Grazing impact on plant spatial distribution and community composition

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Background and aims – Re-introduction of large grazers in the few remaining natural and semi-natural grasslands are thought to be an effective management tool to prevent dominance of late successional plant species and restoration of plant biodiversity. The main objective of this study was to test whether the introduction of large herbivores retard the succession by reducing the abundance of highly competitive tall species and whether it is accompanied with changes in plant community composition and spatial distribution of plant species.

Methods – In order to test this hypothesis, we studied the effect of grazing by large herbivores on vegetation at three hierarchical levels: individual plant species, emergent groups of functionally similar herbaceous plant species, and the main gradients of plant community composition. Study sites were thirteen spatially separated, dry coastal dune grasslands in western Belgium and north-western France.

Key results – Grazing had a predominantly negative effect on high competitive dominant species and led to changes in composition of emergent groups toward less competitive plant species. Additionally, these changes in plant community composition were accompanied with changes in spatial distribution patterns of individual plant species and community richness.

Conclusions – Our results suggest that the current grazing management applied in these nature reserves is able to prevent the expansion of dominant highly competitive species and establishment of functionally different plant species.

Key words – alpha diversity, box-counting fractal dimension, emergent groups, gamma diversity, self similarity, species turnover.

INTRODUCTION

Free-ranging large herbivores are key determinants of grassland plant species composition and diversity (Bakker 1998, Olff & Ritchie 1998). Through land use changes, decreasing size of (semi-)natural grassland areas as well as increasing habitat fragmentation, these animals have long disappeared from many European grassland sites. Coastal dune vegetation in Belgium and many other European countries evolved as a result of natural succession towards coarse grassland with *Calamagrostis epigeios*, *Avenula pubescens* or *Arrhenatherum elatius*, or to scrub vegetation with *Hippophae rhamnoides*, *Ligustrum vulgare* or *Salix repens* or woodland (Provoost & Van Landuyt 2001, Hoffmann et al. 2005). Re-introduction of large grazers in the few remaining natural and semi-natural grasslands is expected to be an effective management tool to prevent dominance of late successional plant species, giving the opportunity of restoration of plant

biodiversity (WallisDeVries et al. 1998, Wardle et al. 2001, Hoffmann et al. 2005). However, only a few studies have investigated the grazing effect by introduced large herbivores on plant community composition and spatial distribution of plant species (but see Wardle et al. 2001, Bakker et al. 2006); the consequences of these introductions on biodiversity are still poorly understood.

There are extensive published studies of effect of grazing on plant community composition. Those which use plant traits provide a more general and mechanistic basis for understanding plant behavior (Lavorel & Garnier 2002). Grouping organisms into categories based on common structural and functional traits, is a tool that ecologists have long used to generalise about properties of ecosystems (Gitay et al. 1999, Díaz et al. 1998). Grazing is generally expected to be accompanied by a shift in plant community composition, i.e. the decline of dominant tall grasses and an increase in plant diver-

sity. This is thought to be due to a shift from competition for light to competition for nutrients, which allows more functionally different species to coexist (Huisman & Olff 1998). From a functional point of view, grazing may induce shifts in trait composition by promoting species with an annual life history, ruderal strategy, rosette habitus, small size and an early flowering and dispersal strategy (Bakker 1998). From a methodological point of view most previous studies considering the effect of grazing on vegetation, have analysed the life traits one by one (Decker et al. 2004). However, the consideration of individual life traits presents a rather abstract view. Obviously, in a real world, environmental factors do not apply directly to each life trait separately but to the species pool as a whole, which is the combination of life traits. This argues for an approach based on emergent groups (sensu Lavorel et al. 1997), an emergent group (EG) being defined as a set of species exhibiting correlations among a set of plant traits (Lavorel et al. 1997, Lavorel & Garnier 2002). Here, we attempted to identify emergent groups of functionally similar herbaceous plants in the coastal grassland flora of Belgium and north-western France. We then tested the hypothesis that grazing by large herbivores may change the composition of EGs.

One other important aspect of herbivory is its effect on the spatial pattern of the vegetation. Such spatial effects may influence the interactions within the plant community, the susceptibility of the vegetation to other disturbances, the distribution of water and nutrients, the movement patterns of organisms and the composition and species richness of animal communities (Williams et al. 2002). Spatial turnover patterns are changes in species composition and distribution over spatial and temporal scales which are studied by self-similarity patterns or fractal distributions (Kunin 1998, Lennon et al. 2002). By definition, a pattern is self-similar or fractal if it does not vary with spatial scale (Arita & Rodríguez 2002, Kunin 1998). The scale-area curves proposed by Kunin (1998) served to define dimension of self-similar distribution of individual species. The slope of a scale area curve measures the degree to which a species population fills its range. The steeper the slope, the more sparsely the species are distributed (Kunin 1998). For the self-similarity of community richness, Harte et al. (1999) argued that if individual species within an assemblage show a self-similar spatial distribution, a linear relationship between the natural logarithm of area and species number should exist (SAR: species-area relationship). The slope of this relationship is correlated with the accumulation rate of species as area increases. A high value of the slope indicates a higher rate of species turnover, and hence less self-similarity at the community level (Arita & Rodríguez 2002, Bossuyt & Hermy 2004). In contrast to the extensive literature, describing the effect of grazing on the relative abundance of plant species and also community composition, little attention has been paid to spatial turnover patterns of individual species and community richness. It is expected that the activity of grazers may increase the rate of plant species turnover compared to ungrazed plant communities, by creating patches suitable for colonisation and seedling establishment (Bakker et al. 2003).

