

Plant diversity partitioning in grazed Mediterranean grassland at multiple spatial and temporal scales

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Summary

1. Grazing by large ungulates may affect plant species richness and diversity at multiple spatial and/or temporal scales, because grazing affects small-scale resource heterogeneity and plant interactions at the local scale, while effects at the landscape scale are related to grazing intensity and timing.
2. We used diversity partitioning to analyse long- and short-term effects of cattle grazing on plant species richness and diversity in an experimental spatial hierarchy in Mediterranean annual grassland. Short-term changes during secondary succession in grazed plots (2003–2005) at two grazing intensities (heavy and moderate) were analysed and compared with long-term protected vegetation. We applied Hill's q -diversity metrics at $q = 0$ (species richness) and $q = 2$ (reciprocal Simpson diversity) to examine the partitioning of species richness and diversity between their alpha (α) and beta (β) components in the different treatments at four spatial scales: quadrats, within exclosures, within plots, within treatments.
3. At $q = 0$, α -diversity was always significantly lower, and β -diversity significantly higher, than predicted by the randomised null model. Diversity partitioning at $q = 2$ showed a similar trend at the quadrat scale. At the exclosure scale, partitioning exhibited a similar trend during the first 2 years of secondary succession but did not deviate from the null model in the third year, as observed in protected vegetation in all years.
4. At $q = 0$, diversity decreased across all treatments in the short term. At $q = 2$, diversity was initially higher in grazed plots than in protected vegetation; α and β components both decreased during secondary succession, to the levels observed in the protected vegetation.
5. *Synthesis and applications.* Lower dominance in grazed vegetation indicates that grazing affects competitive exclusion at the local, small scale and accentuates natural heterogeneity (e.g. patchiness of soil resources, presence of rocks in the landscape) at a larger scale. The results of this study emphasise the importance of grazing as a management tool for maintaining plant diversity at multiple scales. This is a major concern worldwide, as the area covered by natural ecosystems continues to dwindle, necessitating management of grasslands for multiple functions such as animal production, resource protection and wildlife enhancement.

Key-words: diversity, dominance, exclosures, *Hordeum bulbosum*, landscape, q -diversity metrics, spatial heterogeneity

Introduction

An important aspect of studying diversity in hierarchical systems is to examine changes in diversity at different spatial

and/or temporal scales. The rationale behind this is that biotic and abiotic factors structuring plant communities may affect different processes at different scales, such that their impact on plant community structure and species diversity may change with scale. Grazing by large ungulates is a case in point, and previous research has highlighted the importance of examining grazing effects on diversity at different scales (Augustine & Frank 2001; Ravolainen *et al.* 2010). The effects of grazing by

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large herbivores on plant species richness and diversity have been studied extensively across a wide spectrum of grassland ecosystems, from arid grasslands (Alrababah *et al.* 2007) to Mediterranean grasslands (e.g. Noy-Meir, Gutman & Kaplan 1989; Verdú, Crespo & Galante 2000), tall grass prairie (e.g. Knapp *et al.* 1999) and montane grasslands (e.g. Stohlgren, Schell & Vanden Heuvel 1999).

Large herbivores affect species richness and diversity by selective defoliation because of dietary choices between species and between plant parts of any given species (Rook & Tallowin 2003). In addition to direct phytomass removal, trampling by large herbivores opens up regeneration niches for gap-colonising species (Hartnett, Hickman & Walter 1996; Collins *et al.* 1998; Knapp *et al.* 1999; Stohlgren, Schell & Vanden Heuvel 1999), and nutrient patches created by animal excreta may alter the competitive balance both directly and by altering dietary choices and soil resource heterogeneity (Rook & Tallowin 2003). Furthermore, large herbivores may influence patterns of litter inputs into the soil, thus altering the composition and spatial patterning of plant species (Augustine & Frank 2001). Such grazing impacts generally affect local, small-scale patterns of diversity and heterogeneity, via direct effects on plant growth and nutrient allocation between different plant tissues, or indirectly, via changes in patchiness of soil properties and resources, thus affecting plant interactions (e.g. competition). In Mediterranean grasslands, these small-scale effects on species richness and diversity are generally positive (Perevolotsky & Seligman 1998; Sternberg *et al.* 2000). At the large scale, grazing may increase patchiness in soil properties because of variation in grazing intensity in response to productivity gradients or changes in grazing seasonality (Stohlgren, Schell & Vanden Heuvel 1999). In contrast, Augustine & Frank (2001) and Ravolainen *et al.* (2010) observed that while grazing may increase the number and evenness of species at the small (e.g. quadrat) scale, promoting fine-scale heterogeneity in the vegetation, at larger scales, there may be no grazing effect at all.

