SPATIAL PATTERNS OF SPECIES DISTRIBUTIONS IN GRAZED SUBALPINE GRASSLANDS

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ABSTRACT

Spatial patterns of species diversity have important influences on the functioning of ecosystems and the effect of livestock grazing on spatial heterogeneity can differ depending on the scale of the analysis. This study examined the effects of grazing on the spatial patterns of species distribution and whether the effects of grazing on the spatial distributions of species vary with the scale of the analysis. Data were collected at three locations in the subalpine grasslands of Ordesa-Monte Perdido National Park and Aísa Valley, Central Pyrenees, Spain, that differed in mean stocking rates. Aspect explained about one-third of the environmental variation in species distribution. In flat

areas, spatial variation in species composition varied with grazing intensity at two scales. At a coarse scale (among vegetation patches), grazing promoted patchiness, and among-transect variation in species diversity and grazing intensity were positively correlated. At a fine scale (within vegetation patches), the disruption of the self-organizing processes of the species spatial distributions resulted in a reduction in the long-range spatial autocorrelations of some of the characteristic species and in the homogenization of species spatial distributions. *Echinopartum horridum* encroachment had a great influence on the effect of grazing on south-facing grassland slopes.

Key words: beta diversity, Detrended Fluctuation Analysis, grazing stocking rates, Information Fractal Dimension, self-organization, spatial patterns.

INTRODUCTION

Spatial patterns in vegetation develop due to restricted dispersal (Willson, 1993), clonal reproduction (Silander, 1985), and plant interactions (Schwarz et al. 2003; Grau 2002), which leads to increased heterogeneity through vegetation succession (Cook et al. 2005; Seabloom et al. 2005) or ecological memory (the degree to which an ecological process is shaped by past modifications) (Peterson 2002) contribute to the development of vegetation spatial patterns. Grazing can disrupt the spatial structure of plant communities and alter dominance hierarchies (Alados et al. 2003; Rebollo et al. 2002; Roques et al. 2001), which affects the spatial distribution of diversity and has significant implications for functioning of ecosystems. The perception of how grazing influences the spatial distribution of species can depend on the scale of analysis (Adler et al. 2001; Spiegelberger et al. 2006).

In rangeland ecosystems, grazing can have a significant effect on plant species diversity (Cingolani et al. 2005) and even Darwin (1859) recognized the favourable effect of grazing on grasslands. Commonly, biological diversity is associated with the efficient use of resources and ecosystem resilience (Tilman and Kareiva 1996; Chapin et al. 1997; Walker et al. 1999); however, high diversity is not always associated with ecosystem performance and resilience. Grazing can foster invasions by weeds and lead to a reduction in the richness of native plants (Hobbs 2001; Prober and Thiele 1995). Until recently, most of the research has focused on phenomena at a local scale, e.g., resource availability, productivity, biotic interactions, and disturbance (Huston 1979; Huston 1994; Grace 1999; Tilman 1988), and the effect of grazing on the spatial distribution of diversity at multiple spatial scales has not been investigated. Today, however, there is considerable interest in the effects of regional phenomena (Ricklefs

1987; Huston 1999); e.g., species pools (Zobel 1997) on community composition and biodiversity.

Herbivores can affect the habitat and influence species distributions (Gomez 2005) by increasing or decreasing heterogeneity, which depends on the pre-existing spatial pattern of vegetation and the spatial distribution of grazing (Adler et al. 2001). Grazers interact with vegetation selectively (WallisDeVries et al. 1999), which creates disturbances and gaps (Steinauer and Collins 2001) that can contribute to high spatial heterogeneity (Brown and Allen 1989), particularly evident in subalpine grasslands, where a thick grassland cover can impair seed germination. Through the consumption of biomass and trampling, grazing can increase spatial heterogeneity (Alados et al. 2004; de Bello et al. 2007; Bakker et al. 2003) by creating a mosaic of patches, which increases heterogeneity in these grasslands (Bakker et al. 2003). Typically, however, in arid and semiarid ecosystems (Alados et al. 2003; Alados et al. 2005; Alados et al. 2004), grassland prairies (Collins and Smith 2006; Chaneton and Facelli 1991), and subalpine grasslands (Alados et al. 2007), grazing is an homogenizing process.

Livestock can be significant contributors to the dispersal of many plant species (Fisher et al. 1996), when they move between habitat patches during their daily movements and increase the similarity in species composition among fragments (Pueyo et al. 2008).

