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Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing

J. Olofsson · C. de Mazancourt · M. J. Crawley

Abstract Herbivores influence spatial heterogeneity in soil resources and vegetation in ecosystems. Despite increasing recognition that spatial heterogeneity can drive species richness at different spatial scales, few studies have quantified the effect of grazing on spatial heterogeneity and species richness simultaneously. Here we document both these variables in a rabbit-grazed grassland. We measured mean values and spatial patterns of grazing intensity, rabbit droppings, plant height, plant biomass, soil water content, ammonia and nitrate in sites grazed by rabbits and in matched, ungrazed exclosures in a grassland in southern England. Plant species richness was recorded at spatial scales ranging between 0.0001 and 150 m². Grazing reduced plant height and plant biomass but increased levels of ammonia and nitrate in the soil. Spatial statistics revealed that rabbit-grazed sites consisted of a mixture of heavily grazed patches with low vegetation and nutrient-rich soils (lawns) surrounded by patches of high vegetation with nutrient-poor soils (tussocks). The mean patch size

(range) in the grazed controls was 2.1 ± 0.3 m for vegetation height, 3.8 ± 1.8 m for soil water content and 2.8 ± 0.9 m for ammonia. This is in line with the patch sizes of grazing (2.4 ± 0.5 m) and dropping deposition (3.7 ± 0.6 m) by rabbits. In contrast, patchiness in the ungrazed exclosures had a larger patch size and was not present for all variables. Rabbit grazing increased plant species richness at all spatial scales. Species richness was negatively correlated with plant height, but positively correlated to the coefficient of variation of plant height at all plot sizes. Species richness in large plots (<25 m²) was also correlated to patch size. This study indicates that the abundance of strong competitors and the nutrient availability in the soil, as well as the heterogeneity and spatial pattern of these factors may influence species richness, but the importance of these factors can differ across spatial scales.

Keywords Spatial heterogeneity · Species richness · Herbivory · Rabbit grazing

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Introduction

Understanding the determinants of species richness is central for many questions in ecology. Species richness is, however, inherently scale-dependent (Olff and Ritchie 1998; Chesson 2000). An understanding of the scale-dependent variation is needed to be able to generalize about the processes determining species richness between ecosystems and spatial scales. Herbivores influence plant species richness in many terrestrial ecosystems (Crawley 1983; Olff and Ritchie 1998; Proulx and Mazumder 1998). Most studies that have recorded species richness in plots of different sizes have reported a shift from positive to neutral or negative effects of herbivory with increasing spatial scale

(Chaneton and Facelli 1991; Gibson and Brown 1991; Glenn and Collins 1992; Olff and Ritchie 1998; Stohlgren et al. 1999; Augustine and Frank 2001). However, the impact of herbivores on species richness was independent of scale in a recent multi-site study (Bakker et al. 2006). The scale-dependent effect of herbivory on species richness indicates a shift in the importance of the processes that regulate species richness (Starr et al. 2005), suggesting that herbivores have unique effects on each of these processes. For example, herbivores can enhance species richness at small scales by reducing competitive exclusion, but reduce species richness at larger scales by selecting for grazing tolerators in the potential species pool (Olff and Ritchie 1998).

The effect of herbivores on diversity at different spatial scales is likely tied to their effect on spatial heterogeneity. Herbivore created spatial heterogeneity may thus drive species richness, as exemplified by the herbivores in Yellowstone National Park, which only increased plant diversity at the spatial scales where they increased heterogeneity of soil nutrients (Augustine and Frank 2001). Herbivores can both increase and decrease spatial heterogeneity within and between plant communities (reviewed in Adler et al. 2001). The immediate effect depends on the interaction between the spatial pattern of grazing and the preexisting spatial pattern of vegetation. When the spatial pattern of grazing and vegetation are generated independently, grazing will increase heterogeneity at scales where grazing patterns are stronger than vegetation patterns and decrease heterogeneity at scales where grazing patterns are weaker than vegetation patterns (Adler et al. 2001).

Although spatial heterogeneity can be one of the driving forces behind species coexistence (Pacala and Tilman 1994; Connolly and Roughgarden 1999; Chesson 1994, 2000), it is not a straightforward task to link spatial heterogeneity to species richness at different spatial scales. Species richness at small spatial scales depends on the size of the individuals and the extent to which they intermingle (Crawley and Harral 2001). The size of individuals should to a large extent be determined by local nutrient availability. The extent to which species intermingle should be determined by local coexistence. Although many processes have been proposed to drive local coexistence of plants, small-scale variation of limiting resources is among the most well-supported candidates (Pacala and Tilman 1994; Chesson 2000). The number of patches with spatially aggregated species, and thus the large-scale patchiness of resources, should be one factor that influence richness at larger spatial scales (Crawley and Harral 2001). The relationship between the spatial distribution of limiting resources and species diversity is not well established because there is no single scale appropriate for measuring variation in resource distribution (Anderson et al. 2004). The spatial scaling model by Ritchie and Olff (1999)

provides one possible method for this, since it shows that a fractal distribution of resources should lead to higher β diversity and thus higher richness at large spatial scales than would a non-fractal distribution of resources (Ritchie and Olff 1999).