One way to examine the impacts of grazing at different scales is to partition diversity into its *alpha* (α) (within sample/community) and *beta* (β) (between sample/community) components (*sensu* Whittaker 1960, 1972). Diversity partitioning has been increasingly applied in recent years to examine diversity within hierarchical systems (e.g. Crist *et al.* 2003; Gabriel *et al.* 2006; Klimek *et al.* 2008). Diversity partitioning may be either additive, where *gamma* (γ)-diversity is the sum of α -diversity and β -diversity, or multiplicative, where γ is the product of α and β . Much debate has been conducted around the additive vs. multiplicative approaches to diversity partitioning (see Baselga 2010; Jost 2010; Ricotta 2010; Veech & Crist 2010a; Wilsey 2010) including the suggestion that the terms 'additive' and 'multiplicative' should be avoided altogether for diversity partitioning (Veech & Crist 2010b). These authors recommend using *q*-diversity metrics (Hill 1973) rather than standard diversity indices to examine common or rare species by weighting α or β by species abundances. *Q*-diversity metrics define 'diversity numbers' (reciprocal of mean proportional abundance), representing the effective number of equally proportionate species in a sample (α) or the effective number of compositionally

distinct samples (β) (Jost 2006; Tuomisto 2010), accounting for the emphasis given to rare or common species. An increase in *q* places greater emphasis on common species and dominance. Moreover, Veech & Crist (2010b) state that *q*-diversity metrics are superior to entropies (e.g. Shannon index of diversity) for diversity partitioning.

We followed this approach to determine how long- and short-term changes in grazing conditions affect species diversity and community structure in Mediterranean grassland. Initially, we analysed differences in diversity partitioning because of long-term previous grazing treatments (CM – moderate and CH – heavy grazing) or lack of grazing (LP – long-term protection) and subsequently monitored the short-term changes in diversity partitioning during secondary succession in exclosures that were set up in the grazed plots. The vegetation at the study site is characterised by changes in dominance, rather than species turnover between different grazing regimes (Golodets, Kigel & Sternberg 2010). Therefore, we applied Hill's *q*-diversity metrics at both $q = 0$ (species richness) and $q = 2$ (reciprocal Simpson diversity) to determine how changing grazing conditions affect species richness and dominance within the plant community and the partitioning of species richness and diversity between their α and β components. We hypothesised that reduced grazing pressure and protection from grazing would lead to 1) a reduction in species richness, because of increased height and density of the vegetation and, 2) a lower reciprocal Simpson diversity, because of changes in dominance patterns within the vegetation. Because grazing may alter local-scale processes as well as large-scale spatial arrangement of the vegetation, leading to changes in both α - and β -diversity, we used diversity partitioning to allow quantitative evaluation of both local-scale (α) and larger-scale (β) effects of grazing on species richness and diversity.

Materials and methods

SITE DESCRIPTION

The research was carried out at the Karei Deshe Experimental Range Station (lat. 32° 55'N, long. 35° 35'E, elevation 150 m a.s.l., 567 mm mean annual rainfall), in the northeast Galilee region of Israel. The vegetation is classified as Mediterranean semi-steppe batha (Zohary 1973), dominated by grasses and forbs. The dominant perennial species are the hemicryptophytes *Bituminaria bituminosa* (L.) C.H. Stürton, *Echinops gaillardotii* Boiss., *E. adenocaulos* Boiss., *Ferula communis* L. and *Hordeum bulbosum* L., forming c. 40% of the cover (Gutman & Seligman 1979; Noy-Meir, Gutman & Kaplan 1989; Sternberg *et al.* 2000). Most other species are annuals, including grasses (*Avena sterilis* L., *Alopecurus utriculatus* Banks & Sol., *Bromus* spp.), legumes (*Medicago* spp., *Trifolium* spp.), composites, crucifers and umbellifers. Growth and development of the vegetation depends almost entirely on seasonal rainfall, from mid-October/late November to late April/early May. During the summer, the vegetation dries out. Productivity is strongly dependent on the amount and distribution of the rainfall. The long-term average annual rainfall (1964–2005) at Karei Deshe is 567 mm. During the 3 years of the research (2003, 2004 and 2005), rainfall was 754 mm (2002–2003), 665 mm (2003–2004) and 395 mm (2004–2005), thus the first 2 years experienced above-average rainfall while the third year experienced below-average rainfall.

EXPERIMENTAL TREATMENTS

The rangeland at the station is grazed by cattle under a controlled grazing system (Sternberg *et al.* 2000). The three experimental treatments included two grazing treatments – continuous heavy (CH) and continuous moderate (CM), with 1.1 and 0.55 cows ha⁻¹ year⁻¹, respectively, for 10 years prior to the onset of the experiment (Sternberg *et al.* 2000) – and grazing exclusion for 30–40 years (long-term protection, LP). The cows grazed for *c.* 7 months during each year of the research, from mid-January to late August. Deferment of grazing after onset of the rainy season in late autumn allows establishment and early growth of the pasture.

