The influence of vegetation structure on spider species richness, diversity and community organization in the Apšuciems calcareous fen, Latvia

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Abstract

The influence of vegetation structure on spider species richness, diversity and community organization in the Apšuciems calcareous fen, Latvia.— Calcareous fens are considered to be among the most threatened ecosystems of Europe. They are also one of the most diverse habitats as they support an incredibly rich and diverse range of plant and animal species. However, in spite of their diversity, calcareous fens are still poorly investigated, especially when referring to fen invertebrates, such as spiders. Because spiders are good bioindicators, knowledge of their ecology in rare and threatened habitats is of interest. The aim of this study was to document the composition and diversity of spider species, families and foraging guilds in the ground– and grass–layers of the Apšuciems calcareous fen, and to evaluate the influence of vegetation structure on spider community organization. In summer 2012, we collected ground–dwelling spiders using pitfall traps and grass–dwelling spiders using sweep–netting. A total of 2,937 spider individuals belonging to 19 families and 80 species was collected in the Apšuciems fen. Our results indicate that spider species and families tend to be stratified across the vertical structure of the habitat; the spider composition in the ground stratum differed from that in the grass stratum. On the contrary, however, the spider foraging guild structure between the ground–layer and the grass–layer was similar. Each of the two studied strata presented similar guilds in similar proportions. Our results also showed that spider composition differed considerably between fen parts and that much of this variability could be explained by the architectural properties of the habitat. More diverse vegetation generally supported a higher number of spider species.

Key words: Araneae, Community structure, Vertical stratification, Foraging guilds, Habitat heterogeneity

Resumen

La influencia de la estructura de la vegetación en la riqueza de especies, la diversidad y la organización de las comunidades de arañas en el pantano en terreno calcáreo de Apšuciems, en Letonia.— Se considera que los pantanos en terrenos calcáreos son uno de los ecosistemas más amenazados de Europa. Asimismo, son uno de los hábitats con mayor diversidad, puesto que albergan una variedad de especies de plantas y animales increíblemente rica y diversa. No obstante, a pesar de su diversidad, los pantanos en terrenos calcáreos se han estudiado poco, especialmente por lo que hace a los invertebrados, como las arañas. Debido a que son buenos indicadores, es interesante conocer su ecología en hábitats singulares y amenazados. Este estudio tiene como finalidad documentar la composición y diversidad de las especies, familias y gremios de alimentación de arañas en los estratos edáfico y herbáceo del pantano calcáreo de Apšuciems, y evaluar la influencia de la estructura de la vegetación en la organización de las comunidades de arañas. En verano de 2012, recogimos arañas que habitan en el suelo utilizando trampas de caída y arañas que habitan en la hierba con redes entomológicas. En total, en el pantano de Apšuciems se recogieron 2.937 arañas pertenecientes a 19 familias y 80 especies. Nuestros resultados indican que las especies y familias de arañas tienden a estratificarse a lo largo de la estructura vertical del hábitat; la composición de arañas en el estrato edáfico difería de la del estrato herbáceo. Por el contrario, la estructura de los gremios de alimentación era parecida en el estrato edáfico y el estrato herbáceo. Cada uno de los dos estratos estudiados presentaba gremios parecidos en proporciones similares. Nuestros resultados también pusieron de manifiesto que la composición de arañas

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difería considerablemente entre distintas partes del gremio y que gran parte de esta variabilidad se podía explicar por las propiedades arquitectónicas del hábitat. En general, cuanto más diversa era la vegetación, mayor era el número de arañas.

Palabras clave: Araneae, Estructura de comunidades, Estratificación vertical, Gremios de alimentación, Heterogeneidad del hábitat

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Introduction

Calcareous fen habitats have a high conservation value because they support an incredibly rich and diverse range of plants and animals, including many endangered species (Moore et al., 1989; Schmidt et al., 2008; McBride et al., 2011). Despite their ecological relevance, however, calcareous fens have been subjected to various destructive land use practices, such as drainage, peat harvesting, and neglect (Johnson, 2000; McBride et al., 2011). As a result, calcareous fens are now less common than they were 40 to 50 years ago (McBride et al., 2011) and are among the most threatened ecosystems in Europe (Seer & Schrautzer, 2014). In Latvia, calcareous fens are also one of the rarest habitats but their exact size is unknown; approximate estimates indicate they cover only 0.01% of the total area of Latvia (Auniņš et al*.,* 2013).

