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Intensive grazing opens spider assemblage to invasion by disturbance-tolerant species

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Abstract. Grazing is an established conservation tool for maintaining grassland habitats and under some circumstances may enrich arthropod assemblages. However, even if enrichment occurs, it is not granted that conservation value signified by rare and specialist species will also increase. To assess how some preset levels of grazing suit conservation aims, we studied spider assemblages of ungrazed, sparsely grazed and intensively grazed areas of a pasture in Hungary for three years by pitfall trapping and suction sampling. At ground level there was no significant difference among grazing areas, while at higher strata increasing grazing intensity negatively affected number of individuals and species. C-score analysis indicated equally neutral community assembly in all three grazing areas. All statistical methods that took into account species identity indicated virtually no difference between the spider assemblages of the sparsely grazed and ungrazed areas; however, there was a marked difference between these and the intensively grazed area. Spider species in the intensive grazing area had significantly lower affinity but wider tolerance for habitat naturalness, preferred more open habitats and had a lower rarity status. In the intensive grazing area a number of disturbance-tolerant species, among them agrobionts, were present, whereas the exclusion of rare or specialist species in the intensively grazed area occurred infrequently. The primary effect seen at the intensive grazing area was the opening of the spider assemblage to disturbance-tolerant species, while species richness was likely maintained by neighboring source populations. Overall, we experienced a marked decrease in the naturalness status of the spider assemblage in the intensive grazing area.

Keywords: Species richness, neutral community, rare species, grassland, agrobiont, trait-based assessment, Araneae

Grazing is a naturally occurring ecosystem process, which can be part of agricultural production, and recently it has also become a management tool for nature conservation. Its impact on the vegetation has been widely studied (e.g., Belsky 1992; Adler et al. 2001), in both vertebrates (Baldi et al. 2005) and invertebrates, including spiders (Gibson et al. 1992; Bonte et al. 2000; Horvath et al. 2009). Grazing can be of many kinds and may affect ecosystems in variable ways. An increase in plant species diversity and spatial heterogeneity has been reported due to the preferential grazing of the dominant grasses and concomitant increases in subordinate species (Hartnett et al. 1996). Others report both increases and decreases in plant diversity attributable to grazing in different communities (Belsky 1992), which might be caused by the different scales of the studies (Kohyani et al. 2008). Spider communities of grazed habitats also show varied responses, which range from 'virtual extinction' (Thomas & Jepson 1997), to a moderate decrease in diversity (Abrous Kherbouche et al. 1997) and the preservation of rare and specialist species (Zulka et al. 1997). Recent Hungarian studies have indicated that grazing created relatively strong local changes in vegetation structure and height, which were more important in shaping spider communities than larger scale factors such as fragmentation or landscape neighborhood (Batary et al. 2008; Horvath et al. 2009). However, in other systems local grazing effects have been overridden by landscape scale factors (Harris et al. 2003).

The effect of grazing gains special importance if we consider it from a conservation point of view. Moderate grazing may fall into the category of intermediate disturbance (Connell 1979), which is known to produce high diversities at patch scale (Whittaker et al. 2001). Moderate grazing in interaction with succession may result in high diversity, because grazing prevents the climax stage, arresting succession at a stage when species diversity is high, as has been proven, for instance, in grasslands of the Carpathian Basin (Ruprecht 2005). The interaction between vegetation succession and grazing is also important at regional scales, where grazing is a major force that maintains grassland areas and prevents homogeneous afforestation, which would be the norm for the largest part of Central Europe. The pollen record suggests that domestic grazing has formed the landscape in Hungary since the Bronze Age (Chapman et al. 2009). As such, maintaining the "right level" of grazing should be a priority for any conservation strategy that aims to maintain biotopes integrated with traditional human activities.

To judge the effect of grazing is not simple. Even though in some situations grazing might contribute to the increase of species richness, that in itself does not guarantee an increase in conservation value; for example, if a natural habitat is disturbed, then the first occurrence of a weed species will result in an increase in richness. Therefore, it is important to judge the effect of grazing on invertebrate (and other) assemblages by assessing how species interactions are affected and by weighting changes with species traits.

Periodic or constant disturbances may disrupt species interactions and may make the coexistence of a wider range of species possible, but may also increase the probability of species invasions (Hobbs & Huenneke 1992). Under grazing pressure assemblages will be more determined by their suitability to the habitat than by their competitive potential. In other words, grazing, for instance by physical perturbation and by creating spatio-temporal patchiness, may prevent species interactions (e.g., competition, intra-guild predation) from playing a major role in the formation of assemblages. The absence of such interactions and the prevalence of stochastic processes (immigration, birth, death) in community assembly are emphasised by neutral community models. Whether grazing shifts spider communities toward neutrality has not been studied so far.

Habitats with different grazing profiles/histories are likely to have assemblages with characteristic species representing different ecological traits and tolerances. It is known that stable natural habitats harbor less dispersive specialized species (Bell et al. 2001; Bonte et al. 2004a), while ephemeral habitats—both natural and human-created, e.g., arable fields—also have very specific, disturbance-tolerant species assemblages (Samu & Szinetár 2002). Species can be ranked with respect to their preference for stable versus disturbed habitats. Such ranking has been shown to be correlated with rarity (Samu et al. 2008) and can be used for the evaluation of conservation value, both of the habitat and the spider assemblage.

In the present study we evaluate spider assemblages at three areas of different grazing levels. 1) We consider general quantitative properties of spider assemblages in the grazing areas, including abundance and species richness. 2) We ask how species coexistence patterns are affected by grazing. We hypothesize that grazing weakens species interactions; therefore, under heavier grazing assemblages will be more neutral. 3) We investigate the concrete nature of assemblage changes in the different grazing areas. Which species, of which foraging strategies, and of which kinds of ecological tolerances can adapt best to the varied grazing levels? And, would assemblages found represent different conservation values?