To gain a better understanding of how grazing influences plant spatial patterns at multiple scales, we performed a measurable experiment to examine the spatial patterns of diversity in subalpine grasslands of the Central Pyrenees, Spain, where grazing pressure and topography were variable. We assessed the spatial contribution of species diversity by partitioning vascular plant diversity into their spatial components (Lande 1996; Wagner 2000) and evaluated whether the observed diversity partitions deviated from the null hypothesis because of non-random patterns of intraspecific aggregation

(Crist et al. 2003). Non-random distributions within species reflects the influence of processes such as environmental filtering acting by the selection of species pool adapted to specific habitats (Grime 1979; Huston 1979; Wassenaar et al. 2005; de Bello et al. 2009). In addition, self-structuring processes such as species modulation, which can alter soil structure and the redistribution of nutrients (Rietkerk et al. 2004; Rietkerk et al. 2002; Meron et al. 2004; Gilad et al. 2004) or niche differentiation and facilitation interactions, can produce an increase in local assemblages and a reduction in random spatial distributions (Venail et al. 2008).

When evaluated at a coarse scale (inter-patch variation; i.e., communities separated by other communities or by bare soil), we predicted an increase in heterogeneity and spatial variation in species composition because of the large turnover in the secondary succession of subalpine grasslands after grazing disturbance (Hawkes and Sullivan 2001; Proulx and Mazumder 1998). At fine scale (intra-patch variation), we predicted that grazing disrupted the structure of the community and favoured the invasion of early successional species, which spread randomly in the landscape and lead to the homogenization of species distributions.

Specifically, we addressed the following questions: (1) Are variation in species composition and distance between sampling sites positively correlated? (2) How does grazing affect the spatial variation in species composition? (3) How does grazing affect the spatial patterns of species distributions?

METHODS

Study Area

The study was conducted at two sites in the Central Pyrenees (Spain): the subalpine grasslands of the Ordesa and Monte Perdido National Park (OMPNP) (42° 36'N, 0° 00'; from 1700 to 2100m a.s.l.; 15608 ha) and the Aísa Valley (42° 40'N, 0° 34'W; from 1500 to 1900m a.s.l.; 8154 ha). The two areas had similar topography, soils, and climate, and the same grassland plant communities (Aldezabal 2001; Benito Alonso 2006). In the Pyrenees, subalpine pastures are secondary plant communities that have replaced the native forest and have been grazed continuously for at least the last 500 years (Montserrat and Fillat 1990). With the exception of a few annuals that predominate in the gaps created by natural erosion or animal disturbances, most of the plants in the pastures are perennial graminoids and forbs that reproduce clonally. Topography constraints habitat and grazing activity in subalpine ecosystems (García-Gonzalez et al. 1990). Flat areas have the highest plant coverage, production, and forage quality, and therefore, are heavily grazed, mainly by cattle (García-Gonzalez et al. 1990; Montserrat and Fillat 1990). Data were collected in the dense pastures of *Bromion erecti* and *Nardion strictae* that are between 1800 and 2000 m a.s.l. (García-González et al. 1991; Aldezabal 2001).

Between July and September, the Aísa pastures (1241 ha) were used by 150 cattle and 2000 sheep. The Ordesa site has two pastoral areas, Góriz and Sesa. Góriz (5700 ha) held 6500 ewes and 200 cows. Sesa (1600 ha) held 2800 ewes, 550 cows, and 91 horses (García-Gonzalez et al. 2007; García-González and Marinas, 2008). In terms of LU (livestock unit equivalent to a cow of 500 kg) the stocking rate for the different areas was 0.344, 0.201 and 0.603 LU ha⁻¹ year⁻¹ respectively, using metabolic weight as conversion system (Heitschmidt and Taylor, 1991).

Data collection and analysis

To quantify the partitioned components of regional diversity and the influence of environmental and spatial components on the spatial variation of species diversity, in the spring of 2004 we selected two sites in the OMPNP (Góriz and Sesa) and one in the Aísa Valley. At each site, we established nine 250-m linear transects (three on northerly oriented slopes, three on flat areas, and three on southerly exposed sites), reaching a total of 27 transects. In 2005, other nine 250-m linear transects were established at each OMPNP sites (18 in total), where two contrasting grazing pressures and identical physical conditions were present. Aísa Valley was not included in 2005 sampling. In 2004 and 2005, the vegetation was surveyed during the period of peak growth (June and July).