The experimental design included two replicate plots (in different parts of the farm) for each treatment, for a total of six plots. The grazed plots were larger than the protected (ungrazed) plots (*c.* 20–30 ha vs. 0.4–2 ha). The actual sampled area, however, was similar between treatments and shares similar habitats. Within each grazed plot, five 10 × 10 m exclosures were established in February 2003, separated by 50–100 m. The exclosures were set up to monitor short-term recovery of the vegetation after protection from grazing, and to compare it with the vegetation in the long-term protected plots. Because of the smaller size of the protected plots, five 2.5-m-long stakes were located randomly within each plot, with each stake marking the centre of the 100 m² area for sampling (Golodets, Sternberg & Kigel 2009).

SAMPLING OF HERBACEOUS VEGETATION

The herbaceous vegetation was sampled at peak biomass in mid spring (April) of 2003, 2004 and 2005, from five 25 × 25 cm quadrats randomly placed in each exclosure in the grazed plots and in the sampling areas in the protected plots. Quadrat positioning avoided rocks and large perennial hemicryptophytes (i.e. *Echinops* spp., *F. communis*, *B. bituminosa*) but included the perennial grass *Hordeum bulbosum*. All above-ground plant material within the quadrats was removed, plants were sorted to species level, identified (Feinbrun-Dothan & Danin 1991), counted and dried at 70 °C for 48 h (Golodets, Sternberg & Kigel 2009), before being weighed.

ANALYSIS OF HERBACEOUS VEGETATION BY DIVERSITY PARTITIONING

We used a spatial hierarchy with four levels ($n = 4$): (i) quadrat (25 × 25 cm; five per exclosure/sampling area), (ii) exclosure/sampling area (100 m²; five per plot); (iii) plot (two per treatment) and (iv) treatment. Therefore, total (γ) diversity (per treatment) = $\alpha_{\text{quadrats}} * \beta_{\text{quadrats}} * \beta_{\text{exclosures}} * \beta_{\text{plots}}$. Diversity partitioning per treatment was determined by pooling the data for each level to partition the next highest level. Partitioning was conducted using PARTITION 3.0 (Veech & Crist 2009) developed specifically for obtaining the different diversity components and conducting nonparametric tests for statistical significance between the components. PARTITION calculates Hill's (1973) q -diversity metrics, where α -diversity (${}^qD_{\text{alpha}}$) at any level in the hierarchy is calculated as follows:

$${}^qD_{\text{alpha}} = \left[\sum_{i=1}^S \sum_{j=1}^S p_{ij}^q w_j \right]^{1/(1-q)} \quad \text{eqn 1}$$

for all species i to S , where p_i is the proportional abundance of species i in sample j , w_j is the weight of the sample, and q is an 'order' determining the sensitivity of the diversity measure to common vs. rare species (Jost 2007). In this study, sample weights

are equal (i.e. = $1/N$, where N = number of samples). At any level in the hierarchy (quadrat, exclosure, plot), the 'sample' j is the appropriate sampling unit for that level (quadrat, exclosure, plot). A q -diversity metric for γ -diversity (${}^qD_{\text{gamma}}$) is calculated by pooling the samples:

$${}^qD_{\text{gamma}} = \left[\sum_{i=1}^S \sum_{j=1}^S p_{ij}^q w_j \right]^{1/(1-q)} \quad \text{eqn 2}$$

In an experimental hierarchy, γ -diversity of any level is α -diversity of the next highest level.

The q -diversity metric for β -diversity is then calculated as follows:

$${}^qD_{\text{beta}} = {}^qD_{\text{gamma}} / {}^qD_{\text{alpha}} \quad \text{eqn 3}$$

When q is < 1 , the emphasis is on rare species; species richness is thus obtained when $q = 0$. When q is > 1 , greater emphasis is given to common species. The inverse Simpson concentration, which is essentially a measure of dominance, is obtained using $q = 2$. As explained earlier (eqn 3), the different diversity components are related multiplicatively when using q -diversity metrics. In the following, we will refer to 'inverse Simpson concentration' as 'reciprocal Simpson diversity'. The q -diversity metric for α -diversity represents the effective number of species, namely, the effective number of equally proportionate species per sample, accounting for the emphasis on rare or common species. The q -diversity metric for β -diversity represents the effective number of samples (or communities), namely, the effective number of compositionally distinct samples (or communities), accounting for the emphasis on rare or common species. It is also a power value, e.g. a value of 2 indicates that the number of effective species doubles from one scale to the next. When $q = 0$, the effective number of species equals the actual number of species. As q increases and more emphasis is placed on common species, the effective numbers of species and samples decrease relative to $q = 0$ until they represent only the dominant species in the community, at $q \geq 2$.