Given the scarce information for nutrient-poor grasslands systems and in order to attempt generalisations on plant community development in the grazed areas, it is important to have insight into the effects of grazing on both plant species composition and spatial distribution of plant species (Hoffmann et al. 2005). First, we tested whether introduction of large herbivores in remaining natural grasslands counteracts the encroachment of tall, highly, competitive plant species. Secondly, we tested whether this process is accompanied by a change in plant community composition and composition of emergent groups. Then, the effect of grazing on the spatial distribution pattern of individual plant species and community was assessed. Hence, the present paper has the following main objectives: (1) to assess the influence of grazing on vegetation at two different hierarchical levels (plant community composition and species level); (2) to construct a trait based classification of plant species to emergent groups; (3) to determine the relevant relationship between emergent groups and grazing; (4) to analyse the possible effect of grazing on spatial distribution of vegetation at two different hierarchical levels (plant community composition and species level). Because these grasslands are predominantly distributed within nature reserves, implications of this study are extremely relevant for nature management and restoration.

MATERIAL AND METHODS

Data collection

After some decades of sparse and scattered nature management, in the late 1990s the manager of Flemish coastal nature reserve decided to introduce different large, ungulate herbivore species (mostly cattle, several horse breeds, donkeys or sheep) to control further expansion of dominant grasses and woody species (Hoffmann et al. 2005). The animals are free-ranging and remain in the area year round. Extensive studies of habitat preference and diet selection along the Belgian coast revealed that grazer distributions among habitats differed. In general, all animals preferentially grazed in the most productive parts of each site (Hoffmann et al. 2005). Thirteen pairs of grazed and ungrazed sites, with pairwise similar edaphic and topographic conditions, were chosen to record the cover of all vascular plants in the coastal dune grasslands of western Belgium and one north-western French site during the spring and summer of 2006 (see table 1 for general information on study sites). For each pair, two 8×8 m² plots were established randomly, one in the grazed and one in the ungrazed site. These neighbouring plots were separated by a fence and located at a distance of about 10–15 m apart. Each plot was divided into four 4×4 m² subplots (A1) which were further subdivided five times up to 4096 0.125×0.125 m² subplots (A6). For each subdivision, $A_{i-1}/A_i = 4$, where A_{i-1} and A_i are the area of the higher and lower scale level, respectively (fig. 1). The cover of every vascular plant species was visually estimated within ten random subplots at each of the seven spatial scales except for the 4×4 and 8×8 m² subplots for which only four and one subplots were sampled, respectively, i.e. 0.125×0.125 m² (10 subplots), 0.25×0.25 m² (10 subplots), 0.5×0.5 m² (10 subplots), 1×1 m² (10 subplots), 2×2 m² (10 subplots), 4×4 m² (4 subplots) and 8×8 m² (1 plot). Soil conditions are a major source of environmental variation, determining species composition and productivity of dune grasslands (Tahmasebi Kohyani et al. 2008). An

Table 1 – General characteristics of the sampled areas and sites, concerning grazed area and introduced grazers.

Introduced herbivore (average weight): SHC: Scottish highland cattle (450 kg); HC: Holstein cattle (450 kg); KP: Konik pony (350 kg); SP: Shetland pony (180 kg); HP: Haflinger pony (400 kg); Sh: Sheep (75 kg); D: Donkey (180 kg); grazed area: area in which grazers were introduced; grassland area: approximate grassland area within the grazed area (the rest of the grazed area consists of woodland, scrub, blond dune or wet tall forb grassland); average grazer 1/2: average number of animals of introduced herbivore 1 and 2 during the last 5 yrs; AU ha⁻¹: average number of animal units per ha, assuming year-round grazing (AU is defined here as an animal of 450 kg); phytomass = sum of aboveground dead and live plant material in the ungrazed plots.