To estimate plant abundance and species richness in each of the transects, we used the Point-Intercept Method (every 20 cm) (Goodall 1952) and calculated Shannon and Evenness diversity indices.

(i) Spatial components of species diversity

Vascular plant species diversity was decomposed (following Whittaker 1972) into different spatial components. γ diversity is total species diversity in a set of samples, which was partitioned between the average diversity within samples (α) and among samples (β); i.e. $\gamma=\alpha+\beta$, (Wagner et al. 2000). In a nested hierarchical design, α_i is the average diversity within samples at level i , and $\beta_i=\alpha_{i+1}-\alpha_i$ (Crist et al. 2003; Gering et al. 2003; Lande 1996; Allan 1975; Wagner et al. 2000). We used an hierarchical design that had $i = 1, 2$, and 3 nested levels, where level 1 was transect, level 2 was site, and level 3 was Central Pyrenees.

To test for non-random β diversity, we performed a standard randomization routine (Manly 2007). In each randomization, the frequency distribution of each species and the distribution of sampling effort of the empirical data were maintained (Freestone and Inouye 2006). Using Matlab 7.01 software, the randomization models were performed at two levels (Crist et al. 2003): sample-based randomizations (samples are randomized at each hierarchical level) and individual-based randomizations (randomization occurs at the individual level, only), and each randomized data set was partitioned into α and β components at each hierarchical level (Crist et al. 2003). Individual-sample randomizations are useful for determining the effect of individual aggregation on the partitioning of diversity and sample-based randomizations reveal how different patches contribute to regional diversity.

(ii) *Factors influencing spatial variation in species diversity*

To calculate the influence of the environmental variables and spatial components on the variance in community composition, we applied canonical partitioning (Legendre et al. 2005; Borcard et al. 1992; Borcard et al. 2004; Legendre and Legendre 1998). We decomposed the variance observed in the response variable $\mathbf{Y}$ (community composition data) as a function of a set of environmental variables $\mathbf{X}_1$ (proportion of bare soil, grazing pressure, and aspect) and a set of spatial variables $\mathbf{X}_2$ (X and Y geographical coordinates). To calculate the partitioning of the spatial and environmental components of the variation in community composition, we used canonical redundancy (RDA) (Rao 1964) in the Ginkgo Analysis System (Bouxin 2005) (<http://biodiver.bio.ub.es/vegana/>). To generate the dissimilarity matrix among sites, the Euclidean distances were calculated (Krebs 1999). To calculate the correlation between the species dissimilarities of communities and the distance between transects, we used a Mantel Test (Legendre

and Legendre 1998) using Ginkgo Analysis System (Bouxin 2005). The distance between transects were calculated based on GPS coordinates.

(iii) *Spatial patterns of species distribution*

The Information Fractal Dimension (D_I) quantifies the homogeneity of a species distribution. The higher the D_I , the more homogeneous is the distribution. We calculated

D_I as $D_I \equiv \lim_{\varepsilon \rightarrow 0} \frac{H'(\varepsilon)}{\ln 1/\varepsilon}$, (Farmer et al. 1983), where $H'(\varepsilon)$ changes with window size (ε)

following the equation $H'(\varepsilon) = \sum_{i=1}^{N(\varepsilon)} p_i \ln \frac{1}{p_i}$, where p_i is the proportion of the intercepts

attributed to plant species i , which depends on the length of the transect segment (window size = ε). We selected scales of size $\varepsilon = 2^n$, for $n = 0$ to 6 ; i.e., 1, 2, 4 ... 64 m.

D_I is equivalent to the z exponent of the species-area relationship

$S_{(A)} = c \left(\frac{1}{A} \right)^{-z}$ (Rosenzweig 1995), where ε is equivalent to $1/A$ and $S_{(A)}$ is equivalent to

the number of boxes $N(\varepsilon)$ of the box-counting fractal dimension equation

$N(\varepsilon) \cong \varepsilon^{-D}$ (Borda-de-Agua et al. 2002). For the box-counting fractal dimension, each

box is either occupied or unoccupied, and the relative occupancy of points inside the

box is not considered. D_I is more precise than D (Farmer et al. 1983; Alados et al. 1999)

because take into consideration the proportion of box occupied.

