other structural and quality variables besides vegetation composition: diversity (species richness and evenness), peak biomass (in S1) and forage quality. Species richness was measured as the number of plant species per plot. The Camargo index was used to measure evenness per sample (Camargo 1995). Additionally, in S2 we estimated an indicator of overall diversity (Shannon-Wiener index), which combines information about both species richness and evenness. This index was generated through bootstrapping techniques (5000 iterations, see Magurran 2004 for a description of the mathematical formulation and properties of each diversity index). The Pastoral Value per sample (PV) was calculated following Daget & Poissonet (1972), after determining the specific quality index (*IS*) for each species. The specific index ranged from 0 (species that have null forage interest) to 5 (excellent forage) (see Daget & Poissonet 1972 for a description of the method, and Sebastià 2007 for details of the *IS* scoring in this study). The Pastoral Value method provides an estimate of forage quality.

To study the effects of abiotic and management factors on the vegetation parameters we used ANOVA tests and Log Linear Poisson regression for species richness. In S1, we conducted two regression analyses per variable of interest, one comparing variation in structural and quality parameters among communities and another one substituting the communities by environmental and management factors. In S2, we used paired *t*-tests to compare diversity indices, and χ^2-tests to compare the *IS* index, in sheep and cattle-grazed areas. To meet the assumptions of the χ^2-test, species were categorized into low (*IS* = 0 - 2) or high (*IS* = 3 - 5) forage quality plants. Regression was applied in S3 to the species response to grazing intensity (determined from species scores on the corresponding p-CCA axis), using the *IS* index (with values 1 - 5) as the independent variable.

Distribution of samples and environmental (abiotic and management) factors on the first two axes of CCA for the S1 dataset. ▉ show the environmental variables when categorical. ▼ show the distribution of the species dominating in each community type. Other symbols represent samples from different plant communities (see legend).

Relative role of abiotic factors and grazing management on vegetation patterns

Four grassland community types were recognized (from DCA and cluster analysis) in S1, and named according to the dominant species in each: *Festuca eskia*, *F. nigrescens*, *F. gautieri* and *Nardus stricta* dominated grassland community, respectively. The DCA distinguished samples dominated by *F. eskia* from others on the first axis (13% of vegetation variability explained) and distributed samples from mesic *N. stricta* to xeric *F. gautieri* communities on the second axis (6%). *F. nigrescens* and *F. eskia* communities occupied intermediate positions on axis 2. The dominant species in

each community segregated according to both abiotic and management variables (CCA, Fig. 1). Sloping areas relatively exposed and south-facing were dominated by *F. eskia* on a variety of bedrocks (Fig. 1). *F. nigrescens* and *F. gautieri* were associated with areas with relatively high livestock pressure and more frequently grazed by cattle compared to *F. eskia* and *N. stricta* (pCCA on management variables).

The abiotic and grazing variables considered explained ca. 40% of the variability in vegetation composition (CCA; Fig. 1). Abiotic factors alone explained 33% (pCCA with abiotic factor as explanatory variables and management as covariates). The management variables accounted for as much as 14%. Stocking rate accounted for 8% and grazer for 6% (percentages calculated from three pCCA, using the variables of interest as the only explanatory variables, all other factors introduced as covariates). Therefore, our results showed a negative overlap effect between abiotic and management factors (–7%), which is likely to indicate a degree of dependence/collinearity among biotic and abiotic factors (Legendre & Legendre 1998). The non-overlap between stocking rate and grazer type indicates that these variables are factors independently affecting species composition.

The four identified plant communities varied in their structural and forage quality characteristics (Table 1). *N. stricta* and *F. gautieri* communities showed the lowest evenness value and *F. nigrescens* communities the highest value (Table 1). *F. nigrescens* communities showed the highest quality but the lowest peak biomass while, *vice versa*, *F. eskia* communities held the highest peak biomass and the lowest quality (Table 1).