An understanding of the scale dependence of the processes determining species richness is needed in order to generalize about the effects of herbivores on species richness between habitats, ecosystems and spatial scales. A better understanding of the link between species richness and spatial heterogeneity of resources is one way to achieve this. The objectives of this study are thus to determine how rabbit grazing influences spatial heterogeneity of vegetation and soil resources in grasslands, and relate this to species richness at different spatial scales. Based on the theory outlined by Adler et al. (2001), we hypothesize that spatial heterogeneity of vegetation and soil resources in grazed areas are determined by spatial heterogeneity of rabbit grazing and deposition of droppings. Based on the reasoning about processes determining species richness at different spatial scales, we hypothesize that mean values and small-scale heterogeneity of soil and vegetation properties influence species richness at small spatial scales, and patchiness of resources and vegetation influence species richness at larger spatial scales.

Materials and methods

Study site

We studied the effects of rabbit exclusion in dry acidic grassland [a variant of the UK National Vegetation Classification MG5 *Centaureo-Cynosuretum cristati* grassland: *Danthonia decumbens* sub-community described by Crawley (2005)] on sandy soils of the Bagshot Series in Silwood Park, Berkshire, UK (national grid reference 41/94469). Four 30 × 30-m large exclosures and four adjacent control plots were established in 1990. The exclosures were constructed of wire netting with a mesh size of 3 cm. Similar perennial grasslands as well as patches of oak forest surround the study area.

Field and laboratory methods

In July 2003, a 15 × 10-m plot was marked out in each control and exclosure. To estimate plant species richness at different spatial scales, we recorded presence–absence data of each plant species within nested subplots ranging in size from 150 to 0.0001 m^2. The species richness was thus recorded in one plot of 150-m^2, two subplots of 25 m^2, four of 6.25 m^2, eight of 1 m^2, 16 of 0.25 m^2, 32 of 0.0625 m^2, 64 of 0.01 m^2, 128 of 0.0025 m^2 and 256 of 0.0001 m^2,

where two subplots are nested in a regular pattern within the larger subplots. Each 150-m^2 plot contains two 25-m^2 subplots, which in turn contain two 6.25-m^2 subplots each, etc.

To estimate heterogeneity in soil conditions and vegetation, we established a grid of 51 sampling points distributed in a partly randomized nested design as follows. Each 150-m^2 plot was divided into a grid of 6×4 subplots (6.25 m^2). This new grid defines 5×3 interior corner points. In total, 17 of these 35 points were randomly chosen. Three sampling positions were placed at a random distance (between 0 and 1 m) from each selected point, in a randomized direction (north, south, east or west). This sampling design provides a good replication of distances from 0.1 to 15 m.

At each of the 51 sampling points, we estimated plant height, plant biomass and number of rabbit droppings in a 0.01-m^2 area. Maximum plant height was measured with a ruler and number of droppings was counted when removing them from the plot. Plant biomass was harvested, oven-dried at 60°C for 48 h, and weighed. Soil water content in the top 5 cm was measured in the center of each plot using a surface capacitance insertion probe. This instrument measures the soil dialectic constant, which is closely related to the soil water content (Robinson and Dean 1993). Finally, we collected a 4-cm-diameter × 10-cm-depth soil core. The cores were transported to a laboratory as quickly as possible (always <2 h), where the cores were maintained at <5°C prior to analysis. Available ammonium and nitrate was extracted from sieved soil by shaking 25 g soil in 100 ml of 1 M potassium chloride for 1 h. The resulting suspension was filtered through Whatman no. 1 paper and analyzed with a SKALAR continuous flow analyzer (SKALAR, Breda, Netherlands).

Heterogeneity in rabbit grazing was quantified by transplanting pot-grown red fescue, *Festuca rubra*, to each of the 51 sampling points in the grazed plots, after soil cores had been collected. The fescues were grown from seeds for 4 weeks in pots (7×7 cm) and one pot was planted at each of the sampling points. The biomass in each pot was estimated nondestructively by a correlation with plant height ($R^2 = 0.62$) before they were exposed to rabbits. The fescues were exposed to grazing for 5 days. Plants were visually inspected for signs of grazing to check that any reduction of biomass was due to grazing and not other factors such as drought, and plant biomass was harvested. Rabbit consumption of each plant was estimated as the reduction in biomass during the period of exposure to grazing.

Statistical analyses

Mean values of soil and vegetation properties were compared between grazed and ungrazed plots using *t*-tests.