To detect intrinsic changes in the control mechanisms, we used Detrended Fluctuation

Analysis (DFA) to distinguish between spatial patterns caused by pre-existing

environmental heterogeneity and those caused by self-organizing processes. DFA

measures the degree of spatial autocorrelation in each species' cover, independent of the

scale of measurement (Peng et al. 1992; see also Alados and Weber 1999). We

calculated the long-range spatial autocorrelations of the vegetated and non-vegetated

patches, and of each species, individually. In the DFA, the integrated sequence

$y(s) = \sum_i^s x(i)$ was subdivided into non-overlapping sequential sets or 'boxes' of size b ($x(i) = +1$ for presence, $x(i) = -1$, for absence). The long-range spatial autocorrelations of individual species were obtained from the presence (+1) and absence (-1) data of each species. A regression line was fit to each box of size b ; i.e., $y_b(s)$ was regressed on s , and the residual variance per each box size was calculated, $F^2(b) = \frac{\sum (y_b(s) - \hat{y}_b(s))^2}{N}$.

To provide the scale of the relationship, $F(b) \propto b^\rho$, that process was repeated for scales 4, 6, 8 256 points along the first 1025 points of each transect. Following Halley et al. (2004), we chose a minimum scale that was greater than the minimum species crown diameter (inter-point separation) and a maximum inter-point distance (coarse resolution) of one-quarter of the set diameter. The DFA exponent reflects the long-range correlation of the plant distribution sequence, which is equivalent to the Hurst Exponent (Hausdorff et al. 1997), but it is a superior method for quantifying long-range correlations (Hu et al. 2001; Taqqu et al. 1995). Long-range power-law correlations cannot be analyzed using correlation analyses because they are non-stationary. DFA exponents can detect the long-range correlations that are embedded in seemingly non-stationary sequences and remove trends that can arise from fluctuations in external factors, e.g., soil structure. Theoretically, the DFA exponent is not affected by the magnitude of the fluctuations, but by the sequential ordering of the fluctuations. Among the 13 species evaluated in this study, only five showed significant correlations between cover and rho values. When $\rho = 1/2$, the sequence is randomly distributed, but when $\rho > 1/2$, the sequence depends on the history of the distribution. An area in which ρ is larger than in another area indicates greater non-randomness and, therefore, is evidence of higher structural self-organization.

RESULTS

Spatial components of species diversity

In the subalpine grasslands of Central Pyrenees, we recorded 156 species of plants from 37 families, of which 108 were forbs, 22 were graminoids, 11 were dwarfs, 10 were shrubs, and one was a tree. Only 19 (12%) of the species occupied > 1% of plant covered.

The additive partitions of the Shannon Index indicated that α_1 diversity accounted for 76% of the regional diversity, and only 8% was attributed to among-transect variation (β_1). Among-site variation (β_2) accounted for 15% of the regional diversity (Table 1). The observed levels of β_1 diversity were significantly lower than the values expected based on the individual-based randomizations ($t = -4.51$, $df = 16$, $P < 0.001$). Among-site diversity (β_2) did not differ significantly from that expected based on individual-based randomizations ($t = 1.73$, $df = 16$, NS).

The Euclidean distance matrix of floristic dissimilarity and the distance between transects were not significantly ($r_s = 0.03$, NS) correlated, which indicates that components other than the spatial component of diversity had an effect on species dissimilarity. The Redundancy Analysis (RDA) revealed that only 29.6% of the variation in community structure was explained by environmental (grazing pressure, proportion of bare soil, and aspect) (20.8%) and spatial (X and Y geographical coordinates) (8.4%) variables. Aspect (0 = flat, 1 = north, and -1 = south) contributed 11% of the variation explained by the environmental variables.

Grazing pressure and spatial variation in diversity

Grazing pressure had a significant effect on species richness and diversity on transects that has a southern aspect, but not on transects on flat ground or those that had a northern aspect (Table 2). On south-facing slopes, richness and proportional diversity indices (Shannon and Evenness indices) were significantly positively correlated with grazing pressure. Nineteen of the 156 species in the OMPNP provided 80% of the vegetative cover. On south-facing slopes, *Echinopartum horridum* provided 50% of the vegetative cover under low grazing pressure, but only 11% on the transects where grazing pressure was high. When the analysis was restricted to the sites on north-facing slopes and on flat ground, the distance between transects and floristic dissimilarity, as measured by Euclidean distance, were significantly correlated ($r_s = 0.216$, $P < 0.01$). Thus, when the effect of aspect was controlled, the spatial component of diversity became more important. Indeed, the average among-transect variation, β_1 , at sites on north-facing slopes and on flat ground grouped together, was almost twice as high when grazing pressure was high (0.290 ± 0.042) as it was when grazing pressure was low (0.150 ± 0.045). Thus, once the effect of aspect was removed, grazing had a significant effect on spatial diversity in the subalpine grasslands of the Pyrenees.

