Effects of the wasp-spider, *Argiope bruennichi,* on planthoppers and leafhoppers

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Abstract: The role of spiders as generalist predators of herbivores is an important issue for prey population dynamics and spatial distribution. We conducted a field experiment in order to study the effects of the web-building spider *Argiope bruennichi* on plant- and leafhoppers in a grassland habitat. Spider densities were manipulated through repeated removal in open plots that were separated by mown strips, and effects on Auchenorrhyncha were recorded in two blocks of different plot sizes by suction sampling. We found significant negative effects of *A. bruennichi* on the abundance and biomass of their prey in both blocks. The most abundant planthopper *Delphacodes venosus* was most severely affected. However, this species is strictly epigeic, and therefore, predation through a web-building spider is unlikely to be the main cause for its decline. We suggest that non-lethal effects of spiders could be an important factor for the dynamics of herbivore communities in grassland foodwebs.

Zusammenfassung: Als generalistische Prädatoren beeinflussen Spinnen die Populationsdynamik und räumliche Verteilung von Herbivoren. Um die Effekte der Wespenspinne *Argiope bruennichi* auf Zikaden zu untersuchen, führten wir auf einer Feuchtwiese einen Versuch in offenen, nur durch gemähte Streifen getrennten Parzellen durch. In zwei Blöcken mit verschiedenen Parzellengrößen wurden die Spinnendichten experimentell reduziert und die Herbivoren mit dem Saugapparat erfasst. In beiden Blöcken fanden wir signifikante negative Effekte von *A. bruennichi* auf die Abundanz und Biomasse der Zikaden. Die häufigste Zikadenart, *Delphacodes venosus*, war am stärksten betroffen. Da diese Art jedoch strikt epigäisch lebt, ist die Prädation durch eine Radnetzspinne als Erklärung des Rückgangs nicht ausreichend, und wir vermuten, dass nicht-lethale Effekte von Spinnen eine wichtige Rolle für die Dynamik von Herbivoren-Gemeinschaften in Grasland-Nahrungsnetzen spielen können.

Keywords: Non-lethal effects, top-down control, field experiment, invasive species, Araneidae, Hemiptera, Auchenorrhyncha, *Delphacodes venosus*

1. Introduction

A number of field studies have shown top-down effects of spiders on insect herbivores (Riechert & Bishop 1990; Riechert & Lawrence 1997; Schmitz 1998; Finke & Denno 2003; Cronin *et al.* 2004). Riechert & Lawrence (1997) found a particularly strong reduction of phytophagous Coleoptera, Diptera and Homoptera through biomass-dominating

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spiders. Recent studies focused on the importance of non-lethal effects. Whereas prey behavioural responses to predators are relatively well understood in aquatic systems, few studies have been dealing with terrestrial systems. Beckerman *et al.* (1997) found that spiders with their mouth parts glued could cause dietary shifts of grasshoppers. They concluded that predator-induced changes of herbivore feeding behaviour may be more important for the dynamics of terrestrial food chains than predation itself. Similarly, Cronin *et al.* (2004) found that spiders can reduce planthopper densities more severely through induced emigration than through predation.

The aim of this study was to test top-down effects of the invasive spider *Argiope bruennichi* on communities of plant- and leafhoppers in order to assess the role of key predators in structuring food webs.

2. Material and Methods

2.1. Study organisms

We chose the orb-weaving spider *A. bruennichi* because it is easily visible and recognizable in the field due to its black and yellowish coloration, and because of its abundance in the study region. The web is built in the herb layer and is provided with a characteristic zig-zag silk construction (stabilimentum). Prey consists of jumping or flying arthropods such as planthoppers, leafhoppers, grasshoppers (Malt 1994) and dipterans (Nyffeler & Benz 1978). *A. bruennichi* is very common in southern Europe and has been expanding its range into central Europe within the last decades (Hänggi *et al.* 2001; Guttmann 1979).

As potential prey group we chose planthoppers and leafhoppers (Auchenorrhyncha: Fulgoromorpha and Cicadomorpha) as the dominating herbivores of our study site. These insects generally account for a high proportion of the biomass and species diversity in most grasslands and are highly responsive to changes in their environment (e.g. Waloff 1980; Biedermann *et al.* 2005).

