Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain

de Bello, Francesco^{1*}; Lepš, Jan² & Sebastià, Maria-Teresa^{1,3}

 ¹Laboratory of Plant Ecology and Forest Botany, Forestry and Technology Centre of Catalonia, E-25280 Solsona, Spain;
²Department of Botany, Faculty of Biological Sciences, University of South Bohemia, and Institute of Entomology, Czech Academy of Sciences, CZ-370 05 České Budějovice, Czech Republic; E-mail suspa@bf.jcu.cz;
³Agronomical Engineering School, University of Lleida, E-25198 Lleida, Spain; E-mail teresa.sebastia@ctfc.es;
*Corresponding author; Fax +34 973481392; E-mail fradebello@ctfc.es

Abstract

Questions: Does grazing have the same effect on plant species richness at different spatial scales? Does the effect of spatial scale vary under different climatic conditions and vegetation types? Does the slope of the species-area curve change with grazing intensity similarly under different climatic conditions and vegetation types?

Location: Pastures along a climatic gradient in northeastern Spain.

Methods: In zones under different regimes of sheep grazing (high-, low-pressure, abandonment), plant species richness was measured in different plot sizes (from 0.01 to 100 m²) and the slope of the species-area curves was calculated. The study was replicated in five different locations along a climatic gradient from lowland semi-arid rangelands to upland moist grasslands.

Results: Species richness tended to increase with grazing intensity at all spatial scales in the moist upland locations. On the contrary, in the most arid locations, richness tended to decrease, or remain unchanged, with grazing due to increased bare soil. Grazing differentially affected the slope (z) of the species-area curve (power function $S = c A^z$) in different climatic conditions: z tended to increase with grazing in arid areas and decrease in moist-upland ones. β -diversity followed similar pattern as z.

Conclusions: Results confirm that the impact of grazing on plant species richness are spatial-scale dependent. However, the effects on the species-area relationship vary under different climatic conditions. This offers a novel insight on the patterns behind the different effects of grazing on diversity in moist vs. arid conditions reported in the literature. It is argued that the effect of spatial scale varies because of the different interaction between grazing and the intrinsic spatial structure of the vegetation. Variations in species-area curves with grazing along moisture gradients suggest also a different balance of spatial components of diversity (i.e. α - and β -diversity).

Keywords: Competition; Heterogeneity; Land use; Management; Mediterranean; Power law species-area curve; Sheepgrazing.

Nomenclature: Bolòs et al. (1993).

Introduction

The role of herbivores in controlling plant species richness is a critical issue in the conservation and management of grazed systems (Olff & Ritchie 1998; Landsberg et al. 2002; Guo 2004). Syntheses and models suggest that herbivore effects on plant diversity vary across environmental gradients of soil fertility and precipitation (Milchunas et al. 1988; Huston 1994; Proulx & Mazumder 1998; Cingolani et al. 2005). A moderate grazing pressure is thought to enhance plant diversity by the direct consumption of competitively dominant plant species, thus indirectly affecting plant competition and promoting species coexistence (Grime 1973; Al-Mufti et al. 1977). However, in water- and nutrient-limited environments, increased grazing is expected to increase plant mortality and ultimately decrease species richness (Huston 1994; Proulx & Mazumder 1998).

The change in species richness after grazing cessation may be consequently different under different climatic conditions. However the conclusions of previous studies differ to a certain extent (Perevolotsky & Seligman 1998; Osem et al. 2002; Rook et al. 2004) causing some uncertainty in terms of conservation purposes and for the generalization of synthetic theories of biodiversity. Discrepancies could be partially caused by the fact that richness depends on the spatial scales considered (Lepš & Štursa 1989; Canals & Sebastià 2000; Magurran 2004).