Welch approximation to the *df* is used to account for unequal variances (R development Core Team 2006). The relationship between different soil and plant properties were analyzed by linear modeling or generalized linear modeling depending on the structure of the residuals of the data (Crawley 2002). The relative variation within each plot was quantified by calculating the coefficient of variation (Zar 1996). The spatial structure of the variation was addressed using geostatistical methods. Semivariograms of the spatial distribution of soil properties as well as vegetation patterns were constructed separately for each grazed and ungrazed plot. For each semivariogram, we fitted random, linear and spherical models by using the geoR package (Ribeiro and Diggle 2001) within the statistical program R (R development Core Team 2006). We compared random, linear and spherical models by selecting the model with the lowest Akaike information criterion (Crawley 2002). We estimated the range (patch size), nugget (variance at the smallest sampled distance, i.e., micro-scale variance and measurement error) and the sill (plateau reached by the variance at the largest sampled distances), when spherical models had the best fit to the data (Fig. 1). The proportion of variance explained by the model is the ratio of the structural variance ($C = $ sill nugget) to the total variance (the sill, $C_0 + C$), i.e., $C/(C_0 + C)$ (Robertson and Gross 1994). Fractal distributions are self-similar at different spatial scales (Sugihara and May 1990). The fractal dimension (D) of a resource varies between 0 and 2; $D = 0$ is a single point, $D = 1$ indicates highly clustered and self-similar distributions, while $D = 2$ is indistinguishable from a random pattern (Anderson et al. 2004). The fractal dimension were estimated as $D = 2 - m/2$ where m is the slope of the log–log regression between the variance and the lag (Burrough 1983; Palmer 1988; Anderson et al. 2004).

Results

Effects of grazing on mean values of soil and plant properties

The vegetation was more than 3 times taller and plant biomass was twice as high in ungrazed exclosures compared with rabbit-grazed sites (Table 1). The soil water content was lower and soil ammonia and nitrate content were higher in grazed sites than within exclosures (Table 1). The mean density of rabbit droppings in the grazed plots was 413.0 ± 13.9 droppings m^{-2} and the grazing intensity on the planted fescues was $23.0 \pm 2.0\%$. The density of rabbit droppings and grazing intensity was highly correlated in all grazed plots ($r = 0.42, 0.42, 0.33$ and 0.17, respectively). Droppings were found in one of the exclosures (1.5 ± 2.8 droppings m^{-2}), but the effect on vegetation and

Fig. 1 Semivariograms for veg-
etation height in **a** one grazed
site and **b** one ungrazed exclo-
sure. Range, nugget and struc-
tural variance are indicated in
the semivariogram for the
ungrazed exclosure
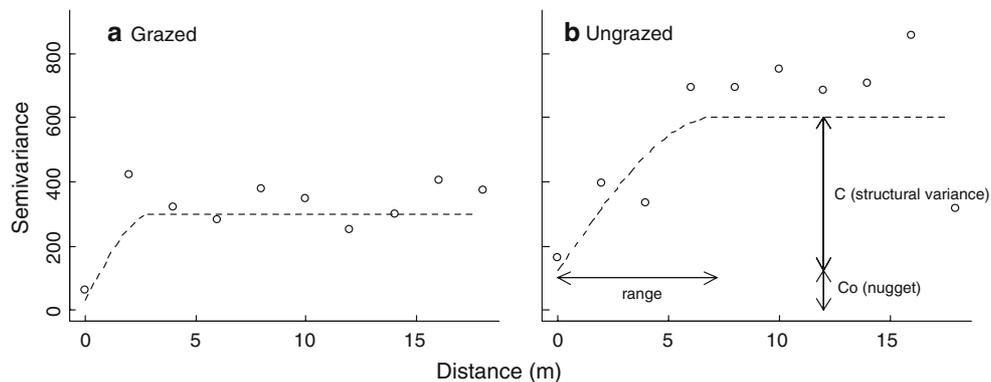
Table 1 Comparison of means (mean ± SE) and coefficients of variation (*CV*) (mean ± SE) of plant and soil variables measured within plots grazed by rabbits and in ungrazed exclosures

Treatments		Grazed	Ungrazed	*t*	*df* [a]	*P*
		Mean ± SE				
Plant height (cm)	Mean	21.7 ± 1.1	61 ± 3.5	11.9	6	<0.001
	CV	92.0 ± 4.8	33.9 ± 0.9	11.9	3.2	<0.001
Plant biomass (g m^{-2})	Mean	420 ± 55	690 ± 20	4.2	6	0.015
	CV	43.4 ± 1.3	26.2 ± 3.8	4.2	3.7	0.016
Soil water content (%)	Mean	1.2 ± 0.5	3.0 ± 0.8	3.5	6	0.075
	CV	83.9 ± 13.8	47.8 ± 4.1	2.5	3.5	0.076
Soil NH$_4^+$ (µg g^{-1})	Mean	255 ± 75	140 ± 50	3.3	6	0.017
	CV	31.1 ± 8.1	15.3 ± 2.3	1.9	3.5	0.014
Soil NO$_3^-$ (µg g^{-1})	Mean	96 ± 10	62 ± 8	2.5	6	0.046
	CV	47.2 ± 14.8	28.9 ± 9.8	1.0	5.2	0.349