Grazing pressure and spatial patterns of species distributions

Livestock grazing had a significant effect on the long-range spatial autocorrelations (DFA exponents) of the species in the flat subalpine grasslands. Of the 13 species that occurred at both grazing sites and were present in most of the slope aspects, more than

half had long-range spatial autocorrelations that were lower where grazing pressure was high than where it was low and, for four of those species, the difference was statistically significant (Table 3). In keeping with the decrease in the long-range spatial autocorrelations of plants with an increase in grazing pressure, the Information Fractal Dimension, D_1 was significantly higher in flat areas (higher homogenous distribution), where the effect of grazing on the spatial distribution of plant species was most evident, than it was at sites that had southern or northern aspects (Table 2).

DISCUSSION

In the subalpine grasslands of the Central Pyrenees, the spatial variation in diversity reflected the importance of self-organizing mechanisms in the ecosystem. As reported by several studies (Freestone and Inouye 2006; Crist et al. 2003; Gering et al. 2003), among-transect variation (β_1) was lower than what was expected based on individual-based randomizations, which reflects the presence of spatial structuring processes. Furthermore, it suggests that multiple mechanisms including spatial heterogeneity, dispersal patterns, and biotic interactions (Bolker and Pacala 1999; Levin 1974; Seabloom et al. 2005) influence the spatial distribution of diversity. Unlike in more highly fragmented ecosystems such as serpentine outcrops (Freestone and Inouye 2006) or the patchy environment of Cabo de Gata National Park (SE Spain) (Alados et al. 2009), in the grasslands of the Central Pyrenees among-site variation (β_2) did not differ significantly from what was expected based on individual-based randomizations. Thus, among-site diffusion processes lead to low among-transect variation, which is characteristic of long-lasting, well-established communities that have prolonged periods

of diffusion (Kareiva 1982). Our results suggest that the traditional grazing practices in the subalpine grasslands of the Central Pyrenees have fostered high connectivity among grassland patches.

Among the factors that influenced the spatial distribution of species, slope aspect explained about one-third of the environmental component of the variation in plant diversity (11% of 30%). The spatial component explained only 8% of the variation in plant diversity when slope aspect was included in the analysis, and floristic dissimilarity and distance between transects were not significantly correlated.

In the Central Pyrenees, *E. horridum*, a thorny-cushion legume, forms large, dense monospecific patches that can cover several hectares in areas where only a few other species persist within the gaps (Alados et al. 2007). The abundance of *E. horridum* on south-facing slopes subjected to light grazing was dramatic. In heavily grazed grasslands, the abundance of *E. horridum* was much lower, which promoted the expansion of populations of species that are less sensitive to, or favoured by, grazing; e.g., *Festuca rubra*, *Thymus praecox*. When the effect of low grazing pressure on south slopes was removed by removing the data from the south slope from the analyses, the spatial component of diversity was a significant factor in structuring spatial diversity, and species dissimilarity and the distance between transects were significantly, positively correlated. In addition, grazing had a significant effect on spatial diversity in the subalpine grasslands. Among-transect variation was higher in heavily grazed sites than it was in lightly grazed sites.

Grazing can act as a landscape modulator by altering soil structure and the redistribution of nutrients, and can increase heterogeneity through vegetation succession (Cook et al. 2005; Seabloom et al. 2005) or ecological memory (the degree to which an ecological process is shaped by past modifications) (Peterson 2002). Grazing in highly productive

sites, that have high ability to recolonize vegetation gaps after perturbation, can increase beta diversity (heterogeneity) (Steiner and Leibold 2004; Bakker et al. 2003), which is in contrast to what can occur in less productive sites, as predicted by Steiner and Leibold (2004); i.e., β_1 diversity was higher in the more productive ecosystem (Central Pyrenees, 0.30) than it was in the less productive ecosystem (Cabo de Gata National Park, 0.17) (Alados et al. 2009).