Given the dependence of species richness on spatial scale, the number of species in a community is better described by the species-area relationship rather than by a single number (Rejmánek & Rosén 1992; Rosenzweig 1995; Gotelli & Colwell 2001; He & Legendre 2002). The species–area relationship, describing the increase in the number of species (*S*) with increasing area (*A*), is one of the most robust patterns in ecology (Huston 1994; Ostling et al. 2003; Magurran 2004). Species-area curves are based on the evidence showing that the number

of species increases with increasing spatial extent of a community and that the rate of increase differs among communities (Lepš & Štursa 1989; Rosenzweig 1995; Wilson & Chiarucci 2000; Desiltes & Houle 2005). The curve is generally formulated as a power function, $S = c A^{z}$, although the semi-logarithmic form S = a + blog A has also been used by botanists (Lepš 2005). The rate at which the species number increases with area (as expressed by z) has been associated to a great variety of theoretical mechanisms suggesting, at least, differences in the processes regulating diversity (Huston 1994). It is generally accepted that z relates to different aspects of spatial heterogeneity (Lepš & Štursa 1989; Huston 1994): resource distribution (Desiltes & Houle 2005), spatial distribution of the species (He & Legendre 2002; Ostling et al. 2003), and spatial display of the species, as, e.g., size and vertical complexity (Huston 1994; Ovaskainen & Hanski 2003; Lepš 2005)

Species-area curves might thus be useful when analyzing the control of disturbance (e.g. grazing) on species richness at different ranges of scales, as they allow the study of the partition of spatial components of diversity (Huston 1999; Loreau 2000). Olff & Ritchie (1998) hypothesized that species-area curves in grazed areas could be less steep compared to curves from ungrazed areas and that these curves should finally intersect. Hence, species richness may increase at small scales while decreasing at wider-regional scales. Intersections of species curves have been reported (Lepš & Štursa 1989; Lande et al. 2000) and they have important consequences for extrapolation of biodiversity patterns (Magurran 2004). More experimental data are however needed to confirm if this different effect of grazing on different spatial scale will hold for different vegetation types and determine the implications for the mutual dependency of local and regional diversity (Rosenzweig 1995; Huston 1999).

In this study, we assessed, under different climatic conditions and vegetation types, whether (1) the effect of grazing on species richness was similar at different spatial scales and (2) the slope of the species-area curve changed with grazing intensity. Changes in plant species richness in grazed (high and low pressure) and abandoned areas were analysed along a climatic and altitudinal gradient in northeastern Spain, from semi-arid lowland to moist-upland areas. Different plot sizes were sampled ranging from 0.01 to 100 m² and the species-area curve was calculated. To our knowledge, this study is the first attempt to investigate the spatial-dependent effects of pastoralism on plant richness with a comparable design for different climatic conditions.

Methods

Experimental design

Five locations were selected along an altitudinal and climatic gradient in northeastern Spain (Fig. 1) including the transition from the Mediterranean to the Boreo-alpine biogeographical region (Bolòs et al. 1993). Climatic parameters covary along the gradient in such a way that selected locations ranged from semi-arid to humid conditions (Moisture index in Fig. 1; Anon. 1992) and each was placed in a different vegetation belt (Vigo & Ninot 1987). The number of species shared between adjacent locations along the gradient was comparable, as it was the similarity in species composition (Fig. 1) calculated with the Jaccard similarity index:

$$J = a/(a+b+c) \tag{1}$$

where a is the number of species shared between the two neighbour locations, b is the number found only in the first location and c the number found only in the second location.

There is a century-long history of livestock (mainly sheep and goat) grazing in the study area. As in most areas of the northern rim of the Mediterranean Basin, rural abandonment is causing successional changes (de Bello et al. 2005). Modernization of livestock production has resulted in a decline of the use of extensive rangelands and grasslands in the last few decades (Rook et al. 2004). Sheep herds in the region have approximately 500-700 animals and the maximum stocking rates are normally encountered next to corrals and water points. In some limited cases traditional transhumance is still practised: shepherds may behave as semi-nomads and flocks of animals are moved up or down the altitudinal gradient according to the state of the vegetation (Etienne 1996).