METHODS

Study area.—The study area was a dry pasture (47° 26′E, 18° 29′N) near Vértesboglár, Hungary (Fig. 1). The area, at an average elevation of 200 m a.s.l., lies at the feet of the Vértes Mountains, a low dolomitic range. This area is at the meeting point of closed forests and steep rock steppe habitats of the Vértes Mountains and wetland areas of the Zámolyi Basin. The original vegetation was forest-steppe mosaic, but it has been used for pastoral farming for hundreds of years. Botanically it can be described as dry grassland of average plant diversity. In this system grazing is the primary factor that maintains the grassland. Without grazing the area would be reforested, and several protected grassland species would lose their habitat.

The pasture studied was 270 ha in area. Since June 2006 the pasture has been grazed by the traditional Hungarian sheep variety "rackajuh". Because of grazing, the grassland vegetation was more homogeneous than the natural grasslands of the mountain slopes. According to vegetation height and vertical stratification two main zones could be identified, which resulted from different grazing pressures affecting the respective areas.

To study the short-term effect of different levels of grazing, we studied spider assemblages in three areas of the pasture (Fig. 1) with different grazing levels. 1) Intensively grazed area. This area of the pasture was directly connected to the sheepfold. The average height of the vegetation was 3–4 cm. Due to their daily activity animals spent more time here; grazing pressure was therefore high. 2) Sparsely grazed area. Animals spent less time in this zone of the pasture and consequent grazing pressure was much lower than in the intensively grazed area. The average height of the vegetation was 5–6 cm. 3) Control, ungrazed area, where livestock were excluded by fencing surrounding a 0.13 ha area, located in the sparsely grazed zone. Fencing was established in 2006. The average height of the vegetation was 10 cm. Sampling locations in the sparsely and intensively grazed areas were ca. 500 m apart. Since each grazing area had only one continuous site, interspersed spatial replication was not possible. Each grazing level was represented by one area, where the samples were taken.

The study was carried out between 13 April 2007 and 28 September 2009 during the early summer and autumn samplings. In all three areas spiders were collected by pitfall trapping and suction sampling. Catches from one trap or one suction sampling transect during a campaign are referred to as subsamples. Subsamples from one area and given sampling campaign constituted a sample. Exact timing, trap opening times and number of subsamples per area are listed in Table 1.

For pitfall trapping we used plastic cups of 75 mm upper diameter, filled with 70% ethylene glycol as preservative and some detergent (Kádár & Samu 2006). We used "Vadóc" game repellent hung on strings above the pitfalls at ca. 60 cm height to prevent domestic and wild grazing animals from demolishing the traps. We also used a hand-held motorized suction sampler to collect spiders (Samu & Sárospataki 1995) during one sampling period (Table 1). The applied suction sampler collected from an area of 0.01 m^2. Ten such applications in a short transect, from a cumulative area of 0.1 m^2, comprised one subsample.

Data analysis.—Spiders were determined using available keys (e.g., Nentwig et al. 2010); nomenclature is according to Platnick (2010). Statistics regarding spider abundance were based on standardized catches: number of spider individuals caught in a subsample per unit sampling duration (one for suction samples; number of days a trap was open for pitfalls). Statistics requiring species level information were restricted to adult spiders, determined to species level.

Species characteristics were quantified in part from the catalogue by Buchar and Růžička (2002). Using the database of the catalogue we assigned ordinal values to species characters that could be ordered: 1) extent of distributional area, 2) preference for elevation, 3) preference for habitat naturalness, 4) preference for habitat humidity, 5) preference for light (habitat openness), 6) vulnerability status of the species and 7) frequency of occurrence. In the case of many species more than one value is listed for the four preference type characters (2–5) in the database, and some of these values were reported to be "typical" or "non-typical". To deal with this, we calculated the mean value of the character, which was either the single ordinal character value for the species, or the mean of the ordinal values in the list or, if typicality was indicated, we applied a typicality weight of 2× (for typical) or 0.5× (for non-typical) in the calculation of the mean. We also calculated the width of the preference-type characters, which was the difference between the largest and the smallest ordinal character values. As an additional species character we calculated Global Abundance Value (GAV), a species