Spiders are among the most dominant insectivores in terrestrial ecosystems, and they inhabit a wide array of spatial and temporal niches (Kremen et al., 1993; Wise, 1995). As predators, spiders are important components of natural ecosystems, playing a vital role in structuring arthropod communities and thus having a significant role in the balance of nature (Gertsch, 1979; Uetz, 1991; Nyffeler et al., 1994; Marc et al., 1999). As spiders have a great potential as good bioindicators (Marc et al., 1999; Pearce & Venier, 2006), by studying them it is possible to assess the conservation value of a particular habitat (Churchill, 1997; Mas et al., 2009). To date, however, the ecology of spider assemblages has been poorly studied in fen ecosystems, especially calcareous fens. Spiders have been widely recommended as good indicator organisms for several reasons: (1) they are widely distributed in high numbers and therefore provide data that are appropriate for statistical analyses (Foelix, 2011); (2) they can be easily collected using standardised sampling methods (Wise, 1995); (3) they are taxonomically well known compared to other invertebrate groups, and can be identified without expensive equipment or techniques (Oxbrough et al., 2005; Cardoso, 2009); and (4) they are good predictors of overall invertebrate biodiversity since they appear to be linked to herbivore and detrivore food webs (Uetz, 1991; Wise, 1995; Willett, 2001).

In previous studies, we investigated several calcareous fens in the Coastal Lowland and focused on either ground–dwelling (Štokmane et al., 2013) or grass–dwelling spider assemblages (Štokmane & Spuņģis, 2014). In the present study, we focused on a single calcareous fen (the Apšuciems fen) and performed a more detailed study of both spider groups (ground– and grass–dwellers). The aims of this study were: (1) to document and compare the species richness, diversity and guild composition of spiders in the ground and in grass layers of the Apšuciems calcareous fen; and (2) to evaluate the potential influence of several vegetation parameters (namely, plant species richness, plant diversity and vegetation height) on the diversity and community organization of ground– and grass–dwelling spider in this fen.

Material and methods

Study area and sampling design

Samples were collected in the Apšuciems calcareous fen, in Lapmežciems parish, Engure district, Latvia. The Apšuciems fen is located in the Coastal Lowland of the Baltic Sea and the Gulf of Riga. The fen covers an area of about 15 ha, and it is situated in the territory of a unique hydrological regime —it is a periodically flooded dune slack. The Apšuciems fen is a nature reserve and a 'Natura 2000' site.

We used a systematic sampling grid in the study (fig. 1). We randomly selected a point in the central part of the fen, and from this point we set up a 50 × 50 m grid in the fen. We then set a 9 × 9 m plot on the northwest corner of each grid cell, for a total of 61 plots. Four of the plots were later discarded because they were located in forested habitats. We therefore used a total of 57 sampling plots.

To characterize the vegetation structure in each plot, we recorded the number of plant species and visually estimated their percent cover. Before data analysis, all vegetation cover values were transformed according to the Braun–Blanquet scale which gives numerical rankings to a range of percentages: (+) < 1% percent cover; (1) 1–5%; (2) 6–25%; (3) 26–50%; (4) 51–75%; (5) 76–100% (Braun–Blanquet, 1964). Vascular plants were identified to species level when possible, otherwise to genus. Bryophytes were considered as a group and were not identified to any taxonomic level. Vascular plant identification followed Pētersone & Brikmane (1980) and Mossberg & Stenberg (2003). Vegetation height (cm) was also recorded in each plot; it was measured as the height of the tallest plant.

Spider sampling and identification

Two collection methods were used to sample either ground–dwelling or grass–dwelling spiders. The ground–dwelling spiders were collected using pitfall traps, consisting of plastic cups with a diameter of 7.5 cm and a volume of 250 mL. Each trap was filled with 100 mL of a solution of 90 mL of 10% formaline, 10 mL ethylene glycol, and some detergent. Traps were placed in the ground with the rim leveled to the surface. Six pitfall traps were installed in each plot; traps were placed in two lines of three traps and spaced 1 m apart. Trapping was continuous, with traps being kept open from 27 VII until 22 VIII 2012. The grass–dwelling spiders were collected using a sweep net with a rim diameter of 30 cm. A sample consisted of 50 strokes of the sweep net taken in a circular manner within ca. 5 m from the plot center. The sweep–netting was carried out on 26 and 27 VII 2012.