Local shepherds, farmers and technicians were interviewed in each location to identify a gradient of sheep grazing intensity. We limited our study to sheep-grazed systems. The selected areas were (1) abandoned for more than 10 years, (2) with low or (3) high grazing pressure. It was not possible to quantify grazing pressure more precisely and thus broad categories were used. Distance of areas from water points and corrals as well as evidences of fresh excrements were taken into account in determining the grazing pressure (Jauffret & Lavorel 2003; Landsberg et al. 2002). Recently burnt land and rock outcrops were avoided. Following Proulx & Mazumber (1998) we applied categorical data on grazing pressure rather than a quantitative scale of grazing pressure. Nevertheless, to allow comparison with other grazing systems and vegetation types, the maximum stocking rates generally encountered in each location was estimated by comparing results from a regional survey (Taüll & Casals unpubl.



Fig. 1. Climate and vegetation of the study locations (PET = potential evapotranspiration). Changes in the relative proportions of different growth forms with grazing intensity in different locations along the climatic gradient (Subshrubs = chamaephytes, small shrubs shorter than 40 cm). The maximum stocking rates (AU = Animal Units) for each location is shown (see Methods). In the species names P. stands for *Pinus* and Q. for *Quercus*.

data) with data from different vegetation types and grazing systems from Etienne (1996). This estimation gives an approximate range of grazing pressures considered in each location, ranging from abandoned grazing to a maximum stocking rate (Fig. 1).

Four independent plots were established per grazing intensity (2 replicates on south and 2 on north facing slopes). Only sloping areas were included as, usually, flat areas are used for cropping. The experiment was established using a factorial design: 3 sheep grazing intensities \times 5 localities \times 2 aspects \times 2 replicates = 60 plots. Slope inclination varied between 19° and 35°. Plots were placed in the approximate centre of a relatively homogeneous zone and were surveyed at the time of the expected peak of vegetation development in the corresponding location.

Vegetation was sampled using 10 m × 10 m plots, divided into 100 1-m² subplots. We recorded all vascular plant species whose vertical projection was included in each subplot. Presence/absence of each species was recorded in every subplot. In addition, one of the subplots, systematically positioned in a corner with respect to the centre of the plot, was further divided into 100 10 cm × 10 cm sub-subplots, and the species present were recorded in each of them. Further details on the experimental design and vegetation changes in the study region are presented in de Bello et al. (2005).

The percentage of bare soil was estimated in each plot within the 3 driest locations (in the moist-upland locations, the bare soil was rare). This was done by the point-quadrat method (Daget & Poissonet 1971) with 5 linear transects of 10 m repeated at regular distances and distributed along the main direction of the slope. A total of 100 points separated by 30 cm were recorded in the five lines.

For every grazing treatment in each location, the Whittaker index of beta diversity was calculated. This was done by dividing the total number of species in one treatment (for instance, the four abandoned plots in the most arid location) with the average number of species in the 10 m \times 10 m plots of that treatment.

Data analysis

For each 10 m \times 10 m plot, the average number of species was calculated for quadrats of increasing size: 1×1 , 2×2 , 3×3 up to 10 m \times 10 m. The average was calculated over all possible different locations for quadrats of a given size in the $10 \text{ m} \times 10 \text{ m}$ plot. This was done to reduce the effect of the starting position in the sampling. Clearly, the number of possible positions decreases with increased quadrat size (100 non-overlapping plots of 1 m × 1 m; 81, partially overlapping plots of $2 \text{ m} \times 2 \text{ m}$, ...; one $10 \text{ m} \times 10 \text{ m}$ plot). We consider each average value to be the best possible estimate of species richness for a given quadrat size, but are aware that no other statistical characteristics (e.g. any measure of variability) would be correctly estimated. Consequently, only the averages were used in further calculations. The same process was repeated for the $1 \text{ m} \times 1 \text{ m}$ subplot divided into $10 \text{ m} \times 10 \text{ cm}$ quadrats ('1×1 small'), with the number of species calculated in quadrats of increasing size from 10 m \times 10 cm to 1-m².