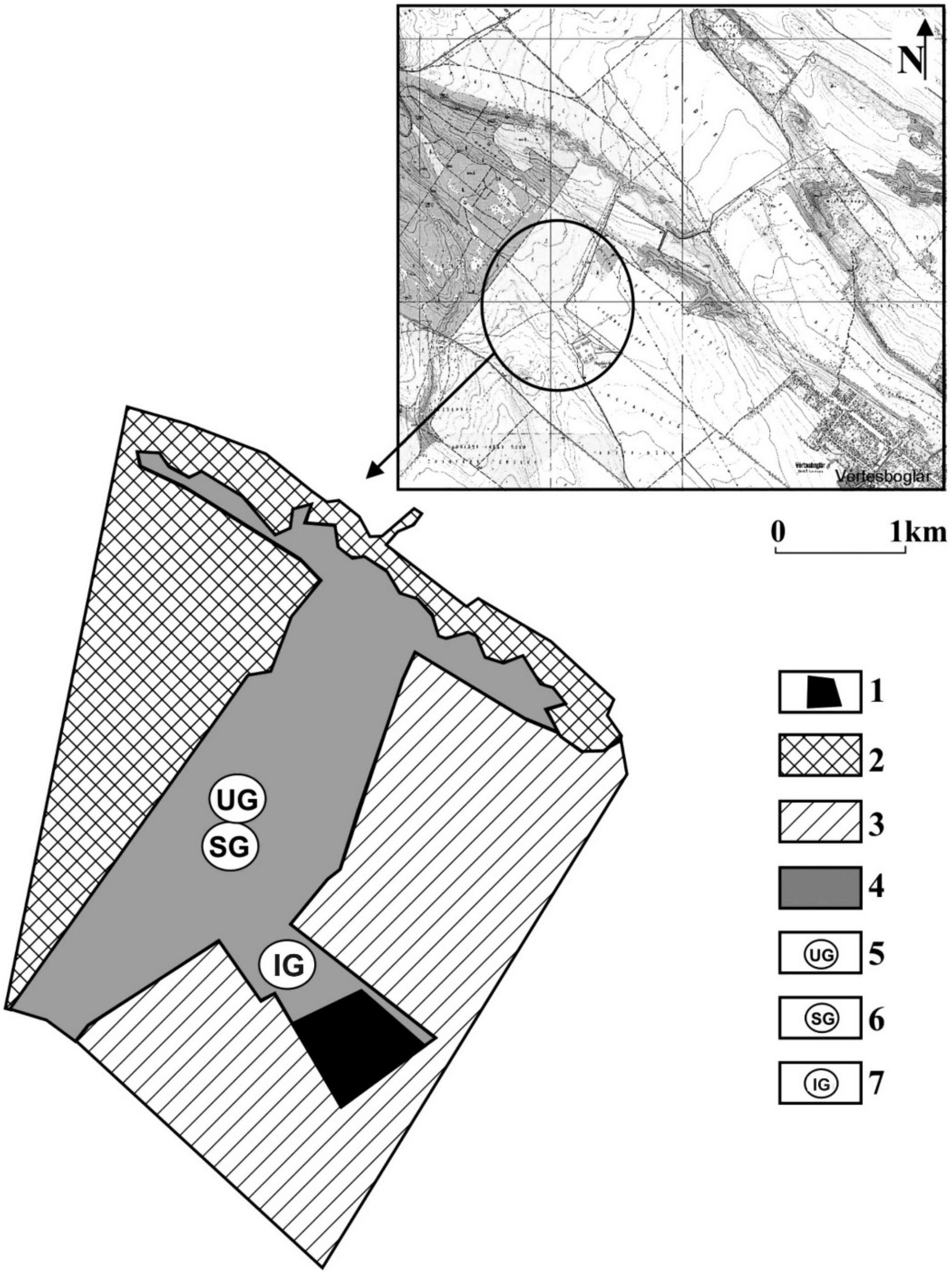

Figure 1.—Arrangement of grazing areas and sampling locations in the study pasture at Vértesboglár 2007–2009. 1, Farmyard and sheepfold; 2, Woodlands; 3, Arable land; 4, Pasture; 5, Ungrazed (= UG); 6, Sparsely grazed (= SG); 7, Intensively grazed (= IG) sampling areas.

Table 1.—Sampling efforts and timing at the three grazing areas. P = pitfall, S = Suction sample × number of subsamples.

Campaign date	Traps open (days)	Exclusion control	Sparsely grazed	Intensively grazed
23.05.2007	40	P × 5	P × 5	
28.09.2007	27	P × 5	P × 5	
08.06.2008	46	P × 5	P × 5	P × 10
21.10.2008	27	P × 5	P × 5	P × 5
06.06.2009	36	P × 5	P × 5	P × 5
28.09.2009		S × 10	S × 10	S × 10

abundance value which is an inverse measure of species rarity. It gives the proportion that individuals of a given species represent out of all individuals in a 'global' background database, which in this case was the Hungarian arachnological database. We included this value, because it has proven to be the best surrogate measure for conservation value in two case studies (Samu et al. 2008).

Following the literature (e.g., Gotelli 2000) we hypothesized that in assemblages structured by biotic interactions the presence of certain species will exclude the presence of others, generating recognizable coexistence patterns, while in neutral communities coexistence patterns generated by such interactions will be weaker or non-existent. We investigated the neutrality of species co-occurrence in the spider assemblages of the grazing areas using Stone and Roberts' C-score analysis (1990). C-score refers to the average number of "checkerboard units" (i.e., no co-occurrence situations) between all possible pairs of species. High C-score values indicate species segregation in a community. C-scores were calculated by samples ($n = 16$: see Table 1), considering subsamples as the units where co-occurrences were recorded. C-score analysis was executed by the program EcoSim 7.72 (Gotelli & Entsminger 2010), which constructs null models by simulation to calculate whether an observed C-score is significantly larger than can be expected by chance. In null-model construction the "sites (= subsamples) equiprobable" and "species fixed" options were used. We compared C-scores between samples using standardized effect sizes, the deviation of the observed C-score from the mean of simulated C-scores scaled to standard deviations, to make comparisons among different samples/assemblages. An effect size greater than 1.96 or less than -1.96 is statistically significant at $P = 0.05$ (Gotelli & Entsminger 2010).

Differences between catches and taxon numbers in the grazing areas were tested by the LME4 package in R (Bates et al. 2011) for generalized linear mixed models. We reached a final model after manual variable selection based on AIC, initially regarding year and subsample as random variables and grazing area as a fixed variable. Species characters were screened in a Canonical Correspondence Analysis (CCA). The similarity of assemblage structures was depicted by Nonmetric Multidimensional Scaling (NMS), and the significance of the differences in species composition between the revealed groupings was tested with Multi-Response Permutation Procedure (MRPP) (Mielke et al. 1976). Species that most characteristically represented the groups were shown by Indicator Species Analysis (ISA) (Dufrene & Legendre 1997). The four latter methods were applied using PC-ORD v. 5.31 (McCune & Mefford 2006).

RESULTS

During the study 1664 individuals were caught, of which 1159 were adults. Apart from the identifiable 63 species we could further identify 11 unique taxa (e.g., juveniles of genera where no adults were found); thus, the total number of taxa shown from the pasture was 74, over 10% of the species on the Hungarian check list (Samu & Szinetár 1999). See the Appendix for a complete list of catches by grazing areas.

Overall we found lower numbers of individuals and taxa where the intensity of grazing was higher (see Appendix). Considering pitfall trap catches, neither the total number of spiders caught (Fig. 2a) nor the number of spider taxa (Fig. 2c) differed significantly between the grazing areas. However, in suction samples both spider abundance and the number of taxa were significantly lower in the intensively grazed area than in the other areas (Figs. 2b–d, Table 2).

Considering species co-occurrences in the spider assemblages at the three grazing areas, we could detect neither species segregation, nor aggregation in the assemblage structures. None of the C-score analyses ($n = 16$) showed significant deviation from the fixed-equiprobable null model (Gotelli 2000), and effect sizes also indicated neutral community organization in all three grazing areas. Effect-sizes among grazing areas did not differ statistically (one-way ANOVA: $F_{2,13} = 1.22$, $P = 0.3$).