[a] *df* vary, as Welch approximation to the *df* is used to account for unequal variances (R development Core Team 2006)

soil is assumed to be minimal. Plant height was positively correlated to plant biomass and soil water content and negatively correlated with soil ammonium and nitrate, grazing intensity and the density of rabbit droppings in all four grazed sites (Table 2). In exclosures, there were no significant correlations between plant height and plant biomass, soil water content, soil ammonia and soil nitrate, respectively, with the exception of the negative correlation with soil water content in two exclosures and the nitrate content in one exclosure (Table 2).

Table 2 Correlations between plant height (cm) and plant biomass (g m^{-2}), soil water content (%), soil NH$_4^+$ content (µg g^{-1}), soil NO$_3^-$ content (µg g^{-1}), density of rabbit droppings and grazing intensity (%), respectively[a]

	Biomass	Water content	NH$_4^+$	NO$_3^-$	Rabbit droppings	Rabbit grazing
Plant height (cm)						
Grazed 1	0.27	0.52	−0.39	−0.41	−0.41	−0.39
Grazed 2	0.27	0.38	−0.22	−0.32	−0.36	−0.41
Grazed 3	0.45	0.56	−0.29	−0.35	−0.54	−0.40
Grazed 4	0.51	0.29	−0.34	−0.22	−0.36	−0.47
Ungrazed 1	–	−0.41	–	–		
Ungrazed 2	–	−0.39	–	–		
Ungrazed 3	–	–	–	−0.46		
Ungrazed 4	–	–	–	–		

[a] Only significant correlations are shown. The correlations were performed independently for each grazed and ungrazed site (*n* = 51)

Effects of grazing on heterogeneity of plant and soil properties

Exclosures decreased the coefficient of variation of plant height and biomass, but had no effect on the coefficient of variation of soil water content, ammonium or nitrate content (Table 1). Geostatistical analyses detected spatial heterogeneity in plant height, soil water content, extractable ammonia, grazing intensity and rabbit droppings. These were best described with a spherical model in all grazed sites. Inside the exclosures, the spatial structures of plant height and soil water content were also best described by spherical models, but the spherical models were just marginally better than a log–log model, implying that the pattern were almost scale-free. The spatial structure of extractable ammonia in exclosures was not significantly different from a random pattern.

Rabbit grazing created 2- to 4-m-diameter patches (range) in vegetation height, soil water content and extractable ammonia (Table 3, Fig. 1). The size of these patches corresponds well to the patchiness in grazing intensity and dropping density (Table 3). Vegetation height is negatively correlated to levels of extractable ammonia and nitrate and positively correlated to soil water content in grazed plots but not in ungrazed plots, while correlations are non-significant or inconsistent in the ungrazed exclosures (Table 2). This indicates that rabbits create heavily grazed patches with low vegetation, dry soils and high nutrient levels (lawns), and lightly grazed patches with tall vegetation and nutrient-poor soil (tussocks). There was no detectable spatial structure in extractable nitrate in any of the grazed or ungrazed sites. Spatial structure in plant biomass was detected in just one of the grazed sites.

Vegetation height showed a significant fractal distribution in all four exclosures, but in none of the grazed plots. The estimated fractal dimension was thus significantly closer to 1 in the exclosures than in grazed plots (Table 3). There were no significant fractal distributions of soil water

Table 3 Analysis of spatial heterogeneity of vegetation height, soil water content and extractable NH_3 (mean ± SE) in controls grazed by rabbits and ungrazed exclosures. Data were analyzed by variograms with spherical covariance structures in two dimensions[a]