area name and Site number	latitude (N)	longitude (E)	km from coastline	grazed area (ha)	grassland area (ha)	introduced herbivore (1/2)	average grazer 1/2	average AU ha⁻¹ grazed area	average AU ha⁻¹ grassland	soil water-pH ungrazed	phytomass (ngrazed plot) (g m⁻²)	strongest syntaxonomical affinity
Ghyvelde1	51°03'33"	02°32'44"	3.1	75.0	52.5	HP/-	13/0	0.15	0.22	5.0 ± 0.1	84	Arrhenatherion
Ghyvelde2	51°03'52"	02°33'12"	2.9	75.0	52.5	HP/-	13/0	0.15	0.22	5.3 ± 0.6	113	Plantagini-Festucion
Cabour1	51°03'55"	02°34'34"	3.1	29.8	20.2	SP/-	13/0	0.17	0.26	5.7 ± 0.1	92	Polygalo-Koelerion
Cabour2	51°03'50"	02°34'46"	3.4	29.8	20.2	SP/-	13/0	0.17	0.26	6.0 ± 0.6	86	Plantagini-Festucion
Oostvoor-duinen1	51°07'30"	02°41'55"	1.9	3.5	3.5	HC/-	10/0	0.36	0.36	6.5 ± 0.7	91	Plantagini-Festucion
Oostvoor-duinen2	51°07'27"	02°42'20"	2.0	1.8	1.8	HC/-	10/0	0.46	0.46	6.5 ± 0.7	108	Koelerio-Corynephoretea
Houtsaeger-duinen	51°05'59"	2° 35' 48"	2.0	10	80	D	15	0.25	0.22	6.5 ± 0.2	85	Koelerio-Corynephoretea
Ter Yde1	51°08'09"	02°41'33"	1.0	16.0	11.0	SP/Sh	5/25	0.26	0.37	6.8 ± 0.1	-	Koelerio-Corynephoretea
Ter Yde2	51°08'05"	02°41'35"	0.9	16.0	11.0	SP/Sh	5/25	0.26	0.37	6.9 ± 0.1	-	Plantagini-Festucion
Ter Yde3	51°07'55"	02°41'40"	0.5	16.0	11.0	SP/Sh	5/25	0.26	0.37	7.0 ± 0.1	-	Plantagini-Festucion
Westhoek-south1	51°04'46"	02°33'10"	1.4	46.6	21.0	SHC/SP	4/16	0.22	0.50	7.3 ± 0.2	106	Koelerio-Corynephoretea
Westhoek-south2	51°04'51"	02°33'53"	1.4	46.6	21.0	SHC/SP	4/16	0.22	0.50	7.4 ± 0.2	174	Koelerio-Corynephoretea
Westhoek-north	51°05'07"	02°33'04"	0.4	52.8	20.3	SHC/KP	4/8	0.19	0.50	7.4 ± 0.2	152	Polygalo-Koelerion

independent survey by the authors confirmed that there was a significant correlation between aboveground biomass (as a proxy for nutrient availability) and soil pH. Therefore, only soil acidity of each sample was measured with a pH meter in water. To do so, sixteen soil samples were randomly collected within each 8×8 m² plot from the upper 10 cm of the soil, using a 7 cm diameter core. The obtained pH values were averaged per area for grazed and ungrazed sites separately.

Data analysis

Plant community and emergent group composition – Relative plant community similarity was assessed by Detrended Correspondence Analysis (DCA), using PCOrd 4.32. Only scores on the first two axes were chosen as response variable for addressing the effects of grazing and soil characteristics on plant community composition. Emergent groups were identified by a cluster analysis on seventeen plant traits, which were related to three key processes in plant communities (persistence, dispersal and establishment) (table 2). Gower's similarity index (Gower 1971) was used to compare the occurring species based on their trait values. In a next step, the species were clustered into emergent groups (EGs), using Ward's method (ClustanGraphics 8). Afterwards, differences in plant traits between emergent groups were assessed by a chi-square test, a Kruskal-Wallis test, or a one-way ANOVA for qualitative, ordinal and quantitative data, respectively. Then, we calculated the relative abundance of each emergent group in every 0.5×0.5 m² subplot, by summing the cover data of all species with that trait value, and dividing it by the sum of the cover of all categorized species in the subplot. The cover of most dominant plant species in this scale was used to test the effect of grazing on plant individual level. To
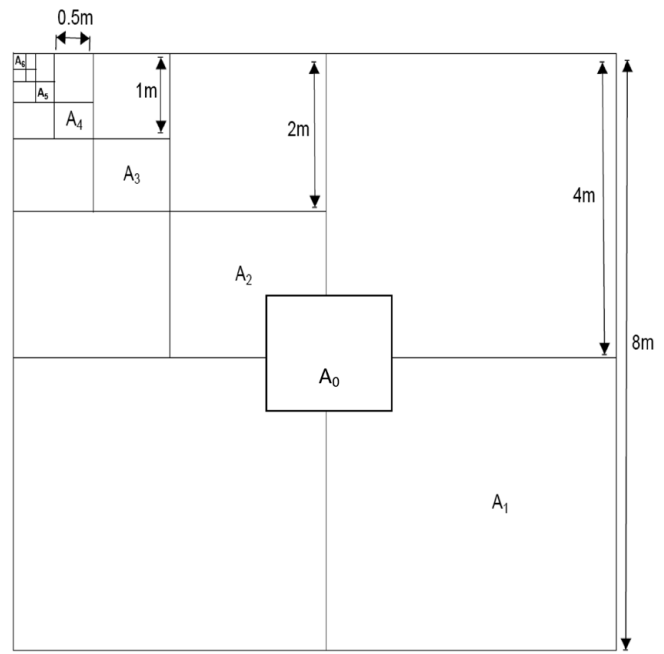
Figure 1 – Plot design with seven scales (from A0 to A6).

avoid pseudo-replication, the relative abundances were averaged per site.