We conducted diversity partitioning of q -diversity metrics of orders 0 and 2, for three consecutive years to examine changes in diversity during the 3-year period of the research. Partitioning of diversity into α and β components was compared with a randomised null model, using 1000 iterations. At the sample level, we used individual-based randomisation; while at the exclosure and plot levels, sample-based randomisation was used to conserve species composition within samples (Crist *et al.* 2003; Veech & Crist 2009). Randomisation tests at the plot level produced spurious results because there were only two plots per treatment and are not presented. The effects of grazing and time on each order of α -diversity were determined by individual repeated-measures ANOVA at each of the first three levels (quadrat, exclosure, plot), using JMP IN 7 (SAS Institute Inc., Cary, NC, USA). Tukey HSD was used for comparison of means when main effects were significant. Data were square-root transformed ($q = 0$) or natural-logarithm transformed ($q = 2$) prior to ANOVA. Because β -diversity values depend on changes in α -diversity and are therefore not independent from one another, we conducted nonparametric repeated-measures ANOVA, at the quadrat and exclosure levels, using PERMANOVA with R software (function 'adonis' in the 'vegan' package; R Development Core Team 2009) to determine the effects of grazing and time on each order of β -diversity. In PERMANOVA, the β -diversity between each pair of plots was randomised 999 times. F - and P -values were calculated according to Anderson (2001). We incorporated the repeated measures by defining plot identity as the nesting factor.

Results

The data were analysed and are presented according to the two orders of the q -diversity metrics. Results for 2003 reflect effects of previous grazing treatments on the vegetation, while results for 2004 and 2005 reflect short-term changes in the vegetation (secondary succession) because of establishment of the exclosures and protection from grazing.

DIVERSITY AT $Q = 0$ – SPECIES RICHNESS

At the start of the study (2003), we analysed differences in diversity partitioning because of long-term previous grazing treatments (CM – moderate and CH – heavy grazing) or lack of grazing (LP, *c.* 30 years). At both the quadrat and exclosure levels, α -diversity was lower than expected compared with the null model ($P < 0.001$, Table 1), while β -diversity was higher than expected, for all treatments. Thus, trends of partitioning were similar among treatments in 2003. The greatest contribution to diversity at $q = 0$ within treatments was from β_{quadrats} and $\beta_{\text{exclosures}}$, both of which were > 2 , i.e. species richness more than doubled from quadrats to exclosures and from exclosures to plots (Table 1).

After setting the exclosures, α -diversity decreased with time (i.e. 2003–2005) at all levels of the hierarchy (Fig. 1), and the decrease was significant between 2004 and 2005 (Table 2). At the quadrat level, α -diversity decreased in CM; however, it did not change in CH or LP (treatment by year [T \times Y] interaction $P < 0.005$). At the exclosure level, α -diversity decreased from 2004 to 2005 (Fig. 1, Table 2), while at the plot level, it decreased between 2004 and 2005, and there was a marginally

significant T \times Y interaction, indicating that the decrease was primarily in the CM treatment (Fig. 1, Table 2). There were no significant changes in β -diversity within or between treatments with time (Table 3). Across years, α -diversity was lower than expected compared with the null model (Table 1), while β -diversity was significantly higher than expected, for all three treatments (Table 1). Gamma (γ)-diversity decreased in 2005 in all treatments (Table 1).

DIVERSITY AT $Q = 2$ – RECIPROCAL SIMPSON DIVERSITY

In 2003, the year reflecting long-term previous grazing treatments, α -diversity was lower than expected compared with the null model, while β -diversity was consistently higher than expected, at the quadrat and exclosure levels in CM and CH treatments (Table 1). For LP, the trends were the same; however, the significant result at the exclosure level is probably not biologically significant, because the values barely changed in 2004 and 2005, and partitioning was not significant in these years (Table 1). In 2003, the greatest contribution to diversity at $q = 2$ (i.e. reciprocal Simpson diversity) within treatments was α_{quadrats} , followed by β_{quadrats} , $\beta_{\text{exclosures}}$ and β_{plots} (Table 1).