In addition, grazing can create gaps in the thick layer of subalpine perennial grasses and provides an opportunity for colonization by seed-dispersed species (Pakeman and Field 2005), which colonize space randomly (Kershaw 1963; Fowler 1990). In our study, in the flat areas that were subjected to the highest grazing pressures from herbivores, the Information Fractal Dimension (D_I) and grazing pressure were positively correlated. As in other studies, grazing increased the homogeneity (high D_I) of species' distributions (de Bello et al. 2007; Collins and Smith 2006; Alados et al. 2003). Moreover, at a fine scale (within patches), grazing disrupted community assemblages, homogenized the spatial distributions of species, and reduced the long-range spatial autocorrelations of half of the most abundant plant species in flat areas. Communities assembled by self-organizing processes such as niche differentiation, allows greater coverage of the heterogeneous environment (Venail et al. 2008), results in an increase in the efficiency of the use of resources (Venail et al. 2008) and the positive effect of plant diversity on primary production (Loreau and Hector 2001). The destruction of the community spatial structure will disrupt the self-organization gene-complex of long standing stable communities. In vitro microcosm experiments have shown that when the community spatial structure is broken by shaking the tubes, diversity is reduced.

In the Central Pyrenees, grazing pressure had a significant effect on the species richness and diversity on transects that has a southern exposure, but not on transects in flat areas

or on those that had northern exposures. The decline in *E. horridum* in heavily grazed areas is more closely associated with traditional management practices, such as prescribed fires, than with depredation by livestock. Traditionally, the grasslands in the Central Pyrenees have been burned, but controlled recolonization from seeds by *E. horridum* in the heavily grazed sites has favoured the spread of other plant species. In contrast, a reduction in grazing pressure can favour an increase in the encroachment by *E. horridum* in lightly grazed sites (Montserrat et al. 1984). In the last 30 yr, the abandonment of grazing practices in the Pyrenees has resulted in a 47% increase in the biomass of woody vegetation (Bartolomé et al. 2005). Thus, heavy grazing after fire, the traditional means of reducing woody plants (Ellenberg 1988; Garcia-Ruiz and Valero-Garces 1998), might be the best practice for maintaining pastures and preventing plant succession in subalpine ecosystems.

We conclude that the spatial structure of subalpine grassland communities in the Pyrenees was altered by grazing, particularly in flat areas, which resulted in an increase in spatial heterogeneity, when evaluated at a coarse scale (among patches), and the homogenization of species distributions at a fine scale (within patches). On south-facing grassland slopes, the reduction of *E. horridum* as grazing intensity increased influenced significantly the spatial diversity of grasslands. The effects of grazing on subalpine grasslands can operate on at least two scales of analysis: a positive effect at a coarse scale because of an increase in heterogeneity, which increases the opportunity for species to colonize gaps and, thereby, increases diversity, and a negative effect at a fine scale because of a disruption in the spatial organization of the community, which has a detrimental effect on niche complementarity. Further research is needed to determine which of the two processes are more important for the conservation grasslands, or whether equilibrium between the two processes is more advantageous.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the Spanish CICYT project CGL2005-01131/BOS. We thank Yolanda Pueyo, Maite Gartzia, Ana Marinas, Beatriz Bueno, and Elena Lahoz for assistance in collecting field data. We thank Bruce MacWhirter for critically reading and providing helpful suggestions on the manuscript.

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Table 1. The observed and the expected alpha, beta, and gamma diversities (based on the individual-based randomization routine) on transects within subalpine grasslands in the Central Pyrenees, Spain. In parenthesis are the 95% Confidence Limits obtained from the individual-based randomization (Crist et al. 2003).

	Observed		Expected
	Values	Percentage	Individual-based randomization
α_1	2.804	76.3	2.797 (2.809, 2.784)
α_2	3.108		3.266 (3.274, 3.258)
α_3	3.673		
β_1	0.304	8.3	0.469 (0.464, 0.473)
β_2	0.564	15.4	0.408 (0.400, 0.415)
γ	3.673	100	3.673

Table 2. Observed means ($\pm$ SE) and F-values from one-way ANOVA with Grazing Pressure as a fixed factor, and plant richness, proportional diversity (Shannon and Evenness indices), proportion (%) of bare soil, and spatial pattern (long-range spatial autocorrelation of vegetated - non-vegetated patches, DFA exponent, and Information Fractal Dimension (D_I) as dependent variables. Analysis based on the presence of species along 36 250-m linear transects in the subalpine grassland of the OMPNP, Central Pyrenees, Spain, collected in 2004 and 2005. * $P \leq 0.05$, ** $P \leq 0.01$.