Spatial turnover – We used the methodology proposed by Kunin (1998), Arita & Rodríguez (2002) and Bossuyt & Hermy (2004) to analyze spatial turnover patterns of individual species and community species richness. For the analysis on the individual species patterns, the slope of the linear relationship between the logarithm of the scale of measurement

Table 2 – Plant traits used to define the emergent groups in the cluster analysis.
Sources: 1: Grime et al. (1988); 2: Zwaenepoel (1992); 3: Bossuyt et al. (2005); 4: Bekker et al. (1998); 5: Ellenberg et al. (1991).

trait	classes	variable type	sources
clonal propagation	no/yes	qualitative	1
seasonal regeneration in gap	no/yes	qualitative	1
height	< 100, 100–299, 300–599, 600–999, 1000–3000	ordinal	1
canopy structure	rosette, semirosette, leafy	qualitative	1
established strategy	Competitors (C), Stress tolerant (S), Ruderal (R), Competitor-Stress-Ruderals (CSR)	continuous	1
leaf phenology	aestival, hibernal, vernal, always evergreen		
life form	chamaephytes, hemicryptophytes, geophytes, therophytes, phanerophytes	qualitative	1
seed length	-	continuous	1
seed longevity index	-	continuous	4
seed weight	-	continuous	2
seed shape: length/width	< 1.5, 1.5–2.5, > 2.5	ordinal	1
time of flowering	spring, summer, autumn	qualitative	2
time of germination	spring, summer, autumn	qualitative	2
time of dispersal	spring, summer, autumn	qualitative	2
palatability	palatable, unpalatable, neutral	qualitative	3
Ellenberg indicator values	light, temperature, nitrogen, salinity, moisture	continuous	5

Table 3 – F-statistic and *P*-value of ANCOVA testing for the effect of grazing and soil pH on plant community composition, as expressed by DCA axes 1 and 2, fifteen individual plant species and six emergent groups.
N: number of observations; EG1: leafy hemicryptophytes with CSR strategy; EG2: semirosette hemicryptophytes with vernal leaf phenology; EG3: semirosette with low nitrogen demand; EG4: large seed length and flowering in summer; EG5: competitive chamaephytes; EG6: annual species with high seed index longevity.

response variable	N	grazing		pH		grazing × pH	
		F	*P*	F	*P*	F	*P*
DCA axis 1	26	11.09	0.006	4.714	0.041	0.67	0.201
DCA axis 2	26	2.07	0.160	5.32	0.031	0.69	0.412
Agrostis stolonifera	20	4.70	0.041	0.004	0.952	0.001	0.978
Anthoxanthum odoratum	14	1.00	0.340	5.50	0.044	0.85	0.387
Arrhenatherum elatius	16	11.40	0.001	1.70	0.211	1.40	0.255
Calamagrostis epigeios	24	9.80	0.011	2.30	0.333	1.80	0.234
Carex arenaria	24	1.50	0.215	0.90	0.451	1.10	0.238
Cerastium fontanum	22	5.30	0.043	0.33	0.915	0.63	0.714
Crepis capillaris	20	6.80	0.031	1.20	0.197	1.10	0.286
Festuca rubra	14	6.70	0.030	0.21	0.120	0.55	0.110
Galium verum	18	5.40	0.047	0.63	0.937	1.20	0.500
Holcus lanatus	18	7.80	0.022	1.90	0.501	4.50	0.049
Luzula campestris	12	5.10	0.053	3.60	0.064	2.10	0.091
Poa pratensis	18	8.10	0.019	0.90	0.120	1.50	0.945
Senecio jacobaea	18	6.40	0.047	2.10	0.180	0.33	0.733
Rosa spinosissima	16	5.30	0.035	4.50	0.048	2.10	0.552
Vicia cracca	18	1.05	0.776	2.50	0.465	0.75	0.107
EG1	26	40.24	0.003	0.12	0.721	0.23	0.632
EG2	26	4.37	0.043	1.47	0.243	0.34	0.568
EG3	26	9.20	0.005	10.16	0.008	1.54	0.234
EG4	26	1.59	0.227	5.70	0.020	2.10	0.157
EG5	26	5.22	0.049	0.60	0.797	0.20	0.656
EG6	26	12.74	0.001	0.01	0.901	0.03	0.953

(ranging from 0.125 to 64 m²) and the logarithm of the species range (Kunin 1998) was considered a measure for the fractal distribution of individual species (Bossuyt & Hermy 2004). This slope (β) is an estimator of 1-DB/2, where DB is the box-counting fractal dimension of species (Lennon et al. 2002). The species range was defined as the sum of the area of the subplots of that particular scale level in which the species occurred. The analysis was executed for fifteen dominant plant species occurring in at least seven grazed and seven ungrazed sites.

For the analysis of community species richness, species turnover was defined as changes in the number of species over the scale levels. Using the multiplicative approach (Whittaker 1972), species turnover (S_β) can be calculated with the formula: $S_\beta = S_\gamma / S_\alpha$, where S_γ and S_α are the number of species in the higher scale (gamma diversity) and the lower scale level (alpha diversity), respectively. In the nested plot design used here, species turnover between two adjacent scales ($S_{i/i-1}$) was hence calculated as the average number of species in the higher scale level i (S_γ) divided by the average number of species in the lower scale level i-1 (S_α).