The species-area curve parameters were calculated based on the number of species within each quadrat size. This was expressed as the power function:

$$S = c A^z \tag{2}$$

where S is the number of species, A is the sampled area and c and z are the parameters estimated by linear regression after log transformation of both variables. The power function starts at the origin (no species present in plot size zero) and implies a linear dependence of the log transformed variables; c is number of species in a plot of

Table 1. Results of the repeated measures ANOVA. Changes in the number of species with increasing plot size (quadrats from 0.01 m^2 to 100 m^2) and its relation with the environmental factors considered (locations along the climatic gradient, aspect orientation, grazing intensity).

		n of species		
	df	F	р	
Between-subjects factors				
Location	4	35.3	< 0.001	
Aspect	1	6.9	0.013	
Grazing intensity	2	9.4	< 0.001	
Aspect × Location	4	5.3	0.002	
Aspect × Grazing	2	0.3	0.709	
Location × Grazing	8	2.4	0.040	
Location × Grazing × Aspect	8	1.0	0.460	
Within-subjects factors				
Size	18	1142.5	< 0.001	
Size × Location	72	11.5	< 0.001	
Size × Aspect	18	3.1	< 0.001	
Size × Grazing	36	5.1	< 0.001	
Size × Aspect × Location	72	1.3	0.055	
Size × Aspect × Grazing	36	0.8	0.810	
Size × Location × Grazing	144	1.9	< 0.001	
Size × Loc. × Grazing × Aspect	144	1.3	0.019	

a given unit size; *z* measures the rate of increase: when doubling the plot size, the number of species increases 2^z times (*z* usually ranges from 0.15 to 0.3; Lepš 2005). Species-area curve parameters were calculated on three ranges of scale: (a) for quadrats ranging from 0.01 to 1 m² ('1 × 1 m small' plot); (b) for quadrats ranging from 1 to 100-m²; and (c) for quadrats ranging from 0.01 to 100 m² (combining 10 cm × 10 cm sub-subplots with the main plot).

A repeated measures ANOVA was performed (after log transformation of the number of species), to test the effect of grazing regime (abandonment, low- and high-pressure), location along the climatic gradient (five locations; Fig. 1) and aspect (north-, south-facing slope) on species richness in different plot sizes. The repeated measures ANOVA was applied because the nested plot design meant that different plot sizes would be correlated. Plot size was used as the repeated measure (='within subject') factor. Whereas the effect of size itself is trivial (the number of species increases with plot size), the interactions with size are of interest. Because the number of species was log-transformed, the interaction tests for the deviation from multiplicative effects. We would expect grazing to have the same effect at all spatial scales if it increases species richness equally by the same proportion (e.g. one third) at all spatial scales. The relative increase would be different for different spatial scales, if the Size × Grazing interaction were significant.

Three-way ANOVAs were used to test the effect of grazing, location and aspect (all introduced as fixed factors) on the calculated z parameters and on bare soil percentage (this variable only in the three driest locations). Standard errors of the z values presented in the graphs refer only to the variability among independent plots (they are not derived from the regression analyses within a plot).

Results

The effect of grazing on the average number of species changed with plot size and along the climatic gradient: all of the first order interactions with Size and also the second order interaction Size × Location × Grazing were highly significant (Table 1). In moist-upland areas (i.e. the two locations at higher altitude), species richness tended to increase with grazing at all scales considered while, in more arid areas, it tended increase only at the largest plot sizes (Fig. 2). In the smallest plot sizes (i.e. 0.01 to 1 m^2) in the most arid location, species richness tended to decrease with grazing (Fig. 2). The percentage of bare soil increased more strongly with grazing with increased arid conditions (Fig. 3).

The z parameters of the species-area curve were



Fig. 2. Number of species under different grazing regimes (legend) and different locations along the climatic gradient (see also Fig. 1). Separate graphs for different plot sizes (10 cm \times 10 cm; 50 cm \times 50 cm; '1 \times 1 small' upper graphs; 1 m \times 1 m; 5 m \times 5 m; 10 m \times 10 m lower) are shown. The error bars denote mean \pm 1 SE. Note that the graphs have different scales. The 'small 1 m \times 1 m' is the single 1-m² quadrat divided into 100 10 cm \times 10 cm sub-subplots. See Table 1 for the ANOVA model.

differently related to grazing intensity under different climatic conditions (Table 2). The results were similar for z calculated between different ranges of scales (0.01 to 1-m^2 ; 1 to 100-m^2 and the combined 0.01 to 100-m^2) even if the adjusted R^2 increased at greater scales (Table 2). Overall, z tended to increase with grazing in arid locations and decrease in moist-temperate ones (Fig. 4). β -diversity covaried with z, showing similar patterns of variations (Figs. 4 and 5). The z parameters calculated between at the 0.01 to 1-m^2 and the 1 to 100-m^2 scale were correlated (R = 0.54) even if the *z*-values calculated at the smaller sizes were significantly higher (paired sample *T*-test; p < 0.001). Overall, species-area curves in arid areas tended to have steeper power functions (Fig. 4). The effect of aspect orientation on *z* also changed in different locations (Table 2) but no interaction with grazing was noted.