Flat aspect	F(1, 10)	Highly Grazed Mean $\pm$ se	Lightly Grazed Mean $\pm$ se
Richness	0.07	46 $\pm$ 4.491	45 $\pm$ 3.266
Bare soil	0.53	5.466 $\pm$ 0.780	7.813 $\pm$ 3.144
Shannon	1.73	2.594 $\pm$ 0.110	2.764 $\pm$ 0.060
Evenness	8.91 **	0.678 $\pm$ 0.013	0.726 $\pm$ 0.010
D_I	4.92 *	0.838 $\pm$ 0.010	0.802 $\pm$ 0.012
DFA exponent	0.04	0.677 $\pm$ 0.33	0.686 $\pm$ 0.022
North aspect	F(1, 10)	Highly Grazed Mean $\pm$ se	Lightly Grazed Mean $\pm$ se
Richness	0.17	51 $\pm$ 1.878	50 $\pm$ 2.662
Bare soil	1.06	4.186 $\pm$ 0.988	6.933 $\pm$ 2.482
Shannon	0.36	2.753 $\pm$ 0.074	2.867 $\pm$ 0.017
Evenness	0.70	0.698 $\pm$ 0.013	0.731 $\pm$ 0.037
D_I	2.79	0.818 $\pm$ 0.011	0.761 $\pm$ 0.032
DFA exponent	0.8	0.684 $\pm$ 0.034	0.638 $\pm$ 0.040
South aspect	F(1, 10)	Highly Grazed Mean $\pm$ se	Lightly Grazed Mean $\pm$ se
Richness	5.04*	52 $\pm$ 3.143	33 $\pm$ 7.757
Bare soil	0.22	4.426 $\pm$ 0.610	6.066 $\pm$ 3.500
Shannon	6.40*	2.773 $\pm$ 0.400	1.742 $\pm$ 0.092
Evenness	6.70*	0.702 $\pm$ 0.023	0.489 $\pm$ 0.078
D_I	2.33	0.781 $\pm$ 0.016	0.841 $\pm$ 0.036
DFA exponent	0.16	0.735 $\pm$ 0.058	0.704 $\pm$ 0.051

Table 3. Observed mean $\pm$ SE and F values of the one-way ANOVAs with grazing pressure as a fixed factor and DFA exponent (long-range spatial auto-correlation estimator) as the dependent variable for the most abundant plant species in the subalpine grasslands flat aspect of the OMPNP in the Central Pyrenees, Spain. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	DFA exponent			
	n2	F (1, n2)	Highly Grazed	Lightly Grazed
			Mean $\pm$ se	Mean $\pm$ se
<i>Nardus stricta</i>	10	2.25	0.738 $\pm$ 0.028	0.786 $\pm$ 0.015
<i>Trifolium alpinum</i>	10	1.17	0.836 $\pm$ 0.017	0.804 $\pm$ 0.027
<i>Trifolium repens</i>	8	11.55**	0.619 $\pm$ 0.008	0.710 $\pm$ 0.025
<i>Agrostis capillaris</i>	10	2.00	0.646 $\pm$ 0.014	0.688 $\pm$ 0.26
<i>Carex sp</i>	10	0.01	0.727 $\pm$ 0.022	0.729 $\pm$ 0.013
<i>Festuca rubra</i>	10	2.98	0.704 $\pm$ 0.028	0.758 $\pm$ 0.014
<i>Sanguisorba minor</i>	4	0.23	0.740 $\pm$ 0.035	0.680 $\pm$ 0.016
<i>Galium verum</i>	10	4.70*	0.595 $\pm$ 0.022	0.659 $\pm$ 0.020
<i>Achillea millefolium</i>	10	6.35*	0.619 $\pm$ 0.018	0.755 $\pm$ 0.051
<i>Hieracium pilosella</i>	8	13.9**	0.632 $\pm$ 0.030	0.772 $\pm$ 0.023
<i>Plantago media</i>	9	0.07	0.667 $\pm$ 0.024	0.677 $\pm$ 0.030
<i>Thymus praecox</i>	10	0.94	0.632 $\pm$ 0.015	0.604 $\pm$ 0.027
<i>Lotus corniculatus</i>	10	0.15	0.677 $\pm$ 0.041	0.699 $\pm$ 0.039