Statistical analysis – Analysis of covariance (ANCOVA) was used to investigate the effect of grazing (binary vari-
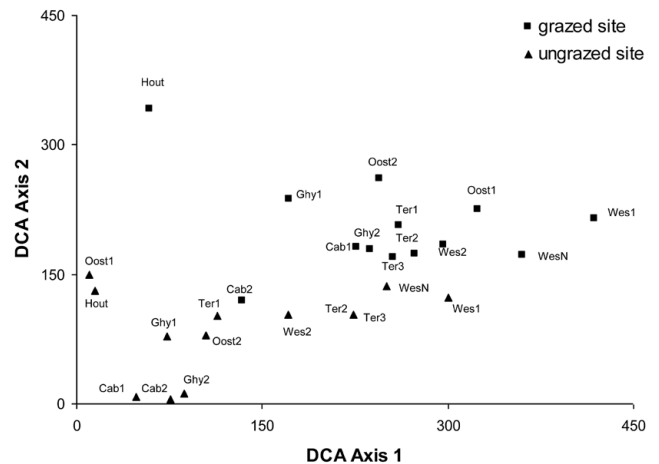
Figure 2 – DCA ordination of thirteen paired grasslands studied (thirteen grazed and thirteen ungrazed sites).

Table 4 – An overview of six emergent groups and the traits associated with them.
♣, Pearson Chi² correlation test. Values are the differences among the expected and observed value for the different classes.
♣♣, Kruskal-Wallis test. Values are the medians. Letters are significantly different at 0.05 level. (a, b, c).
♣♣♣, ANOVA test, Values are the means. Letters are significantly different at 0.05 level. (a, b, c).
* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001 and ns: not significant.

	P	hemicryptophytes, clonal propagation, vernal leaf phenology, CSR strategy (EG1)	unpalatable forbs (EG2)	tall grasses, palatable (EG3)	leafy structure flowering summer, high seed length (EG4)	woody, competitive chamaephytes (EG5)	annulus, high seed index longevity (EG6)
clonal propagation ♣	***	7/-7	4.3/-4.3	-6/6	2.4/-2.4	4.7/-4.7	-12.5/12.5
seasonal regeneration in gap ♣♣	ns	2.9/-2.9	-4.4/4.4	0.5/-0.5	-1.8/1.8	0.7/-0.7	2.1/-2.1
height ♣♣	***	2^{a}	2^{a}	2^{a}	2^{a}	4^{b}	2^{a}
canopy structure ♣	***	0.2/3.5/-4.7	-0.4/-5.2/5.7	-0.5/-6.4/5.1	-0.9/0.5/0.4	0.7/8.3/-9	0.9/-2.5/1.6
established C ♣♣♣	***	0^{a}	0.25^{ab}	0^{a}	0.25^{ab}	0.5^{b}	0^{a}
established S ♣♣♣	***	0^{a}	0.25^{ab}	0.25^{ab}	0^{a}	0^{a}	0.25^{ab}
strategy R ♣♣♣	***	0^{a}	0.25^{ab}	0.25^{ab}	0^{a}	0^{a}	0.5^{b}
CSR ♣♣♣	***	0.5^{b}	0^{a}	0.5^{b}	0.25^{ab}	0^{a}	0^{a}
leaf phenology ♣	***	-2.2/3.6/-0.4/-1	4.3/3.2/-9.9/2.4	1.6/-1.3/-1.3/1	-0.1/0.7/0.2/-0.5	-7/3.7/3.4/-0.2	3.5/-9.9/7.7/-1.9
life form ♣	***	0.8/-15.5/1.8/9/3.5	0.2/-5/1.2/4.1/0.4	-0.8/0.1/0.2/0.1/0.4	0.4/1.4/-2.5/1.4/-0.5	1.4/4.5/-2.5/5.5/-6.1	1.9/14.2/1.9/-20.3/2.3
seed length ♣♣♣	*	2^{a}	1.7^{a}	2.4^{a}	5.1^{b}	2.8^{a}	1.4^{a}
seed Index ♣♣♣	***	0.22^{abc}	0.32^{bc}	0.31^{bc}	0.02^{a}	0.12^{ab}	0.43^{c}
seed weight ♣♣♣	ns	1.3	0.97	1.34	1.4	1.6	0.29
seed shape ♣♣	ns	2	2	2	2	2	1
time of flowering ♣	***	7.4/5.4/-12.8	3.2/-3.4/0.2	-2.2/-4/6.2	1.3/-3.9/2.6	-2.4/3.4/-1	-8.7/2.5/6.2
time of germination ♣♣	**	3.9/1.1/-0.4	-0.6/-3.2/-0.6	-1.6/0.6/-3	-2.6/0.3/1.3	-1.2/0.3/0.8	2.2/0.9/0.8
time of dispersal ♣	***	0.2/4.2/-3.1/-1.3	0.8/-6.4/3/2.7	0.8/-4.6/2/1.7	-1/6/2/-1.1/-4	0.3/2/-4.2/1.7	-1/-1.4/3.1/-0.7
palatability ♣	**	3.2/-2.2/-1	1.6/-3.8/1.2	-2.2/2.5/-0.3	0.1/.3/-0.4	-5.4/3.6/1.8	2.8/-1.5/-1.6
Ellenberg indicator value ♣♣ temperature	ns	6	6	6	6	6	7.5
moisture	***	7^{c}	6^{b}	5^{a}	6^{b}	7^{c}	6^{b}
nitrogen	***	7^{c}	6^{b}	4.5^{a}	6^{b}	6.5^{bc}	5^{a}
salinity	ns	5	3	5	4	3	6^{b}
light	ns	8	7	7	7	7	-

able, fixed factor), soil pH (covariate) and their interaction on vegetation composition in both community and emergent groups. The site scores on the first and second DCA axes for the analysis of the community, and the relative abundance of each emergent group were used as response variables.