2.2. Study site and experimental design

The study was carried out on a moist meadow near the village of Atzenhausen, about 20 km south of Göttingen, Germany. This site had not been mown for several years, and the most abundant monocots were rushes (Juncaceae) and sedges (*Carex* spp.), with grasses (Poaceae) being more prominent in drier parts. Abundant dicotyledonous plants included *Filipendula ulmarina, Geranium palustre, Lotus uliginosus* and *Potentilla* spec. The treatment was maintained for 6 weeks starting in late July 2005, when *A. bruennichi* was clearly the dominating spider (in terms of biomass), reaching an average density of about 1 ♀/sqm.

We installed 12 plots arranged in two rows of 1 m and 2.5 m width, respectively. Both rows occurred as unmown natural vegetation strips on the meadow, each of which treated as a different block and fragmented into six plots by lawnmower lanes of 72 cm width. Plot size was 1 m² in Block A and 6,22 m² in Block B (Fig. 1). In order to study effects on Auchenorrhyncha we manipulated densities of *A. bruennichi* in the established plots through repeated removal of spiders and their webs (removal treatment). For comparison, we left three spatially alternating plots per block with near-natural densities (Fig. 1, spider treatment). Spider numbers were counted regularly and complemented, if necessary. In order to establish homogenous densities, we kept 8 individuals of *A. bruennichi* per large plot (Block B) and 1 individual per small plot (Block A). After two weeks, with an average of 0.84 ♀♀ per sqm, spider densities apparently reached a natural level in our study site.
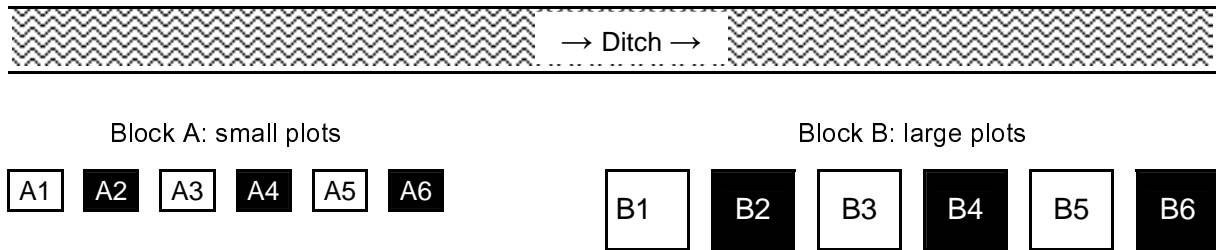
Fig. 1: Study site and arrangement of experimental plots (not to scale). Spider removal plots are shown in white, spider non-removal (= spider treatment) plots in black.

On the removal plots mean densities of *A. bruennichi* (based on two-day surveys) decreased highly significant to 0.03 ♀♀ per sqm (Tab. 2). Missing data for the abundances were calculated by means of the previous and the following day.

We also manipulated another dominant orb web spider on the plots, *Araneus quadratus,* but numbers of this species decreased strongly within the first two weeks, apparently for phenological reasons. Therefore, its effects were discarded from interpretation.

2.3. Sampling and statistical analysis

Samples were taken by two persons by quickly putting up a tube-shaped soil corer (height 32 cm, diameter 21 cm, area size 0.034 m²) onto the surface in order to prevent insects from escaping sidewards, and by immediately inserting the tube of a suction sampler (Stihl SH 85, Germany). We took two samples per small plots and 10 per large plots. Auchenorrhyncha were identified to species level and dried for 72h at 60° C for calculation of biomass. Other arthropods were identified to higher taxonomic levels.

Statistical analyses of data was performed using a two-factorial analysis of variances with spider treatment and patch size as categorial factors (ANOVA). The effects of patch size are not independent from possible gradients in vegetation, as the plots are spatially patched (Fig. 1). The factor patch size (e.g. block factor) can be accounted for statistically because it is independent from the factor spider treatment. However the statistical effect can not be interpreted by one of these causal factors.

Density data of plant- and leafhopper species were analysed by detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) using CANOCO 4.5 (Ter Braak & Smilauer 2002). Data on plant species cover and predator densities (Araneidae, Nabidae, Miridae) were used as explanatory (environmental) variables in the CCA. In order to depict correlations between Auchenorrhyncha species and environmental factors and within the Auchenorrhyncha assemblage, spider treatment and block were included in the analyses as passive variables, i.e. without affecting the ordination.