Treatment	Nugget	Sill	Range (m)	Explained variance	Fractal dimension[b]
Vegetation height (cm)					
Grazed	47.4 ± 25.0	378.7 ± 25.9	2.1 ± 0.3	0.87 ± 0.07	1.97 ± 0.05
Ungrazed	63.8 ± 25.7	493.7 ± 37.0	7.2 ± 1.3	0.88 ± 0.04	1.80 ± 0.01
t	−0.5	−2.6	−3.9	−0.1	−3.7
df[c]	6.0	5.4	3.4	5.0	3.4
P	0.663	0.048	0.024	0.925	0.027
Soil water content (%)					
Grazed	0.50 ± 0.17	0.99 ± 0.16	3.8 ± 1.8	0.52 ± 0.13	1.90 ± 0.02
Ungrazed	0.91 ± 0.17	2.32 ± 0.04	5.0 ± 1.3	0.61 ± 0.07	1.92 ± 0.03
t	−1.6	−8.0	−0.5	−0.6	0.6
df	4.4	3.4	5.0	4.7	4.8
P	0.183	0.003	0.621	0.601	0.593
Extractable NH_3 (µg g^{-1} dry soil)					
Grazed	919 ± 574	3,087 ± 992	2.8 ± 0.9	0.66 ± 0.15	1.99 ± 0.01
Ungrazed	–	–	–	–	1.97 ± 0.03
t					0.6
df					4.8
P					0.593
Grazing intensity (%)					
Grazed	327 ± 131	701 ± 137	3.7 ± 0.6	0.58 ± 0.08	1.97 ± 0.03
Rabbit droppings (no. m^{-2})					
Grazed	21.7 ± 8.9	64.8 ± 27.2	2.4 ± 0.5	0.61 ± 0.07	1.95 ± 0.02

[a] Variogram parameters (nugget, sill, range and proportion of the variance explained) were estimated only when the model showed a significantly better fit to the data than alternative models. The spherical models were just marginally better than a log–log model in the exclosures. Although ranges were estimated in the exclosures, the spatial pattern is close to being scale free

[b] Fractal dimension was calculated as explained in the methods; a fractal dimension of 2 is indistinguishable from a random pattern. Only vegetation height in ungrazed plots shows a significant fractal structure

[c] df vary, as Welch approximation to the df is used to account for unequal variances (R development Core Team 2006)

Table 4 Plant species richness in grazed plots and ungrazed (exclosure) plots, recorded at different spatial scales from 0.0001 to 150 m^2 (mean + SE)[a]

	Area (m^2)								
	0.0001	0.0025	0.01	0.0625	0.25	1	6.25	25	150
Species richness									
Grazed (mean)	2.2	3.1	4.4	5.5	7.6	10.3	15.3	16.5	19.8
Grazed (SE)	0.1	0.3	0.4	0.2	0.4	0.4	0.5	0.3	1.0
Ungrazed (mean)	1.2	2.1	2.3	2.8	3.8	5.5	8.8	10.8	13.5
Ungrazed (SE)	0.2	0.4	0.3	0.3	0.3	0.3	0.5	0.8	1.5
t (7 df)[b]	3.1	2.0	4.7	6.9	8.5	6.3	9.1	6.4	3.2
P	0.022	0.098	0.003	<0.001	<0.001	<0.001	<0.001	<0.001	0.018
Correlations[c]									
Mean	0.88	−0.70	−0.93	−0.91	−0.92	−0.88	−0.98	−0.95	−0.87
Nugget	–	–	−0.86	−0.91	−0.92	−0.88	−0.91	−0.91	−0.87
Range	–	–	–	–	−0.81	−0.77	−0.93	−0.96	−0.89
Sill	–	–	–	–	–	–	–	–	–
Coefficient of variation	0.75	0.57	0.93	0.92	0.97	0.93	0.98	0.96	0.75
Fractal dimension	–	0.73	0.79	0.91	0.80	0.89	0.84	0.80	–

[a] The difference in species richness between grazed and ungrazed treatments was tested separately at each spatial scale with a generalized linear model with quasi Poisson errors

[b] All statistical tests were performed with 7 df

[c] Correlation between species richness at different spatial scales and the different spatial and non-spatial estimates of vegetation height in the plots. Only significant correlations are presented

content or nitrate either in grazed plots or in the exclosures, and there were no significant differences in fractal dimension between the treatments. The ammonia was significantly fractal in one of the ungrazed plots, but there were no significant differences between the treatments. Grazing intensity was fractal in one plot but rabbit droppings were not fractal in any plot.

Effects of grazing on species richness at different spatial scales

Species richness was significantly higher in grazed plots than in exclosures at all censused spatial scales except for one (0.0025-m^2 plots; see Table 4). Grazing increased species richness in the same way at all scales on a log scale: the linear regression lines of log(species richness) and log(area) (Fig. 2) had a higher intercept for rabbit-grazed sites ($t = 10.0$, $P < 0.001$), but there was no significant difference between slopes for the two grazing treatments ($t = 0.5$, $P = 0.583$). The combined slope was 0.173 (CI = 0.012).