Table 2. Results of the 3-way ANOVA for the slope (z) of the species-area curve ($S = cA^z$). The slope was calculated for three ranges of scales: quadrats doubling from 0.01 to 1 m² ('1×1 small' plot), 1 to 100 m² (main plot) and from 0.01 to 100-m² (combining the '1×1 small' plot with the main plot). The adjusted R^2 (adj. R^2) for each ANOVA is shown.

	d.f.	$z (0.01 \text{ m}^2 - 1 \text{ m}^2)$		$z (1 \text{ m}^2 - 100 \text{ m}^2)$		$z (0.01 \text{ m}^2 100 \text{ m}^2)$	
		F	р	F	р	F	р
Location	4	8.2	< 0.001	10.2	< 0.001	24.0	<0.001
Aspect	1	0.7	0.409	2.5	0.127	1.7	0.195
Grazing intensity	2	2.2	0.123	1.2	0.316	1.9	0.162
Aspect × Location	4	1.3	0.292	3.2	0.025	11.4	< 0.001
Aspect × Grazing	2	0.3	0.729	0.1	0.966	1.1	0.341
Location × Grazing	8	2.6	0.029	3.8	0.003	5.1	< 0.001
Location × Grazing × Aspect	8	0.7	0.682	1.3	0.260	0.4	0.929
Error	30						



Fig. 3. Changes in the percentage of bare soil with grazing regime in different locations. Bare soil was estimated by the point-quadrat method. The error bars denote mean ± 1 SE. The *p*-value refers to the results of location × grazing interaction in the ANOVA model that showed a significant effect of ($R^2 = 0.76$ for the whole model). The study was restricted to the three most arid locations.

Discussion

This study shows that grazing has different effects on the species-area relationship under different climatic conditions. This offers a novel insight into the patterns behind the effect of grazing on plant species diversity in moist vs. arid conditions, which has been proposed by several authors as a critical issue in the conservation and management of landscapes (Milchunas et al. 1988; Huston 1994; Proulx & Mazumder 1998; Cingolani et al. 2005; Lepš 2005).

In the most arid locations included in our study, we found that grazing reduced species richness at small scales while promoting it at larger scales (Fig. 2). The vegetation in arid regions is normally clumped in patches that can be separated by bare soil (Cipriotti & Aguiar 2005). In these conditions, grazing might cause an increase in plant mortality (Milchunas et al. 1988) and, thus, increase the proportion of bare soil (Landsberg et al. 2002). These observations are consistent with our results, which indicate that the percentage of bare soil increased more strongly with grazing in arid conditions. Thus, in arid environments, the chance of encountering only bare soil increases in small-scale plots and the number of species would tend to decrease, or remain the same, with grazing. This was also found by Osem et al. (2002) in 20 cm \times 20 cm plots.

The increase of bare soil caused by grazing in arid areas might also increase the degree of patchiness and,



Fig. 4. Slope (z) of the species-area curves for different grazing intensity in different locations along the climatic gradient. The error bars denote mean ± 1 SE (see Table 2 for the ANOVA model). The slope was calculated using different ranges of scales (**a**; **b**; **c**; see Methods) Note that the three graphs have different scales.



Fig. 5. Variation in β -diversity (calculated with the Whittaker index, see Methods) with grazing intensity on different locations.

thus, the spatial heterogeneity for species establishment (Huston 1994; Alados et al. 2004) and resource distribution (Adler et al. 2001; Desiltes & Houle 2005). This will ultimately increase the slope (z) of the species area curves. This implies that the negative effect of grazing on species richness at small scales in more arid conditions might be reversed at larger scales (Fig. 6). The suppression of potential dominants (preventing competitive exclusion) probably functions at all spatial scales, but this effect is more than compensated for at small spatial scales by the increased amount of bare soil.