3. Results

3.1. Auchenorrhyncha species composition

Altogether 15 Auchenorrhyncha species were recorded. Large plots contained almost twice as many species than small plots (14 vs. 8), and also their mean species number was much higher (10.3 vs. 4.3). The Shannon-Wiener index for the small plots was 0.51 and for the large plots 0.68. Tab. 1 shows the summarised sampling results, with a distinction between epigeic and hypergeic species (after Nickel 2003). The planthopper *Delphacodes*

Tab. 1: Abundance and dominance of Auchenorrhyncha on removal treatments versus spider treatments (= non-removal). Significant values are shown in bold. n for small plots were multiplied by 5 to achieve comparability between plots. § indicates log-transformed data to achieve homogeneity of variances.

Species	Spider removal		Non-removal		P
	n	%	n	%	
Predominantly epigeic					
Delphacodes venosus (Germ.)	354	61.67	123	43.77	**0.030**
Muellerianella fairmairei (Perr.)	86	14.98	68	24.2	0.933§
Megophthalmus scanicus (Fall.)	18	3.14	5	1.78	**0.030**§
Kelisia punctulum (Kbm.)	14	2.44	2	0.71	0.235§
Dicranotropis hamata (Boh.)	10	1.74	1	0.36	0.116
Anoscopus flavostriatus (Don.)	8	1.39	0	0	0.063§
Streptanus aemulans (Kbm.)	2	0.35	2	0.71	1.000
Predominantly hypergeic					
Macustus grisescens (Zett.)	28	4.88	26	9.25	0.889
Errastunus ocellaris (Fall.)	18	3.14	15	5.34	0.818
Arthaldeus pascuellus (Fall.)	16	2.79	26	9.25	0.964§
Cicadula flori (J. Shlb.)	8	1.39	3	1.07	0.372
Macropsis cf. prasina (Boh.)[a]	7	1.22	1	0.36	0.258§
Stenocranus fuscovittatus (Stål)	3	0.52	4	1.42	0.760
Javesella pellucida (F.)	1	0.17	4	1.42	0.320
Philaenus spumarius (L.)	1	0.17	1	0.36	1.000
Total	574	100	281	100	0.0251

a = arboricolous species (vagrant)

venosus was by far the most abundant species, occurring on all plots in high densities (on average 111 Ind./sqm) irrespective of patch size.