Species richness was highly correlated with mean vegetation height and coefficient of variation at all scales. Correlation coefficients of species richness and coefficient of variation were greatest at intermediate scales, between 0.01 and 25 m^2. The range was correlated to richness in plots larger than 0.25 m^2. The proportion of variance in plant
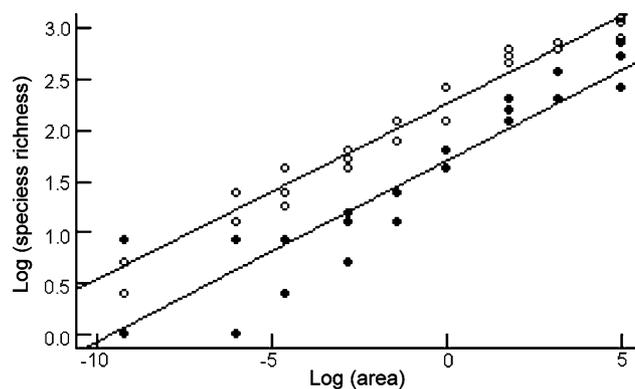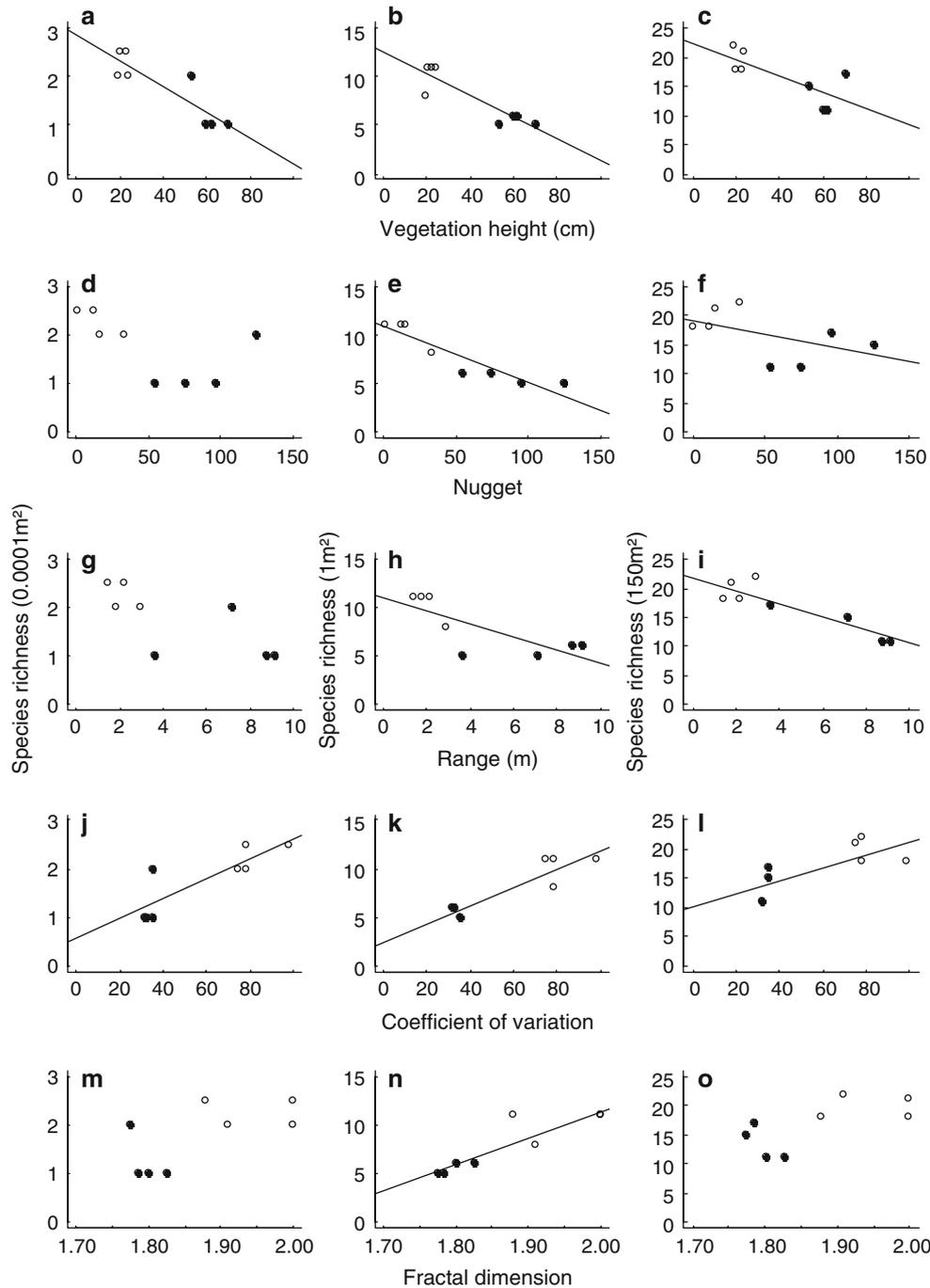