Although assemblages in the different grazing areas all proved to be neutral in terms of species co-occurrence, species compositions in the intensively grazed area were different from that of the sparsely-grazed or ungrazed areas in both years (Fig. 3, MRPP difference between the arising two groups [intensive vs. (sparse + control)] for 2008: $T = -7.374$, $P < 0.0001$; for 2009: $T = -8.489$, $P < 0.0001$). The ordination plot from the NMS analysis also reveals that, in the summer samples of both years, sparsely grazed subsamples and control subsamples did not separate as distinct groups (Fig. 3).

The other ordination method, CCA, made a grouping of the samples very similar to the NMS result. In the CCA plot, samples of the intensively grazed area were placed apart from the group of control and sparsely grazed samples (Fig. 4). The pairing of samples by study year is observable in the control + sparse grazing group, underlying that difference between 'sparse grazing' and 'control' was a mild effect compared to the effect of 'year'. The distinct separation of samples from the intensive grazing area, on the other hand, shows that intensive grazing creates a much stronger difference than yearly variation or sparse grazing. The CCA depicted samples in the species space. The ordination was not constrained as usual by a second matrix of environmental variables, but by the matrix of species characters. The separation of intensively grazed samples was related to light (habitat openness) preference and habitat naturalness preference of the species, as shown by the highest inter-set correlations; i.e., the correlations between species character variables and the ordination axes 1 and 2, weighted by the eigenvalues of those axes (naturalness mean: $r_1 = 0.417$, $r_2 = 0.649$; light preference mean: $r_1 = -0.745$, $r_2 = 0.005$).

Apart from species preference for habitat naturalness and openness as chief main factors, CCA also identified that abundance, width of preference for naturalness, and humidity are also important characters along which spider assemblages of different grazing areas differ from each other. We have tested for the significance of all these characters and found highly significant differences between grazing areas for all of them (Fig. 5). A post-hoc test indicated that the intensively grazed area's spider assemblage was the one that differed from the other two for all characters (Fig. 5).

Finally we wanted to identify which families and species are mostly responsible for the separation of the assemblages in the intensively grazed vs. ungrazed or sparsely grazed areas.

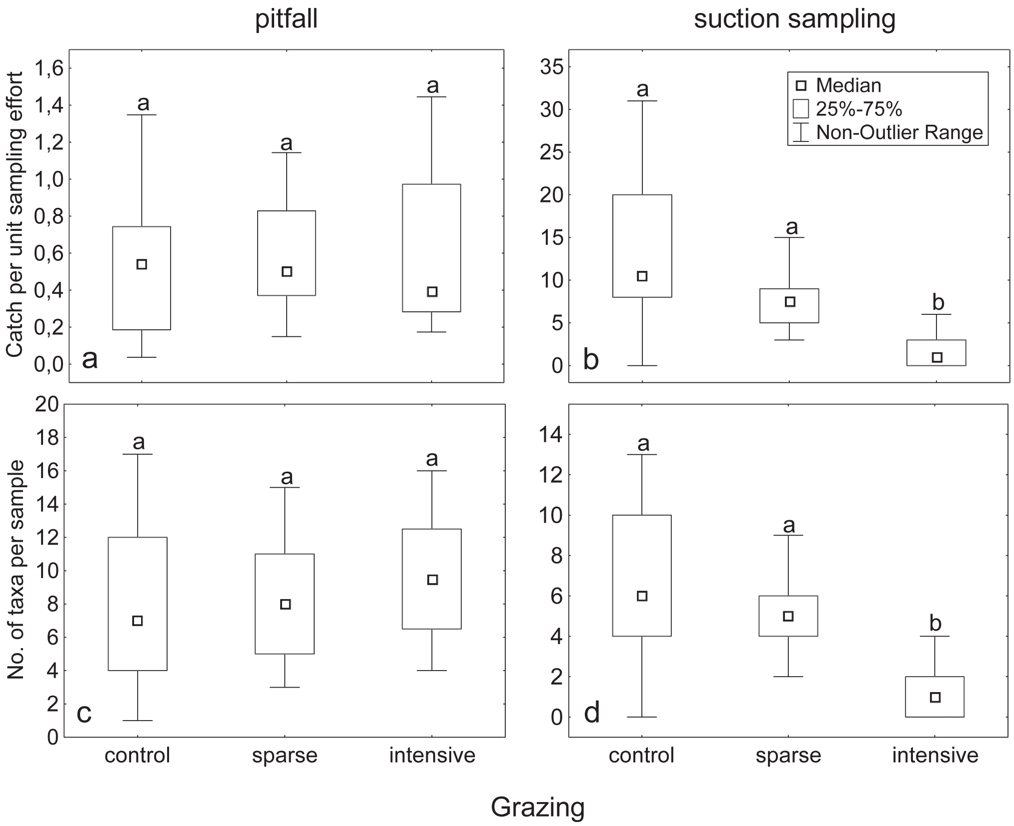

Figure 2.—The effect of sampling method and grazing intensity on number of individuals caught per unit sampling effort (a, b), and on the number of spider taxa caught per sample (b, c). Groups denoted with the same letter are not significantly different at the $P = 0.05$ level under Tukey HSD test.

Considering differences at the family level, Hahnidae had preference for the less-grazed or ungrazed areas, while Linyphiidae and Thomisidae had significant preference for the intensive grazing area (Table 3). An ISA was conducted at the species level to reveal the affinity of species to the grazing areas (Table 4). Over twice as many species were significant indicators of the intensive grazing area than of the less-grazed or ungrazed areas. In the Lycosidae, for instance, the larger *Alopecosa* species had a clear preference for the less grazed areas, while many of the smaller lycosids (*Pardosa* and *Xerolycosa* spp.) were more numerous in the intensively grazed areas. Certain 'disturbance tolerant' species [e.g., *Ostearius melanopygius* (O.P-Cambridge 1879)] and a number of 'agrobiont species' that are strongly associated with arable fields (Samu & Szinetár 2002) were among the indicators of the intensive grazing area (see species marked in Table 4).

Table 2.—Result of Generalized Linear Mixed Models of spider catches and taxon numbers. The models were executed separately by sampling methods, grazing was ordinal fixed variable, sampling date (in case of pitfalls) and subsample were entered as random variables. Poisson error structure and log link function was used. For the overall effect of grazing χ^2 statistics is reported.