PCA of the Auchenorrhyncha assemblages clearly separated the species studied; the first and second axis representing 35.6 and 10.0% of the variation in species data, respectively. The first axis is closely associated with the vegetation and moisture gradient along the ditch from the moister large plots to the slightly drier small plots. Including vegetation cover and predator abundance (the orb web spiders and Heteroptera taxa studied) as predictor variables for the plant- and leafhoppers studied in canonical correspondence analysis (CCA) resulted only in a slight decline in the variance of the species data represented by the first and second axis (34.3 and 15.3%, respectively) compared to the DCA (Fig. 2). This indicates that the plant species composition is a major structuring force for the herbivore community. Hygrophilous and sedge-feeding leafhoppers such as *Kelisia punctulum*, *Stenocranus fuscovittatus* and *Cicadula flori* were closely associated with Block B, whereas grass feeders, like *Anoscopus flavostriatus*, *Dicranotropis hamata* and *Errastunus ocellaris*, clustered with Block A, which is characterised by a higher cover of Poaceae and *Geranium palustris*. Also, spider removal plots were clustered close to small and grass-dominated plots, whereas spider treatment plots were clustered with large plots, characterised by higher vegetation, higher sedge densities and a higher biomass of predatory mirid and nabid bugs. For predatory Heteroptera biomass we found significant differences between block
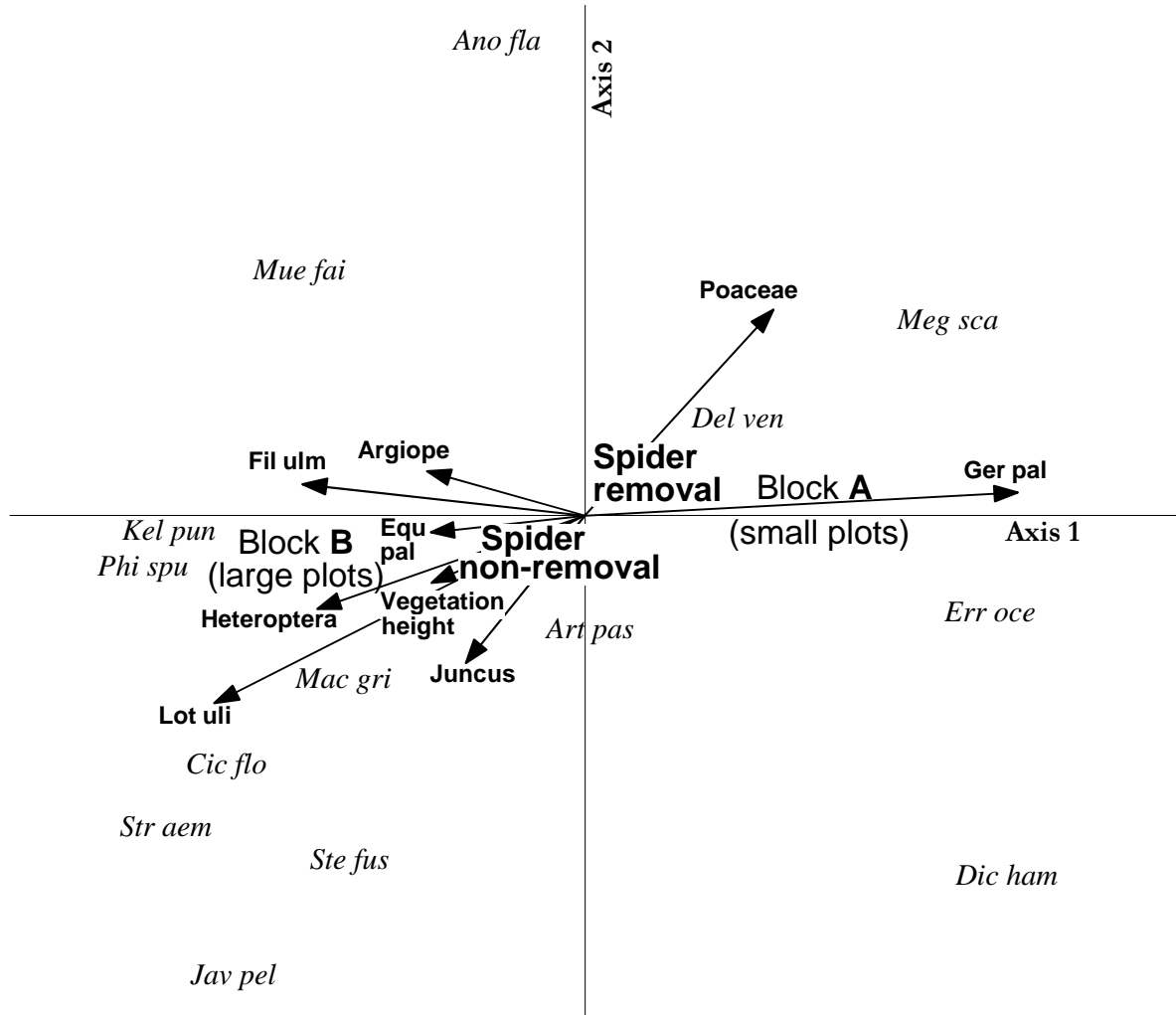
Fig. 2: CCA ordination biplot of the density of plant- and leafhoppers on the studied plots, with the cover of dominant plant species (**Lot**us **uli**ginosus, **Fili**pendula **ulm**aria, **Equi**setum **pal**ustre, **Ger**anium **pal**ustre), vegetation height and biomass of predators (**Argiope** bruennichi and predatory **Heteroptera**) as explanatory variables (arrows). Carex density was highly inter-correlated with other explanatory variables (notably vegetation height and Heteroptera bio-mass) and was therefore omitted. Treatments (spider removal and block) were included as passive variables. For Auchenorrhyncha species names see Tab. 1; we used the first three let-ters of the genus and species names, respectively.

Tab. 2: Response of predatory Heteropta and Araneida, using a two-way ANOVA ($F_{1, 8}$ ra-tios). Bold digits indicate statistical significancies (p<0.05).