As for $q = 0$, α -diversity at $q = 2$ decreased with time at all levels of the hierarchy (Fig. 1). This was significant at the quadrat and exclosure levels, between 2004 and 2005 (Table 2, Fig. 1). At the quadrat level, α -diversity decreased from 2004 to 2005 in CM, while there was no change in CH or LP (T \times Y interaction; Table 2, Fig. 1). At the exclosure level, α -diversity was higher in CM than in LP and decreased significantly from

Table 1. Partitioning of effective number of species (α -diversity) and effective number of samples (β -diversity) at different levels of the experimental hierarchy, and total (γ) diversity, as affected by grazing treatments

Treatment	Hierarchical level	2003				2004				2005			
		$q = 0$		$q = 2$		$q = 0$		$q = 2$		$q = 0$		$q = 2$	
		α	β	α	β	α	β	α	β	α	β	α	β
CH	Quadrat ($n = 50$)	7.52	2.13	2.8	1.51	7.34	1.96	2.93	1.5	6.52	2.15	2.02	1.6
	Exclosure ($n = 10$)	16	2.19	4.22*	1.41*	14.4	2.33	4.39	1.64	14	2.29	3.23	1.33
	Plot ($n = 2$)	35	1.4	5.94	1.28	33.5	1.43	7.22	1.22	32	1.31	4.28	1.02
	Total (γ)	49		7.60		48		8.81		43		4.37	
CM	Quadrat ($n = 50$)	7.42	2.29	2.78	1.64	6.76	2.26	2.63	1.86	4.72	2.22	1.66	1.33
	Exclosure ($n = 10$)	17	2.26	4.55*	1.38*	15.3*	2.19*	4.9†	1.53†	10.5	2.29	2.21	1.13
	Plot ($n = 2$)	38.5	1.27	6.26	1.27	33.5	1.43	7.52	1.09	24	1.38	2.49	1.02
	Total (γ)	49		7.95		48		8.20		33		2.54	
LP	Quadrat ($n = 50$)	7.2	2.29	2.04	1.23	6.06	2.43	1.95	1.36	5.86	2.3	1.89	1.46
	Exclosure ($n = 10$)	16.5	2.03	2.5*	1.11*	14.7*	2.24*	2.65	1.05	13.5*	2.04*	2.75	1.04
	Plot ($n = 2$)	33.5	1.43	2.78	1.06	33	1.45	2.77	1.03	27.5	1.42	2.86	1.05
	Total (γ)	48		2.95		48		2.85		39		3.00	

CH, heavy grazing; CM, moderate grazing; LP, long-term protection from grazing.

Bold values are higher, and italicised values are lower, than expected from individual-based (quadrats) and sample-based (exclosures) randomisations.

Values significant at $P < 0.001$ unless otherwise specified (* $P < 0.01$; † $P < 0.05$). Values at the plot level were not compared with randomised null models because of low sample size.

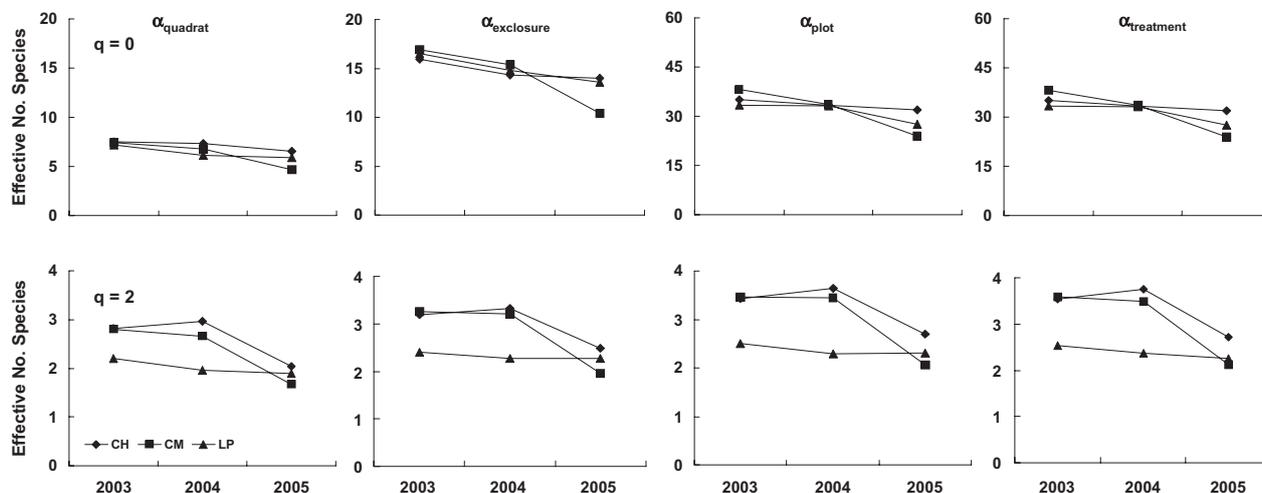


Fig. 1. Effective number of species (α -diversity) at $q = 0$ and $q = 2$ as a function of time, for each level in the experimental hierarchy (quadrat, exclosure, plot, treatment), per treatment. Treatment abbreviations: CH, heavy grazing; CM, moderate grazing; LP, long-term protection from grazing. Effective number of species: effective number of equally proportionate species per sample, accounting for the emphasis on rare ($q = 0$) or common ($q = 2$) species. Note change in scale of y-axis at plot and treatment scale for $q = 0$.