In moist-upland locations, species richness tended to increase at all scales considered with grazing (Fig. 2), while the slope of the species area curve (z) decreased (Fig. 4). The decrease of z with grazing suggests a shift towards a more homogeneous spatial plant distribution. The vegetation in these moist regions is normally composed by a majority of herbaceous species, with similar size and reproductive strategies (de Bello et al. 2005), that form a relatively compact vegetation layer with scarce bare soil. In these environments grazing might increase plant species richness by creating gaps necessary for establishment (Rook et al. 2004; Pakeman & Small 2005), decrease dominance of more competitive species (Grime 1973; Huston 1994; Olff & Ritchie 1998; Lepš 2005) and decrease the spatial heterogeneity of the vegetation. In fact, the presence of shrubs would increase this spatial heterogeneity, due to their vertical complexity and size (Huston 1994; Lepš 2005), but this life form is relatively infrequent in the species pool of these moist locations (Fig. 1, de Bello et al. 2005) and



Fig. 6. Grazing effect on plant species richness at different spatial scales. (a) Olff & Ritchie's model (1998) with arbitrary axes scales; (b) Schematic species-area relationship for grazed (dashed line) and abandoned/ungrazed (solid line) communities in the most arid location; (c) Schematic species-area relationship for the most moist and cold location.

it almost disappeared under grazed conditions.

These differential effects of grazing on the speciesarea relationship under different climatic conditions (i.e. semi-arid vs. moist-temperate; Fig. 6) might depend on the interactions between grazing and the pre-existing spatial patterns of the vegetation. Alados et al. (2004) found that the degree of spatial heterogeneity of the vegetation was responsible for different trajectories in the changes in species richness along grazing gradients under different climatic conditions. In this sense, Adler et al. (2001) noted also that selective grazing (e.g. sheep grazing) operating on a patchy vegetation should ultimately result in an enhanced spatial heterogeneity and contrast between vegetation types, while on more homogeneous vegetation the opposite pattern could be expected.

Our data confirm the observation by Adler et al.

(2001), which also suggests that, under different climatic conditions, the various effects of grazing on the spatial heterogeneity of the vegetation might result in a different partition of spatial components of diversity (i.e. α and β). β -diversity might thus increase with grazing where pre-existing vegetation is more heterogeneous (i.e. in more arid conditions) and *vice versa* in more homogenous vegetation (i.e. upland-moist conditions; Figs. 4 and 5). It should also be noted that in the conditions where grazing had only positive effects on alpha diversity (i.e. moist upland-locations in plots up to 100 m²), β -diversity decreased. This confirms that the spatial components of diversity (i.e. α and β) are mutually dependent (Rosenzweig 1995; Huston 1999) and possibly complementary (Loreau 2000).

The hypotheses that the slope of the species-area curve might be affected by the grazing regime (Olff & Ritchie 1998) and that disturbance may cause an intersection of species-area curves of grazed and ungrazed zones in a given location (Lande et al. 2000) were also confirmed by our data. However, our results did not match the prediction from the Olff & Ritchie model (Fig. 6) that grazing enhances richness at small scales (due to reduced competition) and depletes richness at larger scales (due to a selection of grazing-tolerant species within the species pool). The lower z found in grazed areas in moist-upland locations might partially support Olff & Ritchie predictions. However the crossing of the curves might occur far from the range of scales considered (Fig. 6) and extrapolations are unjustified outside the range at which species area curve were originally assessed (Lepš & Štursa 1989; Lepš 2005), because, for example, at the landscape scale community replacement with topographical changes are likely to occur (Sebastià 2004).