Variable	Method	d.f.	χ^2	P
Taxon number	suction	2	13.37	0.0013
Catch	suction	2	17.40	0.0002
Taxon number	pitfall	2	0.93	0.629
Catch	pitfall	2	0.72	0.697

DISCUSSION

Our survey found that spider assemblages in the ungrazed and sparsely grazed areas had similar spider abundance and species richness, while these measures of spider assemblages were lower in the intensively grazed part of the pasture. Since grazing livestock remove biomass from pasture ecosystems, they can produce a negative cascading effect for arthropod populations along the entire food web (Hobbs 1996; Boyer et al. 2003). Grazing also removes microhabitats, with similar negative effects (e.g., Hutchinson & King 1980). Both these processes are likely to result in lower spider density, and species richness is also likely to follow this pattern of spider abundance (Bell 2000).

In the present experiment two methods were used: suction sampling is more geared toward species living in higher strata of the grass; pitfall trapping more toward species at the ground surface. Since suction sampling catches spiders with higher efficiency from the higher strata in the grass, if the volume of this stratum becomes smaller due to grazing, a decrease in catches can be expected (Greenstone 1984). Pitfall catches, unlike suction samples, showed no significant difference between the grazing areas. Grazing means not only physical disturbance but also altered trophic relationships (Meyer & Reinke 1996). In pasture soil fauna, the subsidy from the manure of grazing animals might compensate for reduced higher strata productivity (Rypstra & Marshall 2005); hence, there is a likely interaction between disturbance and productivity (Bonte et al. 2004b; Svensson et al. 2010). Thus, in an indirect way, differences between the pitfall trap and suction

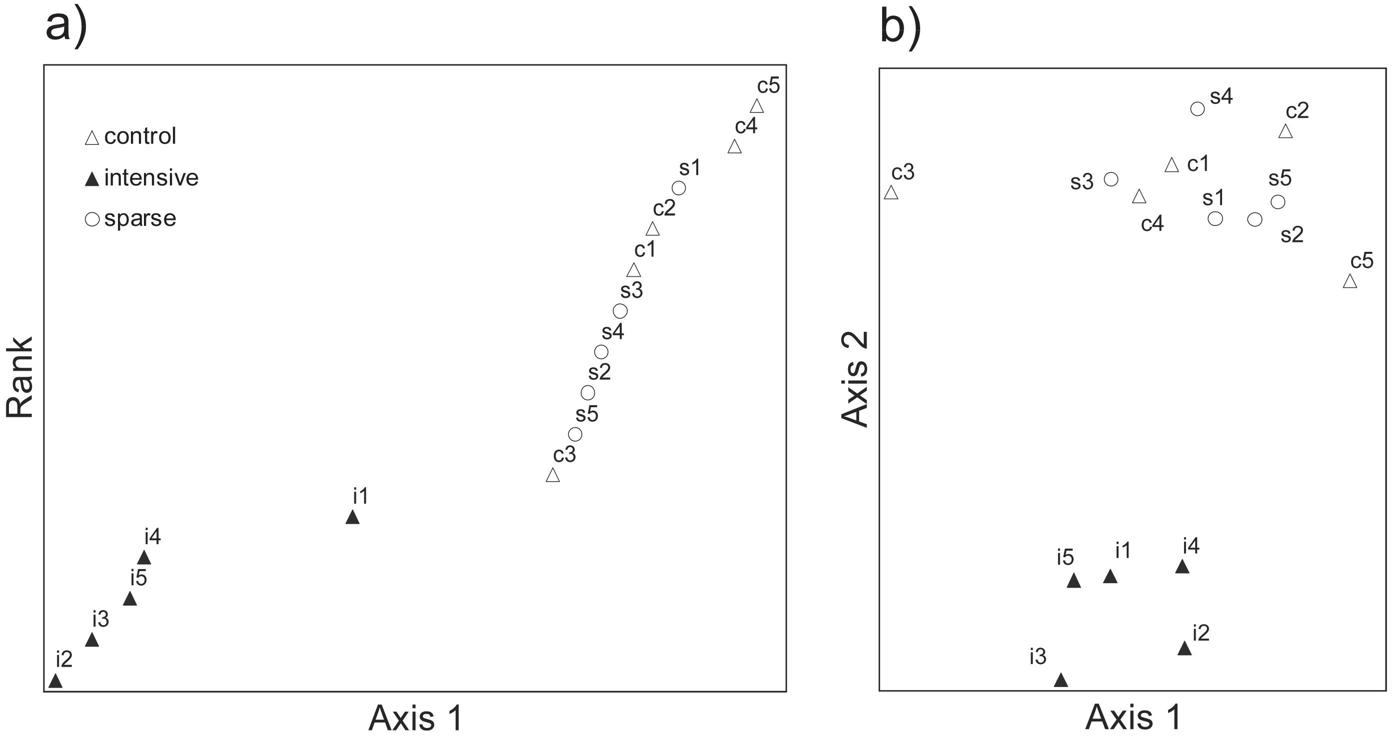

Figure 3.—NMS plots of the spider assemblages from pitfall trap catches in the three grazing areas; note how control grazing points envelop sparse grazing points in both plots. Analyses were done by PC-ORD v. 5.31 with NMS autopilot "thorough" option, Bray-Curtis distance measure. a) 2008 summer (from intensive grazing area only pitfalls 1–5): final stress $S = 24.63$ (one-dimensional solution is the best), Monte Carlo probability of obtaining smaller stress $P = 0.008$; b) 2009 summer: $S = 10.91$ (two-dimensional solution is the best), $P = 0.004$.