	Heteroptera biomass		A. bruennichi abundance of ♀♀		Linyphiidae abundance		Pisauridae abundance		Lycosidae abundance	
	F	P	F	P	F	P	F	P	F	P
Spider	1.35	0.2781	189.93	**<.0001**	1.92	0.2028	0.01	0.9218	0.45	0.5191
Block	6.73	**0.0319**	0.01	0.9108	9.32	**0.0157**	7.29	**0.0271**	6.44	**0.0348**
Sp × Bl	1.35	0.2781	0.00	0.9850	0.28	0.6088	0.01	0.9218	0.45	0.5191

A and B (Tab. 2), whereas spider reduction had no effect. Also, the densities of sheet-web weavers (Linyphiidae), nursery-web spiders (Pisauridae) and wolf spiders (Lycosidae) showed only significant responses to different blocks, but not to *A. bruennichi* treatment (Tab. 2). Spiders of other families showed no significant response at all.

3.2. Effects of *Argiope bruennichi*

3.2.1. Auchenorrhyncha densities

We found a strong and significant negative effect of *A. bruennichi* on Auchenorrhyncha densities, but differences between the two blocks were not significant (Fig. 3a, Tab. 3). In both blocks, densities declined by about one half. The reduction through *A. bruennichi* was relatively distinct in plots of either size (no statistical interaction between spider and block), although variation was more pronounced on small plots (Fig. 3a). The mean numerical relationship between adult Auchenorrhyncha and nymphs increased from 3.9 on spider plots to 5.9 on removal plots, and as a consequence, the negative effects are stronger on larger and more mobile herbivores.

The planthopper *Delphacodes venosus* was the most abundant species and was most severely affected by the spider (Tab. 1), with a mean density reduction from 165 Ind./m² to 57 Ind./m², again without any measurable block effect ($F_{1.8}= 0.0$; $p= 0.97$). The leafhoppers *Megophthalmus scanicus* and *Anoscopus flavostriatus* also responded negatively; *A. flavostriatus* was even exclusively confined to removal treatments (Tab. 1). *Kelisia punctulum*, *Dicranotropis hamata* and *Cicadula flori* showed a non-significant trend to be more abundant on removal plots. *K. punctulum* and *C. flori* occurred exclusively or predominantly in block B.

3.2.2 Auchenorrhyncha diversity

Total as well as mean species numbers of Auchenorrhyncha were lower in spider treatment plots. Total species numbers dropped from 8 to 6 on small plots and from 14 to 12 on large plots (Fig. 3e). However the larger proportional decrease of the dominant species *D. venosus* in spider treatments results in a higher evenness. Shannon-Wiener indices for both spider treatment variants were higher than on the removal plots (0.58 vs. 0.41 in small plots and 0.71 vs. 0.64 in large plots; Fig. 3f).

3.2.3 Auchenorrhyncha biomass

We also found a strong, though not significant, reduction of total Auchenorrhyncha biomass on the spider plots (Tab. 3; Fig. 3b) ranging between 119.5 mg/m² and 53.4 mg/m² (mean: 78 mg/m²) in the large plots. In presence of *A. bruennichi* biomass values ranged between 61.1 mg/m² and 12.2 mg/m² (mean: 42.3 mg/m²). The standard deviation was high, which may be explained through differences in host plant species composition.

Tab. 3: Response of plant- and leafhoppers (from suction samples), using a two-way ANOVA ($F_{1,8}$ ratios). Bold digits indicate statistical significance ($p<0.05$).