Indeed the effect of grazing on the species-area relationship might be also determined by the degree at which the local community is linked to the species and trait pools of the surrounding landscape (Olff & Ritchie 1998; Pärtel 2002; Frank 2005; Reilly et al. 2006), opening up the field for further studies. Nevertheless, deviations from the Olff & Ritchie model can be expected for arid areas, as the selection effect of grazing on the species pool could be less likely to occur in these conditions. As a matter of fact, in arid environments species often show a suite of traits that confer common sets of adaptations to both grazing and water limited environments (Osem et al. 2004; de Bello et al. 2005). Facilitation processes are also common there (Pugnaire et al. 2004). A study in arid environments in Australia (Landsberg et al. 2002), for example, did not show any negative effect of grazing on species richness at regional scales (rather an increase of diversity within 0.5-km² paddocks).

Overall, our study shows that, similarly to predic-

tions (Milchunas et al. 1988; Huston 1994; Proulx & Mazumder 1998; Lepš 2005), the effects of grazing on diversity patterns changed along climatic gradients. In our study it is further suggested that the different effects of grazing along moisture gradients are detectable in different spatial-area relationships. This might be basically related to a different interaction of grazing with the pre-existing spatial heterogeneity of the vegetation, in terms of species distribution and, possibly (as envisaged by Adler et al. 2001), in resource distribution (Desilets & Houle 2005). This interaction also produces different partition of spatial components of diversity. More work is certainly needed to analyse the evolutionary implications of the link between the effect of grazing at the community scale with the regional diversity and the regional pool of species/traits (Olff & Ritchie 1998; Pärtel 2002; Díaz et al. 2004; de Bello et al. 2005).

Indeed, the results shown in this study deserve further comparisons with other systems. Employing an altitudinal gradient leaves uncertainty of what exactly drives the major changes across climatic gradients, even assuming the fact that in our case aridity was the most likely (Anon. 1992). At the same time, topography (Osem et al. 2002; Sebastià 2004), grazing selectivity (Adler et al. 2001), historical evolution of disturbance (Milchunas et al. 1988) and time and intensity of grazing regimes (Pakeman & Small 2005) might give further insight on the variations of the species-area relationship and their relevance for generalizing ecological patterns. Overall, the main implication of these results is that to attain general theories of biodiversity we should encourage comparative studies in terms of spatial scaling law patterns. The differential spatial effect of grazing along the productive-moisture gradient in this study is an example.

Acknowledgements. We thank T. Torrigiani, C. Dal Zennaro and A. Pardini for collaborating in the analysis of the pointquadrat method and M. Taüll and P. Casals for sharing data for stocking rates. J.M. Ninot and J.A. Conesa collaborated in species identification. K. Edwards reviewed the English language. Three anonymous reviewers provided important insights thereby improving the manuscript significantly. The research was partly funded by grants to FdB from the University of Nuoro, the Government of Catalonia (DURSI; FI-2002-2004 programme) and was partially developed within the CARBOCAT and CARBOPAS projects. The Fundació Territori i Paisatge facilitated field sampling in the Alinyà Valley. Participation of JL in this study was partially supported by the MSMT 600-766-5801 grant.

The generosity and cooperation of local shepherds made this study possible.

References

- Anon. (UNEP) 1992. World atlas of desertification. UNEP, Edward Arnold, London, UK.
- Adler, P.B., Raff, D.A. & Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479.
- Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 769-791.
- Alados, C.L., ElAich, A., Papanastasis, V.P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D. & Cabezudo, B. 2004. Changes in plant spatial patterns and diversity along successional gradients on Mediterranean grazing ecosystems. *Ecol. Model.* 180: 523-535.
- Bolòs, O., Vigo, J., Masalles, R.M. & Ninot, J.M. 1993. Flora manual dels Paisos Catalans. 2nd ed. Pòrtic, Barcelona, ES.
- Canals, R.M. & Sebastià, M.-.T. 2000. Analyzing mechanisms regulating diversity in rangelands through comparative studies: a case in the south-western Pyrennees. *Biodiv. Conserv.* 9: 965-984.
- Cingolani, A.M., Noy-Meir, I. & Díaz, S. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol. Appl.* 15: 757:-773.
- Cipriotti, P.A. & Aguiar, M.R. 2005. Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. J. Veg. Sci. 16: 55-66.
- Daget, P. & Poissonet, J. 1971. Une méthode d'analyse phytologique des praires. Critères d'application. Ann. Agron. 22: 5-41.
- Davis, M.A., Curran, C., Tietmeyer, A. & Miller, A. 2005. Dynamic tree aggregation patterns in a species-poor temperate woodland disturbed by fire. J. Veg. Sci. 16: 167-174.
- de Bello, F., Lepš J. & Sebastià, M.-T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J. Appl. Ecol.* 42: 824-833.
- Desilets, P. & Houle, G. 2005. Effects of resource availability and heterogeneity on the slope of the species-area curve along a floodplain-upland gradient. J. Veg. Sci. 5: 487-496.

- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Marti, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. 2004. The plant traits that drive ecosystems: Evidences from three continents. J. Veg. Sci. 15: 295-304.
- Etienne, M. (ed.) 1996. Western European silvopastoral systems. INRA Editions, Versailles, FR.
- Frank, D.A. 2005. The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia* 143: 629-634.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- He, F. & Legendre, P. 2002. Species diversity patterns derived from species-area models. *Ecology* 83: 1185-1198.
- Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.
- Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in diversity of plants and animals. *Oikos* 86: 393-401.
- Gotelli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379-391.
- Guo, Q. 2004. Slow recovery in desert perennial vegetation following prolonged human disturbance. J. Veg. Sci. 15: 757-762.
- Lande, R., DeVries, P.J. & Walla, T.R. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* 89: 601-605.
- Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J. & Tynan, R. 2002. Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. J. Appl. Ecol. 39: 427-444.
- Lepš, J. 2005. Diversity and ecosystem function. In: van der Maarel, E. (ed.) *Vegetation ecology*, pp. 199-237. Blackwell Publishing, Oxford, UK.
- Lepš, J. & Štursa, J. 1989. Species-area relationship, life history strategies and succession – a field test of relationships. *Vegetatio* 83: 249-257.
- Loreau, M. 2000. Are communities saturated? On the relationship between a, b and g diversity. *Ecol. Lett.* 3: 73-76.
- Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, UK.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* 132: 87-106.
- Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13: 261-265.
- Osem, Y., Perevolotsky, A. & Kigel, J. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal

variation in primary productivity. J. Ecol. 90: 936-946.

- Ostling, A., Harte, J., Green, J.L. & Kinzig, A.P. 2003. A community-level fractal property produces power-law species area relationships. *Oikos* 103: 218-224.
- Ovaskainen, O. & Haski, I. 2003. The species-area relationship derived from species-specific incidence functions. *Ecol. Lett.* 6: 903-909.
- Pakeman, R.J. & Field, C. B. 2005. The role of seed bank, seed rain, and the timing of disturbance in gap regeneration. *J. Veg. Sci.* 16: 121-130.
- Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83: 2361-2366.
- Perevolotsky, A. & Seligman, N.G. 1998. Role of grazing in Mediterranean rangeland ecosystems – Inversion of a paradigm. *BioScience* 48: 1007-1017.
- Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581-2592.
- Reilly, M.J., Wimberly, M.C. & Newell, C.L. 2006. Wildfire effects on plant species richness at multiple spatial scales in forest communities of the southern Appalachians. J. *Ecol.* 94: 118-130.

- Rejmánek, M. & Rosén, E. 1992. Influence of colonizing shrubs on species-area relationship in alvar plant-communities. *J. Veg. Sci.* 3: 625-630.
- Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biol. Conserv.* 119: 137-150.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Sebastià, M.-T. 2004. Role of topography and soils in grassland structuring at the landscape and community scales. *Basic Appl. Ecol.* 5: 331-346.
- Vigo, J.P. & Ninot, J.M. 1987. Pirineos. In: Peinado M. & Rivas-Martinez, S. (eds.) *La vegetación de España*, pp. 349-384. Servicio de Publicaciones de la Universidad de Alcalá de Henares, Madrid, ES.
- Wilson, J.B. & Chiarucci, A. 2000. Do plant communities exist? Evidence from scaling-up local species-area relations to the regional level. J. Veg. Sci. 11: 773-775.

Received 21 September 2005; Accepted 12 July 2006; Co-ordinating Editor: M. Pärtel.