The response of the structural and forage quality characteristics to changes in the environmental variables also varied. While species richness was the structural parameter most affected by environmental variables, evenness was not responsive to them (Table 2). Forage quality was also more dependent on environmental factors than peak biomass (Table 2). Species richness and forage quality (PV) had a tendency to increase with grazing intensity, and peak biomass to be higher in sheep than in cattle-grazed areas (Table 2).
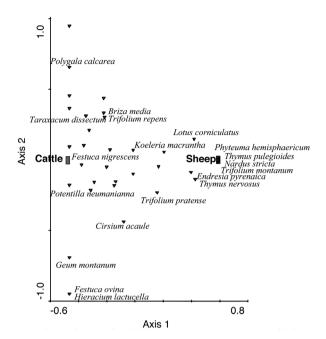
Estimated mean ± 1 SE for several structural and use characteristics of the four plant communities recognized in a survey on grassland vegetation in S1: plant diversity (species richness and evenness in four 0.25 m × 0.25 m plots), peak biomass and Pastoral Value (PV). Values estimated through regression models including plant community type as the only factor (Poisson regression in Log Linear Model for species richness and linear regression for the other variables). Different superscript letters indicate significant differences between communities for a particular variable. Only the back-transformed mean is given for richness.

Community	No. species per m^2	Evenness	Peak biomass (g.m^{-2})	PV
Nardus stricta	15	0.244 ± 0.021	214 ± 28.6[a]	18 ± 5.64[a,b]
Festuca eskia	15	0.317 ± 0.037	307 ± 15.9[b]	14 ± 3.13[a]
Festuca nigrescens	18	0.356 ± 0.043	162 ± 33.1[a]	37 ± 6.51[b]
Festuca gautieri	18	0.226 ± 0.037	211 ± 28.6[a]	27 ± 5.64[a,b]

Vegetation changes with sheep vs cattle grazing

Sheep- and cattle-grazed areas presented a marked differentiation in species composition (Fig. 2), and grazer type accounted for half of the variability in vegetation in the S2 dataset (52% in the ordination analyses). DCA, cluster analysis and CCA consistently revealed two groups of samples, one was very compact and included all sheep-grazed areas, the other group, less compact, included all cattle-grazed areas. In addition, the analyses revealed that there was a group of plants closely associated with sheep-grazed areas, mostly including typical acidic species commonly found in *N. stricta* grassland communities, such as *N. stricta*, *Endressia pyrenaica* and *Phyteuma hemisphaericum* (Fig. 2). On the contrary, in cattle-grazed areas a much higher variety of species and vegetation heterogeneity than in sheep-grazed areas was found; species spread more widely in the ordination space, particularly over the second axis (20% of explained variability; Fig. 2). Among the species, *F. nigrescens* showed an overall frequency of 43% in cattle-grazed compared to only 4% in sheep-grazed areas. In contrast, *N. stricta* had an overall frequency of 59% in sheep-grazed areas but was absent in cattle-grazed areas. Therefore, based on these results, the dissimilarity in species composition between samples was lower within sheep-grazed areas (Bray-Curtis dissimilarity index, 0.212) than within cattle-grazed areas (0.447) and the maximum dissimilarity was found when comparing samples from both treatments (0.729), indicating a strong grazer type effect on vegetation differentiation and a homogenization in vegetation with sheep grazing (see App. 2).

Diversity parameters responded differently to grazer type (see App. 1). Species richness increased while evenness decreased in sheep-grazed areas (mean
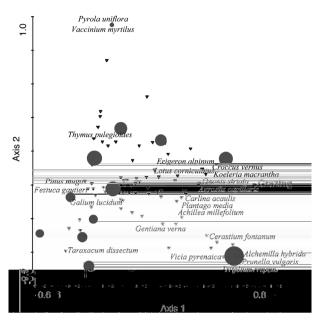

Species distribution from CCA in relation to grazer type in survey S2. ▪ Boxes represent grazing variables, ▼ the species. The most significant species in the analysis are labelled.

number of species per plot 25 ± 1.2 SE, $P = 0.036$; 0.431 ± 0.0223 evenness per plot, $P = 0.039$) compared to cattle-grazed areas (20 ± 1.3 number of species; 0.557 ± 0.0184 evenness). Accordingly, the overall estimated Shannon-Wiener diversity index was not significantly different between treatments. Samples from sheep-grazed areas had more species with low specific quality index ($IS = 0 - 2$) than cattle-grazed areas and, *vice versa*, cattle-grazed areas more species with high IS values ($IS = 3 - 5$) than sheep-grazed areas, when compared using χ^2 tests ($P = 0.053$).