A simple linear regression analysis was performed for each of the fifteen species, with log-transformed scale as independent and log-transformed species range as dependent variable for grazed and ungrazed sites separately. A regression line was thus obtained for each species and each plot. Differences in the slope of this regression line between plots in grazed and ungrazed sites were then analyzed for each species by an ANCOVA, in which grazing and soil pH were used in the linear model as fixed factor and covariate, respectively.

For the analysis of spatial turnover of community species richness, grazing, scale level and their interaction were entered in the model as fixed factors, and pH as a covariate. A Tukey post hoc comparison was used to reveal the differences of plant turnover between the scale levels in grazed and ungrazed sites separately. All statistical analyses were computed with SPSS 11.0.

RESULTS

Response to grazing of plant community composition and individual plant species

The ANCOVA revealed a significant effect of grazing and soil acidity on plant community composition measured as scores on DCA axis 1 (table 3, fig. 2). We were only able to investigate the grazing response of fifteen plant species in our dataset. There was a large difference in response of individual plant species to grazing (table 3). Overall, *Agrostis stolonifera*, *Cerastium fontanum*, *Crepis capillaris*, *Festuca rubra*, *Galium verum*, *Poa pratensis* and *Senecio jacobaea* responded positively to grazing and no interaction between grazing and soil acidity was observed for all considered individual plant species. In contrast, the cover of *Arrhenatherum elatius*, *Calamagrostis epigeios* and *Rosa spinosissima* significantly declined under grazing. *Anthoxanthum odoratum*, *Carex arenaria* and *Vicia cracca* were the only plant species without any significant response to grazing (table 3).

Emergent group identification

Cluster analyses resulted in six emergent groups, which significantly differed in plant traits (table 4). Life form, canopy structure, leaf phenology and palatability were the main life traits driving the clustering. Most species in the first emergent group (EG1) were hemicryptophytes with a clonal propagation that mostly possessed vernal leaf phenology and CSR strategy. Unpalatable forb species were classified into the second group (EG2). Tall graminoid species that could typically be characterized as highly competitive and palatable plant species built up the third group (EG3). Plant species with a generally leafy structure, flowering in summer belonged to the fourth EG. This group was also characterized by large seed length in comparison with other groups. All woody plant species (chamaephytes) that are highly competitive formed
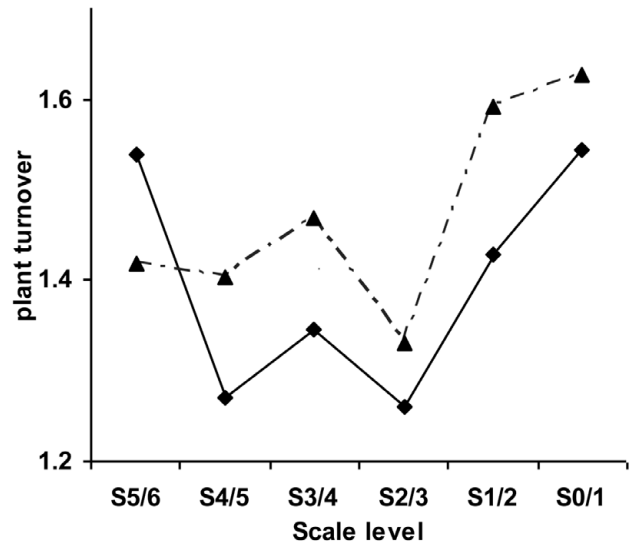
Figure 3 – Total species turn over in grazed (full line) and ungrazed sites (dashed line). Species turn over ($S_{i/}S_{i-1}$) was defined as the number of species in the higher scale level i divided by the number of species in the lower scale level i-1.

EG5. Finally, EG6 contains annual species with high seed index longevity (table 4).

Grazing response of emergent groups

In general, there were large variations in response of the emergent groups to grazing (table 3). Relative abundance of EG1 and EG2 was higher in grazed conditions. Oppositely, EG3 and EG5 were significantly less abundant in grazed conditons. EG4 did not significantly differ between grazed and ungrazed conditions. As expected, the relative abundance of EG6, which contained annual plant species, was more prominent under grazing (table 3).

Spatial turnover

Community species richness – Grazing (df = 1; F = 6.11; P < 0.05), scale level (df = 5; F = 8.55; P < 0.001) and their interaction (df = 5; F = 5.8; P < 0.05) had a significant effect on plant species turnover. Plant turnover was higher between the smallest scales [0.125 × 0.125 m² and 0.25 × 0.25 m² ($S_{5/6}$)] in grazed sites than in ungrazed sites. However, at higher scale levels the rate of plant turnover became larger in the ungrazed compared with grazed sites (fig. 3). The post-hoc comparison among the scales revealed that in the grazed sites, there was a fast accumulation of species at both the lower and the higher scale levels, while species turnover remained relatively constant at the intermediate scale levels (fig. 3). In contrast, for the ungrazed sites, a fast accumulation of species was only observed at the higher scale levels.