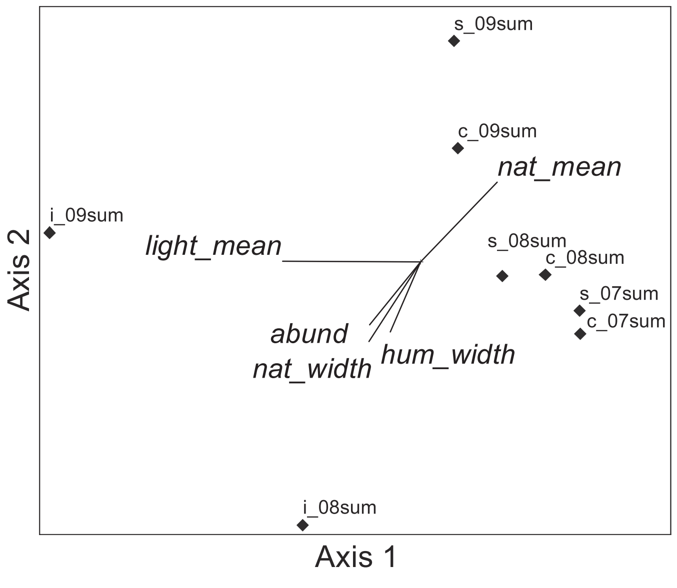

Figure 4.—Canonical Correspondence Analysis plot of yearly pitfall trap samples during the summer trapping period in the three grazing areas, constrained by a second matrix of species characteristics. See text for the explanation of how species character variables were derived. Abbreviations: abund = abundance (GAV), nat = naturalness, sum = summer; 0x = year, c = control, s = sparse grazing, i = intensive grazing. Eigenvalue $\lambda_{axis1} = 0.406$, $P = 0.017$; $\lambda_{axis2} = 0.081$; Samples-species characters correlation $r_{axis1} = 0.813$, $P = 0.025$; $r_{axis2} = 0.501$.

sampler catches underline the importance of vegetation height/volume as a predictor of species richness and abundance (Kruess & Tscharntke 2002; Schwab et al. 2002), and show that different process might act in different strata.

Little is known about how disturbances affect species interactions and assembly; specifically, the effect of grazing on invertebrate species co-occurrence is virtually unknown. Communities may show non-random species co-occurrence patterns as a result of competitive interactions (Ulrich & Gotelli 2007), but in spiders such interactions can seldom be classified as exploitative competition (Wise 1993). More often they take the form of direct interactions, such as intraguild predation and cannibalism (Samu et al. 1999; Wise 2006). Recently there have been a few studies that indicate the disruption of non-random community structure in invertebrate groups by disturbances other than grazing, such as fire (Sanders et al. 2007; Pitzalis et al. 2010) or tourism (Ulrich et al. 2010). By analogy, we expected that with stronger grazing more neutral co-occurrence patterns would emerge. However, C-score analysis suggested no deviation from neutral species assembly in any of the grazing areas. We suggest that in the grassland systems studied, neutral communities and fairly species-rich assemblages are the norm; while climax, low diversity, highly structured spider assemblages may be non-existent, in part because some level of disturbance (e.g., grazing by wild animals) occurs naturally. In such neutral communities fine-tuned habitat filtering might be an important process; thus, differences should be sought more in the actual composition of the assemblage.

Some spiders have good dispersal capabilities because of ballooning; therefore, they can track down habitat changes

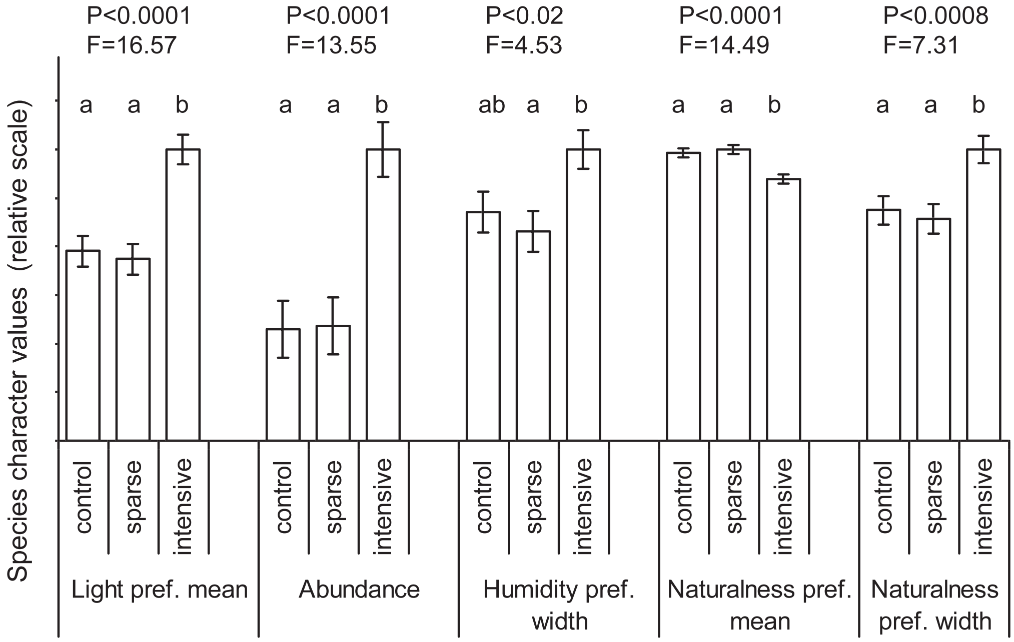

Figure 5.—Species mean character values per pitfall trap (subsample) by grazing areas in the summer samples. One-way ANOVA and Tukey HSD test were performed separately for each character. The effect of year as random factor was originally included, but left out from final models, because in all cases it explained $< 1\%$ of variance. Different letters indicate a significant difference by Tukey HSD test at the $P = 0.05$ level. For plotting, each character was relativized by the maximum mean value.

fairly rapidly. Their assemblages, for instance, can recover rather quickly after a major disturbance like fire (e.g., Spuogis et al. 2005; Samu et al. 2010). Thus, after one year of grazing exclusion we could already expect – and indeed we found – a response from the spider assemblage. However, one of the main findings of the present study was that this qualitative difference (grazing vs. no grazing) was relatively small compared to the quantitative difference we found between the sparsely and intensively grazed areas. Comparing the spider assemblage in the intensively grazed area to the less-grazed or ungrazed areas, we found a striking difference in assemblage structure. By classifying spider species according to their ecological traits, it turned out that less-grazed or ungrazed areas had significantly more species, with a preference for natural habitats. By contrast, in the intensively grazed areas species that also attained high abundances elsewhere in Hungary prevailed, and we could also show that these species generally have wider habitat tolerances (in terms of naturalness and humidity) and have higher preferences for open areas.