Regression analysis on three structural and use variables in relation to abiotic and management factors in survey S1. Modelling through Poisson regression in Log Linear Model for species richness and linear regression for the other variables. Significant effects in bold.   indicates an effect of ca. $P = 0.1$.

Source	df	No. species per m² P-value	Evenness P-value	Peak biomass (g m⁻²) P-value	PV P-value
Acidic	1		0.699	0.734	0.253
Altitude	1	0.786	0.872	0.945	0.876
South aspect	1	0.187	0.792		
Slope	1	0.154	0.939	0.846	
Protected micro	1	0.435	0.188	0.521	0.365
Exposed macro	1		0.807	0.974	0.720
Stoniness	1		0.503	0.888	0.600
Grazer type	1	0.950	0.852		0.545
Grazing intensity	1		0.611	0.387	

Species distribution from CCA based on sheep grazing intensity in survey S3, introducing abiotic factors as covariates in the analysis. Grey circles represent samples with size proportional to species richness (32 - 53 species per 100 m² plot). ▼ represent the species. The most significant species in the analysis are labelled.

Vegetation changes along grazing intensity gradients

In the third survey (S3), all the environmental variables considered (abiotic and management) explained 65% of the variability in grassland vegetation in a CCA analysis. Grazing intensity alone explained more than half of this variability (36%; pCCA including grazing intensity, all abiotic factors as covariates). Species typical of sub-alpine forests (e.g. *Pinus mugo* ssp. *uncinata*) distributed on the negative side of axis 1, while species typical of grasslands were found towards the positive part of this axis (Fig. 3). Plants typical of acidic and mesic forests, such as *Vaccinium myrtillus* and *Pyrola uniflora*, were found at the positive end of axis 2 (Fig. 3). This was probably related to acidic forest species increasing on northern aspects.

Species diversity was affected by grazing, and the lowest species richness was found in the abandoned areas (Fig. 3). Grazing explained the changes in species richness better in small ($R^2_{adj} = 0.931$ for 1 m × 1 m plots) than in large ($R^2_{adj} = 0.447$ for 10 m × 10 m plots) areas, indicating a higher sensitivity of the system to grazing at smaller scales. Regression analysis indicated a decrease in the forage quality of species (measured through the *Is* index) with abandonment ($P = 0.049$).

Relative role of abiotic and grazing factors on vegetation structural patterns

Our data showed that vegetation composition within a region was affected by environmental factors hierarchically, changing first according to abiotic factors, which constituted the first species filter, and then to grazing management, which acted as a successive environmental filter (survey S1, Fig. 1). This result is consistent with findings in the Pampa in Argentina (Cingolani et al. 2003) and in mountain grasslands in the Alps (Barbaro et al. 2004). However, our results also reveal the strong susceptibility of grassland vegetation composition to the specificity of the grazing management practices, in particular grazer type (Fig. 2) and grazing intensity (Fig. 3).

In addition, this study shows that the sensitivity and direction of the response of the variables representing different vegetation structural properties in front of abiotic and management factors may differ from each other. Species composition was highly responsive to management variables (Fig. 1) compared to diversity components (Table 2). The two components of species diversity (richness and evenness) varied independently, and forage quality was more responsive to the environment than productivity (Table 2). Overall, these results confirm the decoupling in the response of the various diversity components with management and other environmental variables, as found by de Bello et al. (2006), and this has to be taken into account when planning management.

Grazing effects on vegetation patterns

Overall, species richness increased with grazing intensity (Table 2; Fig. 3), as found in other studies (e.g. Milchunas & Lauenroth 1993; Cingolani et al. 2005; de Bello et al. 2006). In addition, our study clearly shows that grazer type is an important factor structuring vegetation (Figs. 1 and 2), which should be considered in macro-ecological studies more often. We found that cattle grazing increased vegetation heterogeneity in landscapes within a region (Fig. 1) and in patches within landscapes (Fig. 2), while sheep reduced it (Figs. 1 and 2). It is agreed that sheep are selective grazers that consume the best forage plants within a patch, while cattle select among big patches but do not select particular species within those (WallisDe Vries et al. 1999; Rook et al. 2004). Therefore, at the local patch scale sheep grazing is highly selective and, in this study, produced a strong vegetation homogenization effect (Fig. 2). In contrast, at the patch scale, cattle grazing is homogeneous, relatively random and, in this study, was associated with high vegetation

heterogeneity (Fig. 2).