After collection, spiders were immediately preserved in 70% ethanol for later examination. In the laboratory, all spiders were sorted, counted and identified using appropriate literature. Mature spider individuals were identified to species when possible; unidentified adult specimens were recorded as morphospecies. Most immatures were identified to family only. We used the identification keys of Locket & Millidge (1953), Roberts

(1996) and Nentwig et al. (2012), and followed the World Spider Catalog version 17.0 (Platnick, 2016) for the nomenclature and taxonomy of spiders. Voucher specimens were stored in 70% ethanol and deposited in the Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia, Riga.

Statistical analyses

To evaluate plant and spider species richness and diversity in the fen, we used three indices: the number of observed species (S) as the primary indicator of plant/spider species richness, as well as the Shannon–Wiener index (H), and the Pielou's evenness index (J) as a measure of species diversity. We chose these indices because they are among the most popular and most frequently used diversity indices in ecology. Mathematical formulae to calculate the Shannon index and the evenness index can be found in Magurran (2004). The calculations were performed for each of the 57 sample plots and then averaged for the whole fen. All diversity indices were calculated using the PC–ORD 5.0 (McCune & Mefford, 2006).

Spider dominance structure was analyzed at family and species levels, as well as by foraging guilds. The dominance level for each spider species was calculated according to the logarithmic dominance classification proposed by Engelmann (1978) in which eudominant species comprise > 32% of the total abundance, while dominant, subdominant, recedent, subrecedent, and sporadic species comprise 10–32%, 3.2–10%, 1–3.2%, 0.32–1%, and less than 0.32%, respectively. On the basis of prey capture method, spider families can be grouped into two or more foraging guilds of differing mobility. In this study, we used the following guild classification (modified from Uetz, 1977; Wise, 1995): (1) web spinners; (2) sit–and–wait ambushers; and (3) active hunters.

We used a simple linear regression analysis to test for relationships between spider diversity parameters (spider abundance, species richness and diversity) and vegetation characteristics: the number of plant species (species richness), plant diversity (Shannon index) and vegetation height. Before testing, data were checked for normality of distribution (using Kolmogorov–Smirnov test) and, if necessary, log–transformed prior to analyses. Regression analysis was conducted using the R software (R Development Core Team, 2011).

The data were also interpreted using an ecological ordination technique —a redundancy analysis (RDA) that is the canonical version of principal component analysis (PCA) (Legendre & Legendre, 1998). RDA is one of the most prominent methods of direct gradient analysis (Lepš & Šmilauer, 2003). This analysis was used to detect patterns in spider community organization in relation to vegetation structure. The RDA was based on the spider species and the number of specimens within each species found in each sample plot. Juvenile spiders and species with fewer than four individuals were excluded from the analysis. The species data were Hellinger–transformed prior to analysis, since the Hellinger distance is supposedly a better ecological distance than the Euclidean distance (Legendre & Gallagher, 2001). The scaling method 2 (= the covariance biplot) was used. We tested the statistical significance of the RDA by means of permutations (number of permutations: 999). The RDA was run by the R (R Development Core Team, 2011) with the VEGAN package (Oksanen et al., 2009).

Results

Habitat characteristics of the studied fen

A total of 50 species of vascular plants were found in the Apšuciems fen. The dominant plant species with the highest mean percent cover were *Cladium mariscus* with 27.81% cover (± 4.69 SE), *Myrica gale* with 21.06% (± 1.79), *Molinia caerulea* with 19.88% (± 3.50), *Phragmites australis* with 13.91% (± 2.03), *Schoenus ferrugineus* with 8.89% (± 1.95), *Frangula alnus* with 5.07% (± 1.68) and *Carex lasiocarpa* with 2.55% (± 0.65). The mean Shannon index for vascular plants was 1.44 (± 0.05) and it ranged from 0.49 to 2.10, while the mean evenness was 0.62 (± 0.02) and ranged from 0.23 to 0.85. The vegetation height also differed considerably between different parts of the Apšuciems fen —the mean vegetation height for the whole fen was 150 cm (± 14.55), but it ranged between 40 and 900 cm.