Fig. 2 Relationship between log plant species richness and log area. Rabbit-grazed sites are plotted as *open symbols* and ungrazed plots as *solid symbols*. *Solid line* shows the common regression for grazed and ungrazed sites together. There were significantly different intercepts between grazed sites and ungrazed exclosures ($t = 10.0$, $P < 0.001$), but there were no significant difference between the slopes ($t = 0.5$, $P = 0.583$)

height explained by spatial pattern, also referred to as the structural variance (see Fig. 1 for an explanation), was not significantly correlated to species richness at any spatial scale. Plant height was chosen because it clearly showed the effect of rabbits on spatial heterogeneity; furthermore, we found here that it is correlated to all other properties that we measured. The results were qualitatively similar when

the same analyses were performed for soil water content or extractable ammonia. Mean vegetation height was clearly the factor most correlated with species richness at the smallest spatial scale (Table 4, Fig. 3). Although coefficient of variation was the estimate most closely correlated to species richness in the 1-m^2 plots, the mean, nugget, range, and fractal dimension of vegetation height were all also closely correlated to the species richness at that spatial scale. The range of the vegetation height was the estimate most correlated to the species richness in 150-m^2 plots, but the mean and the nugget were also highly correlated to the species richness at that spatial scale.

Fig. 3a–o Relationship between plant species richness at three spatial scales (0.0001, 1, 150 m^2) and mean value, nugget, range, coefficient of variation and fractal dimension of vegetation height. Rabbit-grazed sites are plotted as *open symbols* and ungrazed plots as *solid symbols*. *Solid line* shows significant correlations for the grazed and ungrazed sites together

Discussion

Rabbit-grazed grasslands in Silwood Park were a heterogeneous mosaic of 2- to 4-m-diameter patches of nutrient-rich and dry soil with short vegetation alternating with nutrient-poor soils with tall vegetation. The spatial distribution of these patches corresponds to the spatial pattern in grazing intensity as measured by consumption of a phytometer (*Festuca rubra*) and deposition of rabbit droppings. These patches seem to become weaker and increase in size (vegetation height) or disappear (extractable ammonia) and the distribution of resources and vegetation became fractal when rabbits were excluded for 15 years (i.e., inside the matched exclosures). Rabbits are known to repeatedly graze the same areas (Iason et al. 2002; Bakker et al. 2005). We infer that rabbit grazing and excretion induce and maintain this patchiness as a result of their repeated use of certain areas.

The rabbit grazing in these grasslands corresponds to a patch-grazing scenario (Adler et al. 2001). Increased heterogeneity induced by patch grazing has been found in a wide range of ecosystems with different types of herbivores (McNaughton 1984; Ring et al. 1985; McNaughton et al. 1997; Cid and Brizuela 1998; Pastor et al. 1998; Posse et al. 2000; Augustine 2004). Adler et al. (2001) proposed that patch grazing typically involves repeated grazing of small areas promoted by a positive feedback between grazing and forage quality (e.g., higher than average nitrogen content in regrowth; Crawley 1983) or confinement of herbivores to areas offering relative security from predators. These two scenarios could both explain patch grazing by rabbits as they forage closer to their burrows to avoid predators (Iason et al. 2002) and enhance their forage quality by repeated grazing (Bakker et al. 2005). In the grassland that we studied, rabbit burrows were located in the forest edges, but the heavily grazed patches were not concentrated along forest edges or in the vicinity of other structures that might serve as protection from predators. Moreover, previous studies have reported that predation risk does not change the spatial distribution of rabbit grazing (Bakker et al. 2005). A positive feedback on the quality of their own food resource (e.g., less dead organic matter in the sward, lower average leaf age, and higher than average leaf nitrogen; Crawley 1983, 1990) may be the most likely explanation for repeated grazing of some patches.

The combined slope for the logarithm of species richness against the logarithm of area in grazed and ungrazed sites (0.17) is much smaller than 0.25, which has been suggested for many ecosystems (Rosenzweig 1995). However, the richness–area relationship is scale dependent (Crawley and Harral 2001) and our estimation do not deviate from what Crawley and Harral (2001) found at similar spatial scales (0.16). The consistent positive effects of rabbits on species

richness at all spatial scales examined are in contrast to most previous studies that have reported a shift from positive to neutral or negative effects at increasing spatial scales (Chaneton and Facelli 1991; Gibson and Brown 1991; Glenn and Collins 1992; Olff and Ritchie 1998; Stohlgren et al. 1999; Augustine and Frank 2001). Contrasting effects of herbivory on species richness at different spatial scales have been explained by shifts in the importance of the processes regulating species richness (Starr et al. 2005), or by hypothesizing that herbivores have unique effects on each of these processes (Olff and Ritchie 1998). However, the multi-site study by Bakker et al. (2006) also reported effects of herbivores on species richness that were independent of the spatial scale investigated.