Table 3.—Difference between standardized catches of families in the pitfall trap catches. A family was included in the analysis if more than 30 individuals were caught in total. Mean of percentage differences in catches at sample dates are given between the control + sparse grazing vs. intensively grazed areas, taking the former as the basis. Difference between catches by families was tested with Generalized Linear Mixed Models, after model selection including the fixed effect of 'grazing', 'sampling date' and 'subsample' as random variables and accounting for overdispersion. Poisson error structure and log link function was used. For the effect of intensive grazing vs. control + sparse grazing. *z* statistics is reported. Note that the Bonferroni-corrected threshold is $P = 0.0055$.

Family	% difference	*z*	*P*
Dictynidae	−14.3	−0.58	0.560
Gnaphosidae	95.3	1.84	0.066
Hahniidae	−83.6	−7.06	0.0001
Linyphiidae	447.2	4.58	0.0001
Liocranidae	8.8	−1.67	0.095
Lycosidae	37.6	−0.57	0.568
Philodromidae	195.5	0.63	0.529
Salticidae	−78.3	−2.43	0.015
Thomisidae	224.7	3.92	0.0001

We note that trait based approaches – because they are functional – have a much better explanatory power in distinguishing various ecological situations than bulk community measures such as taxon richness. Trait based statistics give more insights into how a community reacts to disturbance (e.g., flooding disturbance: Lambeets et al. 2008; post-fire responses: Langlands et al. 2011). Better insights on changes in assemblage structure are gained by using species' ecological characteristics, even at local scales and with few spatial replicates. The difficulty lies in the availability of good background datasets about specific ecological characteristics. Spiders are good candidates to become a successful indicator group, because databases develop rapidly (Hänggi et al. 1995; Buchar & Růžička 2002; Nentwig et al. 2010). On such bases spiders could reliably indicate conservation value for habitats such as peat bogs (Scott et al. 2006) and grasslands (Samu et al. 2008).

Although species character values gave mean responses broken down by specific ecological traits, family distributions and ISA revealed the families and species that responded to differences in grazing regimes. At a family level, web-building spiders and spider families that typically live on foliage of the grassland vegetation were affected severely by intensive

Table 4.—Results of Indicator Species Analysis comparing the grazing levels 'intensive grazing' vs. 'no or sparse grazing'. IV = Indicator Value, IVRnd = mean of IVs obtained by 4999 random permutations, STD(IVRnd) = standard error of IVRnd, P = probability of obtaining a higher than observed IV in the permutations (all species with $P < 0.1$ are listed), agrobiont status (constant dominance in arable fields) of species is given according to Samu and Szinetár (2002). Authorities for species names are found in the appendix.

Species	IV	IVRnd	STD(IVRnd)	P	Agrobiont
No or sparse grazing					
Hahnia nava	62.3	34.0	5.46	0.0004	
Drassyllus pumilus	44.9	25.1	5.22	0.004	
Alopecosa cuneata	28.8	17.8	4.65	0.0298	
Phrurolithus pullatus	22.4	12.9	4.20	0.0438	
Intensive grazing					
Haplodrassus signifer	52.6	15.7	4.57	0.0002	
Pardosa agrestis	43.5	11.9	3.98	0.0002	yes
Pardosa palustris	34.7	10.5	3.91	0.0002	
Xerolycosa miniata	35.0	9.4	3.58	0.0002	
Trichoncus affinis	25.0	7.4	2.94	0.0008	
Xysticus kochi	49.5	23.6	5.19	0.0012	yes
Ozyptila scabricula	31.3	12.1	4.15	0.0018	
Ozyptila claveata	24.5	11.9	4.04	0.0162	
Haplodrassus dalmatensis	15.0	5.1	2.58	0.02	
Drassyllus praeficus	16.9	10.1	3.66	0.046	
Enoplognatha thoracica	10.0	4.3	1.69	0.0796	
Ostearius melanopygius	10.0	4.4	1.74	0.086	
Meioneta rurestris	15.3	9.0	3.67	0.096	yes

grazing, which is in line with changes found in other studies (Churchill & Ludwig 2004; Horvath et al. 2009). Analyzing the species compositions showed that spiders indicate, not only in relative but also in absolute terms, a very good naturalness state of the less-grazed or ungrazed areas. Sparse grazing seems to halt succession at a favorable state, while the disturbance remains minimal for the spider assemblage. During the three years' study, considering the whole pasture, we found many rare and/or specialist species that are representative of good quality dry grasslands. Among these *Chalcoscirtus brevicymbialis* Wunderlich 1980, new for the Hungarian fauna (Samu & Szinetár 1999), occurs from Germany to Kazakhstan in natural xerothermic rock steppes (Buchar & Růžička 2002; Nentwig et al. 2010). Two other species *Panamomops inconspicuus* (Miller et Valesova 1964) and *Ipa terrenus* (L. Koch 1879), also new for Hungary, are mentioned as rare by Buchar and Růžička (2002). Maybe because of the sporadic occurrence of the rarer species, these species could not become significant indicator species of the less-grazed or ungrazed areas. Although many rare species appeared sporadically in our catches, there were statistically more rare species in the less-grazed or ungrazed areas than in the intensively grazed area.

At the intensively grazed area some of the well-known Central European agrobiont species [*Pardosa agrestis* (Westring 1861), *Xysticus kochi* Thorell 1872, *Meioneta rurestris* (C. L. Koch 1836)] were indicators. The indicator status of *Ostearius melanopygius* (O. P.-Cambridge 1879), a typical cosmopolitan species for disturbed habitats, is also notable, occurring for instance in intensive pastures of New Zealand (Topping & Lövei 1997; Szymkowiak & Woźny 1998).