Spider diversity

A total of 2,937 spiders was collected, representing 80 species in 19 families. All spider species were sorted into two groups: ground–dwellers and grass–dwellers. Since we could not find any strict classification in the literature concerning which spider species are considered ground–dwellers and which are grass–dwellers, we classified all the collected spider species according to the method by which they were caught, *i.e.,* if the particular species was collected by pitfall trapping, it was considered to be a ground–dweller, but if the species was collected by sweep netting, it was considered to be a grass–dweller. Of all 80 spider species collected, only eight were obtained using both methods. In this case, a species was put in one or the other group taking into account in which samples there was a greater number of individuals of the particular species. Thereby, *Pardosa fulvipes* (89% of all individuals found in pitfall traps) and *Episinus angulatus* (two of three individuals found in pitfall traps) were classified as ground–dwelling spider species, whereas *Dolomedes fimbriatus* (89% of all individuals found in a sweep net), *Pisaura mirabilis* (86%), *Evarcha arcuata* (87%), *Xysticus ulmi* (85%), *Oxyopes ramosus* (98%) and *Cheiracanthium punctorium* (two of three individuals found in a sweep net) were considered grass–dwelling species. Fifty–five of the collected spider species were classified as ground–dwellers and 25 as grass–dwellers.

The mean Shannon index was 1.69 (± 0.06 SE; range: 0.50 to 2.25) for ground–dwelling spiders and 0.85 (± 0.07 SE; range: 0.14 to 1.86) for grass–dwelling spiders. Species evenness was 0.87 (± 0.02) for the ground–dwelling spiders and 0.68 (± 0.04) for the grass–dwelling spiders.

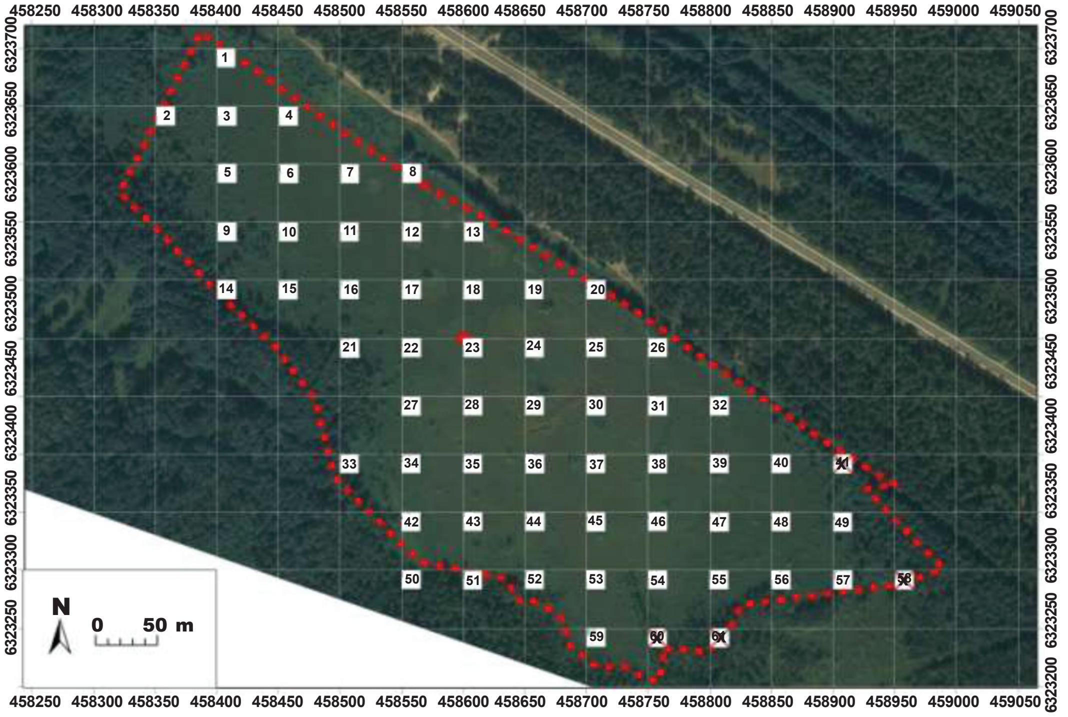

Fig. 1. The study area and the arrangement of the sampling plots in the Apšuciems calcareous fen. In total, 57 out of 61 sample plots were used in the study (the four discarded plots are crossed out).