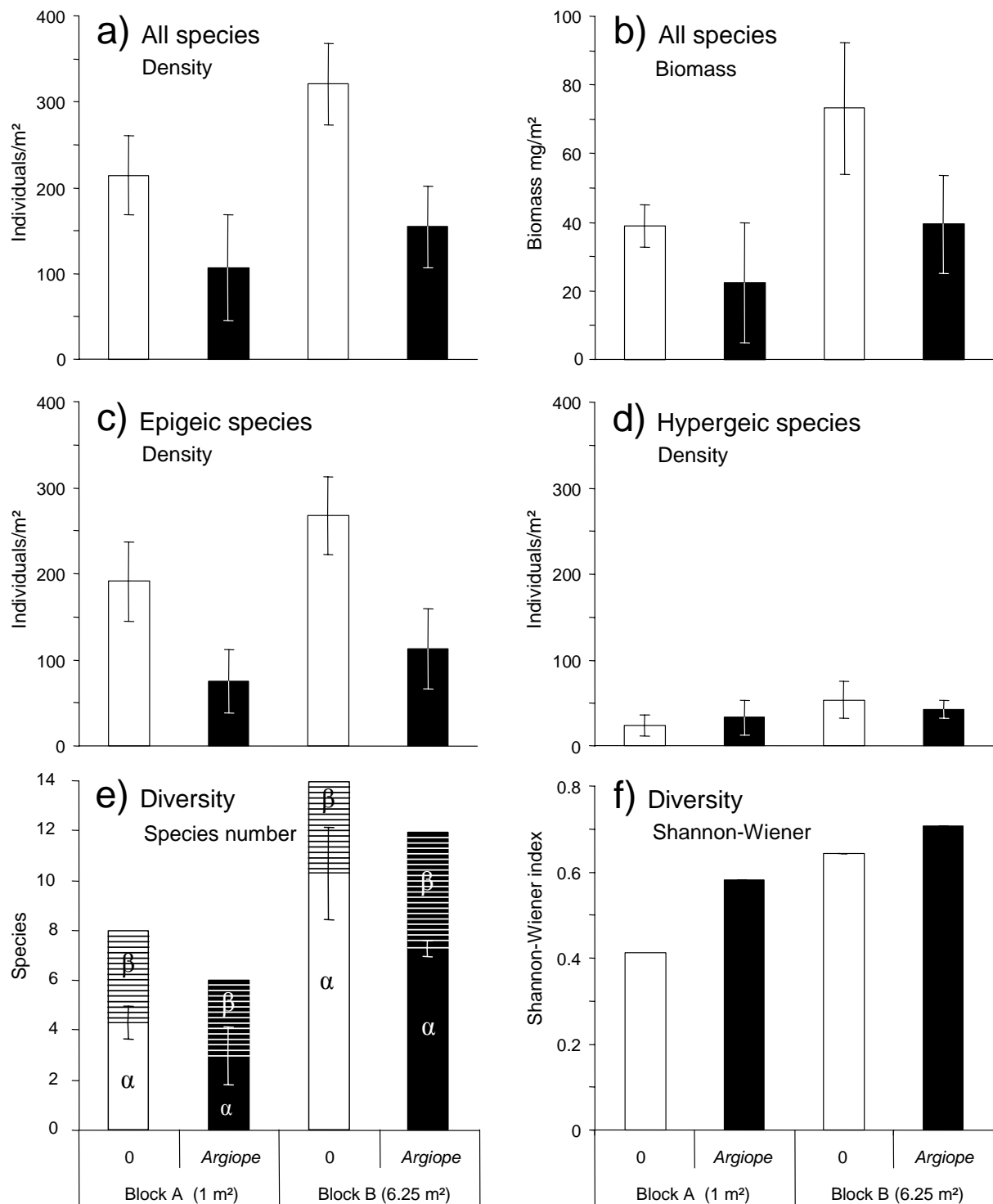|	All species abundance		All species biomass		Epigeic species abundance		Hypergeic species abundance		Mean species number	
	F	P	F	P	F	P	F	P	F	P
Spider	7.56	**0.0251**	2.79	0.1337	9.61	**0.0147**	0.00	0.9576	3.52	0.0974
Block	2.40	0.1602	2.88	0.1281	1.72	0.2264	1.33	0.2824	20.02	**0.0021**
Sp × Bl	0.35	0.5708	0.32	0.5874	0.19	0.6738	0.36	0.5628	0.52	0.4910

Fig. 3: Auchenorrhyncha responses to spider removal on small (A) and large (B) plots with (black bars) and without (white bars) *Argiope bruennichi* (means ±SE). **a**: mean total densities (all species) **b**: mean total biomass, **c**: epigeic species, mean densities, **d**: hypergeic species, mean densities, **e**: mean (α) and total ($\alpha+\beta$) numbers of all species (species turnover between plots: hatched section of bars), **f**: Shannon-Wiener indices.

4. Discussion

The orb-weaving spider *Argiope bruennichi* is apparently an efficient predator with dramatic effects on the Auchenorrhyncha assemblage of our study site. We found a pronounced decline of Auchenorrhyncha densities on *A. bruennichi* plots compared to removal plots. Block and patch size, however, seemed to be unimportant for the strength of top-down effects. We believe that these spider effects are direct, although we cannot fully exclude alternative explanations, e.g. indirectly through downward shift of predatory Heteroptera preying upon epigeic Auchenorrhyncha (intraguild trait-mediated effects). However, we did not find any significant *Argiope* effect on other predators, which provides further evidence for a direct effect of *Argiope* on Auchenorrhyncha.