In the central Pyrenees it was found that sheep fed on a higher variety of plant communities than cattle (Aldezabal et al. 2002). Sheep are generally conducted by shepherds and consequently will be expected to present a relatively homogeneous grazing pattern, as shepherds will give the animals less choice to select feeding patches. Cattle are most often left relatively free to roam within an area and can, therefore, select patches of their choice. At the landscape scale, a higher diversity of communities was associated with sheep grazing (Fig. 1), while sheep grazing seemed to limit the heterogeneity in vegetation and decrease the beta diversity (de Bello et al. 2007). This study points out that grazing patterns and their effects on vegetation can change for the same grazer type with scale. The ecology of grazing is complex (Garcia et al. 2003) and the consequences of interactive effects across scales need to be unravelled.

The effects of grazer selectivity on vegetation composition, apparent in the S1 survey (Fig. 1), were most evident in S2 (Fig. 2), under controlled variability. In sheep-grazed areas a specific set of species was selected, including *N. stricta* (Fig. 2), which became dominant. *N. stricta* is an unpalatable species, and its expansion has been related in the UK to grazing by selective animals such as sheep (Perkins 1968; Welch 1986; Grant et al. 1996), following complex patterns (only at low fertility; Pakeman 2004). Changes in initial plant composition modifying environmental conditions after small-scale disturbances have been reported to lead to persistent changes in grassland vegetation in the western Pyrenees (Canals & Sebastià 2002). Our hypothesis is that a similar mechanism works in sub-alpine *N. stricta* communities on limestone, and that the resulting vegetation patterns in S2 were the consequence of positive feed-backs relating sheep grazing, soil evolution and vegetation composition (Sebastià 2004).

Furthermore, the results stress the important role of grazer type in terms of conservation of particular plant species and community types within a region. Although cattle-grazed areas favoured higher a variety of plant species and heterogeneity in vegetation composition than sheep-grazed areas (Figs. 1 and 2), sheep grazing contributed to the maintenance of some specific species and communities (Fig. 2) that have important value in terms of conservation in the region. In fact, acidophilous *N. stricta* communities on limestone in the Pyrenees are relatively rare and known to include some species (Fig. 2), such as the endemic *Endressia pyrenaica*, not or only rarely found in other situations (Vigo 1976). Therefore, the combination of sheep and cattle-grazed areas increased the diversity of plant species and communities at regional (Fig. 1) and landscape (Fig. 2) scales, through the scaling up of effects by local processes occurring in patches at smaller scales.
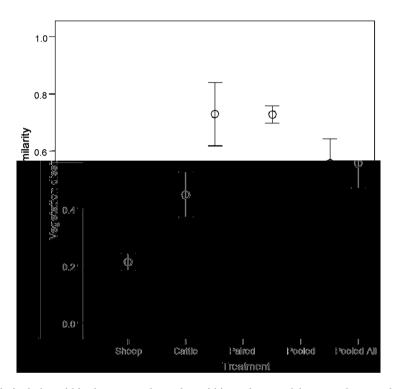
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Several structural characteristics in the cattle- and sheep-grazed areas in survey S2: species richness (number of species per plot recorded on 100 points), the Camargo evenness index per sample (*E*), the Shannon-Wiener diversity index (*H*) and the Bray-Curtis dissimilarity index. The Berger-Parker dominance index (frequency of the dominant species / overall frequencies), the Bray-Curtis similarity index and the Shannon (generated by randomization) presented for each grazer type refers to the within treatment single value or the mean, depending on index calculation. Estimated mean ± 1 SE shown for the other two variables.

Grazer type	Richness	*E*	*H*	Dominance	Dissimilarity
Cattle	16 ± 1.31	0.5568 ± 0.0184	3.6898	0.2048	0.4473
Sheep	25 ± 1.19	0.4305 ± 0.0223	3.4668	0.1533	0.2117

Bray-Curtis dissimilarity index within sheep-grazed samples, within cattle-grazed, between sheep- and cattle-grazed, paired and pooled and among all samples pooled.