Table 2. Repeated-measures ANOVA on the effects of grazing treatments and year on effective number of species (α -diversity) at $q = 0$ and $q = 2$ for each of three levels of the experimental hierarchy: quadrat, exclosure, plot. Bold values are significant at $P < 0.05$; values in italics are marginally significant at $P < 0.10$

$q = 0$	Quadrat			Exclosure			Plot		
	Source	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>
Treatment	2	0.613	0.542	2	0.291	0.749	2	1.83	0.216
Year	2	27.7	< 0.0001	2	11.3	< 0.0001	2	11.6	0.003
Treatment \times Year	4	3.84	0.004	4	1.79	0.139	4	2.79	<i>0.093</i>
Error	441			81			9		
$q = 2$	Quadrat			Exclosure			Plot		
	Source	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>
Treatment	2	5.39	0.005	2	5.26	0.007	2	3.84	<i>0.062</i>
Year	2	11.0	< 0.0001	2	5.15	0.008	2	4.66	0.041
Treatment \times Year	4	3.16	0.014	4	2.24	<i>0.072</i>	4	1.85	<i>0.204</i>
Error	441			81			9		

2004 to 2005. There was also a marginally significant treatment by year [T \times Y] interaction (Table 2), showing that the decrease in α -diversity from 2004 to 2005 was because of a decrease in CM. At the plot level, α -diversity decreased from 2004 to 2005, while differences between treatments were only marginally significant, and there was no treatment by year interaction (Table 2, Fig. 1). Across years, β -diversity at the quadrat level was higher in CM than in LP (Table 3). In addition, β -diversity at the exclosure and plot levels decreased in 2005 compared with 2004 (Table 3). In 2004, partitioning between α - and β -diversity was significant at both quadrat and exclosure levels for CM and CH, while in LP only at the quadrat level. In 2005, partitioning at the exclosure level was not significant in any treatment (Table 1). γ -diversity was higher in CM and CH compared with LP in 2003 and 2004, while in

2005, it decreased in CM and CH to the levels measured in LP (Table 1).

Discussion

Partitioning of diversity in the studied Mediterranean grassland initially appeared to be similar to other vegetation systems (Summerville & Crist 2005; Chandy, Gibson & Robertson 2006; Erös 2007). However, in this system, it was notable that α -diversity was lower than expected, while β -diversity was higher than expected between quadrats. There are several possible explanations for the lower-than-expected α -diversity, including competitive interactions between plants (e.g. competitive exclusion by dominants), aggregation (Crist *et al.* 2003), or small-scale heterogeneity of soil resources which may limit

Table 3. Nonparametric repeated-measures ANOVA on the effect of grazing treatments and year on effective number of samples (β -diversity) at $q = 0$ and $q = 2$ for each of two levels of the experimental hierarchy: quadrat, enclosure. Bold values significant at $P < 0.05$

$Q = 0$		Quadrat				Enclosure			
Source	df	<i>F</i> Model	R^2	<i>P</i>	df	<i>F</i> Model	R^2	<i>P</i>	
Treatment	2	8.31	0.159	0.241	2	1.01	0.120	0.393	
Year	2	0.241	0.005	0.757	2	1.46	0.172	0.296	
Treatment \times Year	4	1.62	0.062	0.142	4	0.735	0.174	0.624	
Error	81				9				
$Q = 2$		Quadrat				Enclosure			
Source	df	<i>F</i> Model	R^2	<i>P</i>	df	<i>F</i> Model	R^2	<i>P</i>	
Treatment	2	7.09	0.127	0.011	2	1.93	0.120	0.236	
Year	2	4.76	0.085	0.012	2	6.63	0.413	0.031	
Treatment \times Year	4	1.70	0.061	0.189	4	1.49	0.186	0.343	
Error	81				9				

the establishment of species to specific soil patches (Augustine & Frank 2001), e.g. moisture, nutrients, availability of microsites. In addition, litter accumulation by tall grasses (*H. bulbosum*, *H. spontaneum*, *Avena sterilis*) should reduce richness as it presents an obstacle for seedling emergence of species with small seeds and therefore small seedlings. Because these tall grasses and other large species have large seeds with large seedlings capable of penetrating the litter layer, they may use litter accumulation to pre-empt competition with smaller species (Sternberg *et al.* 2003; Aboling *et al.* 2008). While all of these alternative mechanisms are plausible, further investigation is needed to determine which one(s) is/are responsible for the low α -diversity observed at the small scale in the current study. In contrast, we maintain that high β -diversity indicates that the intrinsic heterogeneity of the vegetation is high at the scale of a few metres, even without the influence of grazing. A likely explanation for the high β -diversity between quadrats (i.e. within enclosures) is the patchy distribution of soil resources. Analyses of soil samples (not shown) revealed very high spatial variability in soil properties within the experimental plots (Golodets, Kigel & Sternberg 2010). Patchiness of soil resources may increase β -diversity by limiting species to specific soil patches (as explained earlier), thus increasing the heterogeneity of species composition between samples.