Individual species patterns – There was a significant linear relationship between log-transformed scale level and species range in both grazed and ungrazed sites for all fifteen plant species considered (table 5). However, the obtained slopes largely differed among the plant species, indicating different

Table 5 – F-statistic and *P*-values of ANCOVA testing for the effects of grazing on the fractal distribution (β) of fifteen individual species.

No significant effect of pH was found on fractal distributions of all plant species represented by β and DB. Slope (β) and *P*-value of the linear regression between the logarithm of scale level and the logarithm of species range. DB = the box-counting fractal dimension.

| species | regression analysis | | | | | | ANCOVA | |
| | grazed sites | | | ungrazed sites | | | grazing | |
	β	*P*	DB	β	*P*	DB	F	*P*
Agrostis stolonifera	0.187	0.003	1.626	0.405	0.001	1.19	7.14	0.020
Anthoxanthum odoratum	0.163	0.053	1.674	0.367	0.001	1.266	7.015	0.029
Arrhenatherum elatius	0.311	0.001	1.378	0.11	0.045	1.78	6.14	0.033
Calamagrostis epigeios	0.341	0.001	1.318	0.131	0.040	1.738	5.17	0.036
Carex arenaria	0.470	0.001	1.06	0.269	0.001	1.462	2.25	0.155
Cerastium fontanum	0.323	0.001	1.354	0.466	0.001	1.068	4.49	0.050
Crepis capillaris	0.315	0.001	1.37	0.501	0.001	1.001	2.52	0.135
Festuca rubra	0.174	0.001	1.652	0.496	0.001	1.008	23.14	0.001
Galium verum	0.173	0.024	1.654	0.197	0.001	1.606	2.57	0.124
Holcus lanatus	0.283	0.001	1.434	0.423	0.001	1.154	0.939	0.352
Luzula campestris	0.329	0.001	1.342	0.421	0.001	1.158	1.35	0.261
Poa pratensis	0.080	0.026	1.84	0.428	0.001	1.144	5.82	0.027
Senecio jacobaea	0.398	0.001	1.204	0.501	0.001	1.001	6.47	0.019
Rosa spinosissima	0.408	0.001	1.184	0.313	0.002	1.374	0.417	0.53
Vicia cracca	0.472	0.001	1.056	0.43	0.001	1.14	0.175	0.684

fractal distributions of plant species (represented by β and DB). Five species had the same self-similarity pattern in absence and presence of grazing, the fractal distribution of the remaining ten species significantly changed in response to grazing and no significant effect of pH was found (table 5).

<div style="text-align:center">DISCUSSION</div>

Plant community and emergent group composition

We found that introduction of large herbivores led to a large difference in plant community composition, as expressed along the two first DCA axes, clearly separating grazed and ungrazed sites (fig. 2). This confirms and quantifies the preliminary findings of Provoost et al. (2004), who described qualitative changes in plant community composition in coastal dune grasslands in response to grazing. As expected, variations in plant community composition result from different response of individual plant species to grazing. Grazing indeed led to retardation of succession by reducing the plant species which are characterized as highly competitive species, *Arrhenatherum elatius*, *Calamagrostis epigeios*, *Holcus lanatus*, *Rosa spinosissima*. Similarly, increase in less competitive plant species with grazing confirmed this pattern. These species can be classified into two groups based on their response to grazing in coastal dune grassland of Belgium (Provoost et al. 2004): *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Calamagrostis epigeios*, *Holcus lanatus*, *Rosa spinosissima* are characterized as decreaser species in term of abundance. In contrast, grazing favours *Agrostis stolonifera*, *Carex arenaria*, *Cerastium fontanum*, *Crepis capillaris*, *Festuca rubra*, *Galium verum*, *Luzula campestris*, *Poa pratensis* and *Senecio jacobaea*. Additionally the observed pattern for the effect of

grazing on composition of emergent groups also confirmed the retardation effect of grazing on succession. The emergent group delineation was primarily driven by life form which indeed correlated with numerous morphological and physiological traits (Lavorel et al. 1997). Among the six identified EGs, plants from five groups significantly responded to grazing either positively or negatively. Furthermore, differences in response among EGs clearly demonstrated their functional significance. Because EGs contained species reacting to environmental factors similarly, they can be considered as true plant functional types (McIntyre et al. 1999) Plant species clustered in EG3 and EG5 were mostly highly competitive plant species characterized as late successional, dominant plant species in coastal dune grasslands (Hoffmann et al. 2005, Provoost et al. 2004). In the present study, tall perennial grasses, being the main contributors to the palatable biomass and dominant in ungrazed sites, were overall negatively affected by grazing. As a result, most of changes in plant community composition may be attributed to the fact that they considerably decreased under grazing. This was due to the extremely high abundance of *A. elatius*, *C. epigeios* in ungrazed sites in comparison with grazed sites. Absence of grazing is associated with competition for light and generally allows the establishment of large, competitive species (Tilman 1988, Grime et al. 1988). These conditions favour species with morphological and phenological characteristics that allow the plant species to compete efficiently for light (Gaudet & Keddy 1995). Competition for light will favour species with traits such as taller growth form, leafy structure, tall shoots and a strong lateral extension, which increase the species' vulnerability to grazing. In contrast, grazing as a disturbance factor has been found to be accompanied by an increase in species with a ruderal strategy (Grime et al. 1988),