Both the synthetic measures (richness, abundance) of spider assemblages and concrete species compositions suggested that the sparse grazing area did not differ from the ungrazed area, and it was the intensive grazing that significantly altered the spider assemblage. The neutrality of spider assemblages also emphasized the habitat filtering process; that is, suitability (ecological traits) determined the presence or absence of species. As opposed to no grazing or sparse grazing, intensive grazing opened up spider assemblages for invasion by species with traits that represented various aspects of disturbance tolerance, the appearance of agrobiont species being an example. Complete exclusion of species sensitive to disturbance occurred to a much smaller extent, possibly because of reestablishments from the nearby non- intensively grazed area. Thus, we can conclude that sparse grazing allowed the persistence of rare and otherwise naturalness indicating species, while intensive grazing shifted the species spectrum toward common and disturbance-tolerant species. From a conservation point of view, the utility of grazing depends on its intensity, and it can be either beneficial or adverse for the spider fauna.

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Appendix.—Complete species catches of spiders in the three grazing areas at the Vértesboglár pasture, Hungary.

Species	Control	Sparse	Intensive
Agroeca lusatica (L. Koch 1875)	1		
Alopecosa accentuata (Latreille 1817)	1	1	
Alopecosa cuneata (Clerck 1757)	41	39	2
Alopecosa mariae (Dahl 1908)	5	6	4
Alopecosa pulverulenta (Clerck 1757)	6	5	1
Alopecosa sp.	14	10	2
Altella sp.	4	1	
Araeoncus humilis (Blackwall 1841)			1
Araneidae sp.		1	
Argenna patula (Simon 1874)	8	1	3
Argenna sp.	52	7	1
Argenna subnigra (O. P.-Cambridge 1861)	7	11	11
Aulonia albimana (Walckenaer 1805)	8	2	4
Cercidia sp.	1	1	
Chalcoscirtus brevicymbialis Wunderlich 1980	1	3	
Chalcoscirtus sp.	1	2	
Cheiracanthium sp.		3	
Clubiona diversa O. P.-Cambridge 1862	3	2	
Clubiona sp.	4	1	
Coelotes sp.	1		
Crustulina sp.		1	
Drassyllus praeficus (L. Koch 1866)	1	3	9
Drassyllus pumilus (C. L. Koch 1839)	25	47	4
Drassyllus pusillus (C. L. Koch 1833)	2	1	2
Dysdera erythrina (Walckenaer 1802)		1	
Enoplognatha thoracica (Hahn 1833)			2
Euophrys frontalis (Walckenaer 1802)	7	4	
Euophrys sp.	13	5	
Gnaphosidae sp.	31	28	42
Gongylidiellum murcidum Simon 1884			1
Hahnia nava (Blackwall 1841)	156	122	9
Hahnia sp.	3	9	
Haplodrassus dalmatensis (L. Koch 1866)			3
Haplodrassus signifer (C. L. Koch 1839)	3		27
Haplodrassus sp.			1
Heliophanus sp.	6	13	2
Hypsosinga sp.	5	4	7
Ipa terrenus (L. Koch 1879)			1
Linyphiidae sp.	21	7	10
Lycosidae sp.	32	46	16
Meioneta rurestris (C. L. Koch 1836)	3	3	5
Micaria dives (Lucas 1846)	3	4	2
Nemesia pannonica (Herman 1879)	3	1	
Oedothorax apicatus (Blackwall 1850)			1
Ostearius melanopygius (O. P.-Cambridge 1879)			2
Ozyptila claveata (Walckenaer 1837)	4	1	9
Ozyptila pullata (Thorell 1875)	3	4	3
Ozyptila scabricula (Westring 1851)	2	5	24
Ozyptila sp.	1	7	1
Pachygnatha sp.			1
Panamomops inconspicuus (Miller & Valesova 1964)		2	
Pardosa agrestis (Westring 1861)		1	12
Pardosa alacris (C. L. Koch 1833)	1	5	1
Pardosa bifasciata (C. L. Koch 1834)	3		
Pardosa hortensis (Thorell 1872)		1	
Pardosa palustris (Linnaeus 1758)	1		45
Pardosa prativaga (L. Koch 1870)	1		
Pardosa sp.		1	2
Phlegra fasciata (Hahn 1826)	2	1	
Phlegra sp.		2	
Phrurolithus festivus (C. L. Koch 1835)	8	8	3
Phrurolithus pullatus Kulczynski 1897	18	13	

Appendix—Continued.

Species	Control	Sparse	Intensive
Phrurolithus sp.	3	8	5
Phrurolithus szilyi Herman 1879			1
Pisaura mirabilis (Clerck 1757)	2	1	
Robertus arundineti (O. P.-Cambridge 1871)			1
Salticidae sp.	4	2	
Sintula spiniger (Balogh 1935)	1		
Stemonyphantes lineatus (Linnaeus 1758)	1	3	
Synageles sp.		8	
Talavera aequipes (O. P.-Cambridge 1871)	2	5	1
Tapinocyboides pygmaeus (Menge 1869)		1	
Tegenaria sp.			1
Thanatus arenarius L. Koch 1872	4	11	7
Thanatus sp.	8	7	8
Theridiidae sp.	7	5	2
Thomisus onustus Walckenaer 1806	1	1	
Tibellus sp.	1	1	
Trachyzelotes pedestris (C. L. Koch 1837)	4		1
Trichoncus affinis Kulczynski 1894			15
Trichopterna cito (O. P.-Cambridge 1872)			1
Trochosa robusta (Simon 1876)			1
Trochosa terricola Thorell 1856	1		
Urocoras longispinus (Kulczynski 1897)	4	2	3
Xerolycosa miniata (C. L. Koch 1834)			15
Xysticus acerbus Thorell 1872	1		
Xysticus audax (Schrank 1803)		1	
Xysticus cristatus (Clerck 1757)			1
Xysticus kochi Thorell 1872	4	10	27
Xysticus sp.	1	1	4
Xysticus striatipes L. Koch 1870	4	15	
Zelotes electus (C. L. Koch 1839)	13	5	13
Zelotes gracilis Canestrini 1868	37	35	32
Zelotes longipes (L. Koch 1866)	25	16	15
Zodarion rubidum Simon 1914			1
Zora parallela Simon 1878	2		
Zora sp.	3		
Number of individuals	649	584	431
Number of species	67	67	59