Although rabbits enhanced species richness at all plot sizes and the relationship between species richness and area were similar for both grazing treatments, the mechanisms involved at different scales might differ. Our results indicate that different processes drive species richness at different spatial scales, although the causal connection cannot be addressed directly. As we hypothesized, there was a strong correlation between plant height and species richness. This may simply reflect that there is room for fewer individuals when plants are getting larger (Crawley and Harral 2001). However, plant height was correlated to species richness at all spatial scales. This may indicate that tall dominant species have expanded in the exclosures and outcompeted subordinate plants. Since there is a strong inverse correlation between plant height and extractable ammonia in the soil, plant height can also be related to the intensity of competition for nutrients. Competition by dominant grasses is probably important for species richness of this grassland at all spatial scales, since two tall broad-leaved grasses (*Dactylis glomerata* and *Arrhenatherum elatius*) dominate the vegetation inside exclosures. This is consistent with previous studies of rabbit grazing that have reported an increased diversity at small spatial scales (Tansley and Adamson 1925; Hope-Simpson 1940; Thomas 1960; Harper 1969; Crawley 1983, 1990; Olofsson et al. 2007).

Heterogeneity of limiting resources is often correlated with species richness (Huston 1980; Pacala and Tilman 1994; Kohn and Walsh 1994; Chesson 2000; Starr et al. 2005) since heterogeneity controls the spatial extent of competitive hierarchies among species and could thus increase the beta and gamma diversity (Starr et al. 2005). The higher coefficient of variation in plant height, plant biomass and soil nutrients in sites grazed by rabbits may thus enhance species richness at all spatial scales, although correlation between species richness and coefficient of variation in plant height suggest that heterogeneity was playing a more important role at intermediate spatial scales. However, as the coefficient of variation often increases with decreasing mean values, these results should be interpreted

carefully as they might at least partly reflect changes in mean value rather than heterogeneity. We found a negative correlation between the fractal dimension of plant height and the species richness, contrary to the predictions by Ritchie and Olff (1999). These correlations are, however, caused by the lower fractal dimension in exclosures compared to grazed plots. There is even a trend for a negative relationship between species richness and the fractal dimension in exclosures at the largest spatial scale. Our results do not contradict the hypothesis that a fractal distribution of resources should increase species richness at larger spatial scales. However, the result shows that changes in the fractal dimension of resources cannot explain the higher species richness in vegetation grazed by rabbits. In two previous studies (Augustine and Frank 2001; Anderson et al. 2004) grazed grasslands were fractal. This difference might reflect that those grasslands were grazed by many different species of herbivores simultaneously, while rabbits alone were the dominant herbivores in this grassland. The patch size imposed by herbivores should be related to body size and multiple species might thus impose multiple sized patches, yielding a distribution that is more scale free.

This study indicates that the spatial structure of resources may be important for species diversity. Patch size was correlated with species richness in large plots. In contrast to numerous theories that link heterogeneity to species richness (Chesson 2000), there are few general theories that link spatial structure of resources to species richness. The theory for fractally distributed resources (Ritchie and Olff 1999) does not explain the pattern that we found, since rabbits actually removed any fractal structure. It is, however, reasonable to assume that an increased small-scale variation should increase species richness at that spatial scale, and this pattern has indeed been recorded in empirical studies (Augustine and Frank 2001; Anderson et al. 2004). A rougher environment (equivalent to a smaller range) increases the probability that different types of environments with their characteristic species will be represented in a sampled plot, and this should enhance species richness. However, too rough an environment does not allow for plants to experience any heterogeneity. The unimodal relationship between species richness and patch sizes recorded by Anderson et al. (2004) reflects these two opposing forces. Patch size should influence species richness most when it is recorded in plot sizes of the same order of magnitude as the size of patches. When plots are much smaller than patch sizes, most plots will sample a relatively homogeneous environment. When plots are much larger than patches, then all plots sample all the environments. This could explain why patch size was only significantly correlated with species richness in plots >0.25 m^2 in our study. However, when interpreting these results, we have to be aware that patches were not only larger but the spatial structure was also weaker and, in some cases, almost indistinguishable from a scale-independent pattern in the exclosures.

As we hypothesized, rabbits create a spatial heterogeneity in the vegetation and soil resources by grazing and depositing droppings. This spatial pattern disappeared and plant species richness decreased when rabbits were excluded for 15 years. Moreover, different factors may be acting on species richness, but the importance of these factors may vary with spatial scale and, consequently, the mechanisms through which herbivores affect species richness may vary with scale as well. The results indicate that the size of individuals and competition determine species richness at small spatial scales. Although these factors might be important at larger spatial scales, the patchiness of the vegetation and soil resources appear to be important as well. It is not a straightforward task to generalize about the effects of grazing on species richness between spatial scales. However, this study provides new information on the link between species richness and the spatial heterogeneity of resources and vegetation and thus provides an explanation for the scale dependence in the effect of herbivores on species richness.

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