an annual life history, a small statute and by an increasing relative abundance of forbs and annual grasses. The mechanism underlying these patterns is probably the differential defoliation on a vertical gradient caused by large herbivore grazing. Tall, erect plants or plants with raised regeneration buds are eliminated, while small or rosette species survive. These traits were classified in two emergent groups in our study: EG2 and EG6. These groups generally contained less competitive plant species. This suggests that two plant communities in grazed and ungrazed sites differed in successional pattern in vegetation, most probably caused by the introduction of large herbivore grazing.

Plant spatial pattern

Individual species – The slopes of the regression between log-transformed scale level and species range were significant for all species, but there were large interspecific differences in box-counting fractal dimension (table 1). Furthermore, species reacted dissimilar with respect to fractal dimensions in response to grazing. Grazing indeed resulted in the break-up of the spatially aggregated pattern of *Arrhenatherum elatius* and *Calamogrostis epigeios* and led to a random distribution of *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Cerastium fontanum*, *Festuca rubra* and *Poa pratensis*. The fractal dimensions of 1.78 and 1.73 for *Arrhenatherum elatius* and *Calamagrostis epigeios* in ungrazed plots indicate that changes in their distribution could be attributed to random processes in ungrazed conditions, while not so in grazed sites (1.37 and 1.31 respectively). These two species are highly competitive species that are affected by herbivory (Tahmasebi Kohyani et al. 2008). Their distribution may, however, be restricted under protection of other species or sites unfavourable for grazing; as recently evidenced by Gomez (2005) and Bossuyt et al. (2005). This may cause a non-random distribution of these species in grazed sites under protection of grazing-resistant species. Herbivore exclusion may enable these plant species to colonize the grassland in a more evenly spatial pattern.

Community species richness – A high species turnover between the smallest scales levels ($S_{5/6}$) in grazed plots (fig. 1) may at the one hand be related to a small number of species in S_7 due to interspecific competitive exclusion (Bossuyt & Hermy 2004). The number of species in a small area depends on the size of the individuals and on the extent to which they are vertically stratified or horizontally intermingled with each other (packing problem) (Crawley & Harral 2001). Other studies also revealed that spatial interactions between plant species and competition for space restricted the co-occurrence of plant species at small scales (Spiegelberger et al. 2006). On the other hand, more species may co-occur in plots of the scale level S_6 because of grazing. The results indicate that the effect of limiting factors on plant species is more likely to be found at the smallest scale (0.125 × 0.125 m²) in grazed plots while in ungrazed situation this factor may still hamper the co-occurrence of a high number of species at smaller and intermediate scales (packing problem in scales lower than 2 × 2 m²). The activity of grazers may increase the rate of plant species turnover by creating patches suitable for colonization and seedling establishment (Bakker et al. 2003). In absence of grazing, interspecific competition may still hamper the co-occurrence of a high number of species at smaller and intermediate scales, resulting in a constant species turnover (self-similarity pattern). However, at the higher scale levels (between 4 × 4 and 8 × 8 m², from $S_{4/5}$ to $S_{0/1}$), the rate of plant turnover increased in both grazed and ungrazed sites. As demonstrated by Olff & Ritchie (1998), this is most likely caused by an increasing number of different microsites, differently colonised by a species. There are several reasons why species accumulate as the sample area increases: (i) probabilities to record rare species increase when more samples are taken; (ii) probabilities to record spatially aggregated species increase accordingly (a spatial clumping effect); (iii) species that are ecologically separated co-occur only at larger spatial scales (a spatial segregation effect); and (iv) distinctive new sets of species appear when environmental conditions become more heterogeneous (a habitat effect) (Crawley & Harral 2001).

CONCLUSION

Our results indicate that the current grazing management is able to conserve species diversity by prevention of expansion of dominant highly competitive species. We studied vegetation changes at three different levels (community, emergent groups and species level) and the results of different levels are consistent. Additionally, the study presented here developed a simple, straightforward methodology for a functional analysis of plant community in relation to grazing. Based on that, different emergent groups with distinct ecological characteristics occurred in grazed and ungrazed grasslands. These changes in plant community composition and composition of emergent groups were accompanied by changes in spatial distribution pattern of plant individual species and community composition. Large mammalian herbivores are increasingly introduced into ecosystems, either as livestock for conservation purposes or as alien species in habitat that lacked grazer during recent evolutionary time (Bakker et al. 2006). The trends shown by our results may help to develop strategies of appropriate biodiversity conservation management. Grazer effects may vary with herbivore density, herbivore functional (physiologically dictated) type or species as well as their interactions with scale and soil. Future studies concerning these processes may gain more insight into the general mechanisms by which herbivores change plant diversity in different habitats.

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