The results of our CCA ordination (Fig. 2) suggest that the community composition of plant- and leafhoppers is shaped mainly by bottom-up forces. We found an association between spider removal plots and small plots occupied mainly by grass feeding species, indicating that *Argiope bruennichi* and vegetation density affected the community of plant- and leafhoppers in a similar way. The effect of spider removal on species composition seems to be less important, although the spider effect on species preferring grass-dominated plots with lower vegetation is more pronounced than on species preferring more complex environments. These findings correspond with recent studies of herbivore systems that are driven predominantly by the quality and distribution of plant resources. Denno *et al.* (2003) found that on the one hand composition of the planthopper assemblage was primarily driven by bottom-up forces, on the other hand there were significant top-down effects on the most abundant planthopper species. Therefore, we conclude that bottom-up as well as top-down forces influence the overall dominance structure of herbivore communities to a varying extent which may strongly be subject to potential interactions between single species.

Predators themselves are also strongly dependent on habitat structure and microclimatic conditions (Wise 1993; Platner 2004). Similar abiotic requirements often result in strong positive correlations between predators and their potential prey even when trophic relations are weak. In our study *A. bruennichi* was positively correlated with density of *Filipendula ulmaria* before the manipulation had started. Therefore habitat structure should mediate top-down forces exerted by *A. bruennichi* on plant- and leafhoppers (Sanders, Nickel & Platner, unpublished data).

A. bruennichi also had a negative effect on the total number of Auchenorrhyncha species. It is unlikely, however, that an average of two new species immigrated into each plot within the short period of our treatment. Instead, we assume that rare species increased relatively, and as a consequence, their probability of being sampled. Moreover, we found changes in the evenness of species composition that can also be contemplated in the context of diversity. Comparing the Shannon-Wiener indices for spider treatment plots versus removal plots, we found slightly higher indices in the spider treatment plots (Fig. 3f), indicating a positive effect of key predators. In other experiments spiders and ants resulted even in higher species numbers of plant- and leafhoppers (Sanders *et al.* 2006).

Our results provide evidence for non-trophic, trait-mediated spider effects on planthoppers and leafhoppers through behavioural mediation or spider-induced emigration, although we have not explicitly tested this hypothesis. There are, however, several arguments that these effects can not plausibly be attributed merely to predation. Most important, strongly epigeic species, such as *D. venosus*, *A. flavostriatus* and *M. scanicus*, which are highly unlikely to be ever caught in spider orb webs, showed the strongest responses.

Web heights in our study ranged between 20 cm and 40 cm (measured from the centre to the ground). It is further unlikely that other web building spiders exerted direct pressure. In fact, webs of *A. bruennichi* are built much lower in the vegetation than those of *Araneus quadratus* (Mensendiek 1997), and therefore, an additional trophic effect of *A. quadratus* is unlikely. We rather assume that spider induced emigration, first described by Cronin *et al.* 2004), may play a more important role. These authors found that in open patches the densities of planthoppers strongly declined at high spider densities, whereas predation itself in caged patches was weak.

Predator cues in arthropod predator-prey interactions were often described in aquatic systems, but few in terrestrial systems (Chivers & Smith 1998). Persons *et al.* (2001, 2002) observed defensive behaviour between intraguild predators in wolf spiders and found that they can distinguish between low-risk and high-risk predators through diet-based predator cues. Detecting predator cues reduced predation rates strongly, and survival in the presence of any cue was significantly increased. More recently, Kortet & Hedrick (2004) found that juvenile crickets use chemical cues to detect spider predators. In a laboratory experiment these insects avoided spider silk, secretions and excreta. However, mechanisms in planthoppers and leafhoppers are still unknown. Altogether, trait-mediated effects of biomass-dominant spiders could be an important driving force for the dynamics of herbivore communities in grassland food-webs.

Dietary shifts due to avoidance of predators could cause strong cascading effects on plants. These behavioural changes might result in strong damages to single plant species, and consequently, could have major implications for biological pest control (Hlivko & Rypstra 2003; Maloney 2003). Some planthoppers, especially Delphacidae, are devastating pests on major agricultural crops (Denno & Roderick 1990). Herbivore behaviour therefore underscores the important link between behavioural ecology and vertical food web interactions (sensu Denno *et al.* 2003).

Further studies need to explicitly exclude possible alternative explanations and to explore mechanisms for the planthopper behaviour. It is unclear, whether perception happens mainly through vision or chemical detection by planthoppers. Future perspectives should also include application for pest control purposes.

Acknowledgements

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