We hypothesised that both species richness and reciprocal Simpson diversity would decrease because of the reduced grazing pressure and protection from grazing. As predicted, reciprocal Simpson diversity responded strongly to protection from grazing – the initial measurements showed that long-term protected vegetation had significantly lower diversity, and within the third year after construction of the grazing enclosures, reciprocal Simpson diversity dropped to the levels measured in the long-term protected plots. The reduction in both α - and β - components of reciprocal Simpson diversity, in response to protection from grazing, supports the notion that grazing effects on the vegetation are expressed at both the small, local scale (quadrat) and at the larger (landscape) scale.

Reciprocal Simpson diversity is a measure of dominance in the vegetation. Its strong response to changing grazing conditions reflects the fact that the studied grassland community is characterised by strong dominance of *H. bulbosum*, a perennial hemicryptophyte (Sternberg *et al.* 2000; Golodets, Kigel & Sternberg 2010). In the grazed plots at the study site, the relative abundance of *H. bulbosum* is between two- and three-fold lower than in the long-term protected plots (Table 4), and short annual grasses and thistles are more prominent (Noy-Meir, Gutman & Kaplan 1989; Sternberg *et al.* 2000; Golodets, Kigel & Sternberg 2010). After establishment of the enclosures, relative abundance of *H. bulbosum* recovered rapidly to the levels recorded in long-term protected vegetation, at least in the moderate grazing treatment (Table 4). Thus competitive exclusion, driven by the recovery of *H. bulbosum* with protection from grazing, probably drives the reduction in the α component of reciprocal Simpson diversity during short-term succession after protection from grazing. Such rapid recovery of the vegetation composition is common in Mediterranean grasslands that have evolved under a long history of grazing (Perevolotsky & Seligman 1998; Sternberg *et al.* 2000) and highlights the high resilience of this ecosystem to perturbations.

Table 4. Average per cent biomass (mean \pm SE) of *Hordeum bulbosum* during secondary succession in enclosures (CH, CM), compared with long-term protected plots (LP)

Treatment	2003	2004	2005
CH	7.57 \pm 1.86 ^c	11.9 \pm 2.95 ^{bc}	30.5 \pm 5.29 ^{ab}
CM	12.9 \pm 3.14 ^{bc}	21.4 \pm 4.11 ^{bc}	47.7 \pm 6.12 ^a
LP	41.0 \pm 4.45 ^a	47.6 \pm 5.05 ^a	47.1 \pm 4.97 ^a

CH, continuous heavy; CM, continuous moderate. Different superscript letters indicate significantly different values ($\alpha = 0.05$) according to repeated-measures ANOVA. Adapted from Golodets, Kigel & Sternberg (2010).

The reduction in reciprocal Simpson diversity after both long-term and short-term protection from grazing indicates that grazing increases between-habitat heterogeneity in the vegetation structure (Klimek *et al.* 2008). Besides the main impact of large herbivores on vegetation heterogeneity because of phytomass removal, grazing also influences the spatial patterning of soil processes (Afzal & Adams 1992; Knapp *et al.* 1999; Augustine & Frank 2001), and these often occur at the fine scale. One of the main mechanisms of herbivore impact on the heterogeneity of soil resources is via excreta, primarily urine (Afzal & Adams 1992). In grazed grasslands, Augustine & Frank (2001) found that large herbivore grazers increased fine-grain heterogeneity in soil N and N-mineralisation potential at small scales because of localised influence of cattle excreta, compared with larger-scale patchiness associated with phytomass removal by grazing and topographical variability. Previous research has shown that the impact of excreta on patchiness of soil resources is a function of grazing intensity (Afzal & Adams 1992; Augustine & Frank 2001). Afzal & Adams (1992) observed that at a grazing intensity of 3 cattle ha⁻¹ c. 27% of the grazed pasture during the grazing period was influenced by urine, with a significant effect on patchiness of soil N resources. In contrast, Augustine & Frank (2001) estimated that 2.5% of the grazed range in the Yellowstone park was influenced by urine, with a grazing density of 0.17–2.5 elk ha⁻¹, and there was no observed effect on heterogeneity of soil N. Based on these estimates, we can suppose that the grazing intensity of 0.55–1.1 cattle ha⁻¹ at Karei Deshe would result in c. 5–10% of the grazed areas being directly affected by urine. If we account for the fact that the cows tend to concentrate in the more level parts of the paddocks (such as where our experiment was conducted), then the area influenced by cattle urine may be closer to 15%, which may increase soil resource patchiness (in particular soil N) sufficiently to cause an increase in reciprocal Simpson diversity.

Between exclosures, grazing may accentuate the patchiness in species composition attributable to the presence of rocks in the landscape. The research site is characterised by variable rockiness, ranging from 0% to 50% cover, although the current study was conducted only in areas with a low percentage of rock cover, to standardise this effect between treatments. Nevertheless, under grazing, seeds that accumulate under the protection of rocks become sources for re-colonisation of overgrazed microsites (Milchunas & Noy-Meir 2002), thus increasing heterogeneity of vegetation composition. In the absence of grazer activity, the vegetation is more homogeneous, and these rock 'refuges' are functionally less important.

In contrast to the clear response of reciprocal Simpson diversity, species richness was not affected by protection from grazing. Initially, species richness (diversity at $q = 0$) was uniform across all treatments at all spatial scales. We had expected that high dominance of *H. bulbosum* in the long-term protected plots would reduce species richness at the local scale (i.e. α -diversity) because of competition for light and space (Perevolotsky & Seligman 1998). However, Noy-Meir (1988) showed that in this grassland ecosystem, there are many small-scale disturbances by small mammals (voles, wild boars etc.) and

insects (e.g. ants) in long-term ungrazed vegetation, which create gaps in the canopy that could maintain species richness even in the absence of large herbivores. In addition, standing dead material, which tends to accumulate in the absence of herbivores, is a significant source of soil nutrients and may be a potential contributor to small-scale soil patchiness in ungrazed vegetation (Augustine & Frank 2001). The uniformity of β -diversity of species richness across treatments is probably because of the large overlap in the species pool between the different treatments, coupled with the fact that most of the gap-colonising species in the long-term protected plots are unique to this treatment and compensate for the species lost because of competitive displacement by *H. bulbosum* (Golodets, Kigel & Sternberg 2010).

We have shown that grazing in the studied Mediterranean grassland primarily leads to changes in dominance, rather than significant turnover of species, as is usually the case in grasslands grazed by large ungulates (Hartnett, Hickman & Walter 1996; Márquez *et al.* 2002; Martin & Wilsey 2006). This relative stability of vegetation composition at Karei Deshe, and in other Eastern Mediterranean sites under grazing, is most probably because of the long history of grazing in the region (Perevolotsky & Seligman 1998; Sternberg *et al.* 2000). This was highlighted by the strong effect of grazing on β -diversity of reciprocal Simpson diversity, which maintained the significant partitioning between α - and β -diversity at the quadrat level for the first 2 years after protection from grazing. However, grazing also contributes to heterogeneity in the vegetation at higher spatial scales, as evidenced by the strong decrease in the β -component of reciprocal Simpson diversity at the exclosure level with protection from grazing, which cancelled out the significant partitioning between α - and β -diversity at this level.

Much research on species diversity has considered only species richness as a measure of diversity, without considering changes in the relative abundances of species (e.g. Collins *et al.* 1998; Gabriel *et al.* 2006; Hendrickx *et al.* 2007). This approach can be misleading, especially considering the fact that human activities usually have a more profound effect on the relative abundances of species than on presence or absence of species (Hillebrand, Bennett & Cadotte 2008; Rundlöf, Bengtsson & Smith 2008). Indeed, ecologically meaningful differences between plant communities are usually related to differences in species frequencies, not in their presence and absence (Jost 2007). Sometimes, it is necessary to combine species richness with other indices of diversity to capture the full complexity of patterns in diversity and their underlying mechanisms (Wilsey *et al.* 2005; González-Megías, Gómez & Sánchez-Piñero 2007). Previous research concerning grazing effects on species richness and diversity has found that species richness was generally not affected by grazing conditions (Márquez *et al.* 2002; Peco, Sánchez & Azcárate 2006; Alrababah *et al.* 2007), while parameters that accounted for changes in dominance (species composition, diversity and cover) were significantly affected (Márquez *et al.* 2002; Alrababah *et al.* 2007), and these parameters were significantly related to ecosystem function (Wilsey & Potvin 2000).

The results of this study emphasise the importance of grazing for maintaining diversity at both the local scale and across landscapes (Hartnett, Hickman & Walter 1996; Collins *et al.* 1998; Sternberg *et al.* 2000; Klimek *et al.* 2008), especially in Mediterranean ecosystems with a long history of grazing (Perevolotsky & Seligman 1998; Verdú, Crespo & Galante 2000) thus maintaining a variety of habitats and enabling high levels of species richness and diversity for conservation purposes (Verdú, Crespo & Galante 2000). This is an especially important concern worldwide, as the area covered by natural ecosystems continues to dwindle, necessitating management of grasslands for multiple functions, e.g. animal production, resource protection, and wildlife enhancement (Sanderson *et al.* 2004).

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