Fig. 1. Área de estudio y localización de las parcelas de muestreo en el pantano en terreno calcáreo de Apšuciems. En total, en el estudio se utilizaron 57 de las 61 parcelas de muestreo (las cuatro que se descartaron están tachadas).

Spider dominance structure

Spider dominance structure in the Apšuciems fen was analyzed both by taxonomic groups (*i.e.,* species and families) and by ecological groups (*i.e.,* foraging guilds). The most dominant species in the ground–layer were *Trochosa terricola*, *Antistea elegans*, *Piratula hygrophilus*, *Zora spinimana*, and *Hygrolycosa rubrofasciata* while in the grass–layer were *Dolomedes fimbriatus* and *Evarcha arcuata* (table 1). No eudominant species were detected among the ground–dwelling spiders, but the number of dominant and subdominant species was relatively large. Findings in the grass–layer differed somewhat as the numbers of spiders among the three most dominant classes were more evenly distributed, *i.e.,* there were one eudominant, one dominant and two subdominant grass–dwelling spider species. Thus, species composition and dominance structure were evidently distinct in each of the two strata. A large number of sporadic spider species was also observed in the fen; 35 ground–dwelling spiders (63% of all ground–dwellers) and seven grass–dwellers (28% of all grass–dwellers) could be considered sporadic.

We observed large differences in dominance at the family level between the ground and the grass layers (figs. 2A–2B). The most abundant family in the ground–layer was Lycosidae, representing 60.8% of all the ground–dwelling spiders, while in the grass–layer the most abundant family was Pisauridae, representing 59.9% of all the grass–dwelling spiders. These two families clearly dominated numerically, despite the fact that the family Pisauridae was represented almost solely by *Dolomedes fimbriatus*, while the family Lycosidae was represented by 13 different species. In turn, the most speciose spider families in the ground–layer were Linyphiidae (34.5% of all ground–dwellers) and Lycosidae (23.6%) while in the grass–layer they were Araneidae (28.0% of all grass–dwellers).

Spiders were grouped into three foraging guilds based on the spider foraging technique: (1) web spinners (detected spider families: Theridiidae, Araneidae, Agelenidae, Linyphiidae, Tetragnathidae and Hahniidae); (2) sit–and–wait ambushers (Lycosidae, Thomisidae and Pisauridae); and (3) active hunters (Gnaphosidae, Clubionidae, Miturgidae, Philodromidae, Salticidae, Oxyopidae, Zoridae, Liocranidae and Corinnidae). The exception was the family Cybaeidae which was not included in any of the mentioned guilds because the single species that we collected from this family (the water spider, *Argyroneta aquatica*) shows different foraging strategies depending on the sex of an individual, *i.e.,* males of *A. aquatica* wander around and catch their prey mainly by active hunting, while

Table 1. The most abundant spider species collected in the ground–layer and in the grass–layer of the Apšuciems fen in 2012. The Engelmann's scale of dominance is used (Engelmann, 1978).

Tabla 1. Las especies de arañas más abundantes recogidas en el estrato edáfico y en el estrato herbáceo del pantano de Apšuciems en 2012. Se ha utilizado la escala de dominancia de Engelmann (Engelmann, 1978).

Dominance class		
	Ground–layer	Grass–layer
Eudominant species (> 32%)		
	–	*Dolomedes fimbriatus* (Pisauridae)
Dominant species (10–32%)		
	Trochosa terricola (Lycosidae), *Antistea elegans* (Hahniidae), *Piratula hygrophilus* (Lycosidae), *Zora spinimana* (Zoridae), *Hygrolycosa rubrofasciata* (Lycosidae)	*Evarcha arcuata* (Salticidae)
Subdominant species (3.2–10%)		
	Pirata tenuitarsis (Lycosidae), *Piratula knorri* (Lycosidae), *Pardosa sphagnicola* (Lycosidae), *Pardosa fulvipes* (Lycosidae)	*Oxyopes ramosus* (Oxyopidae), *Heliophanus cupreus* (Salticidae)
Recedent species (1–3.2%)		
	Pirata uliginosus (Lycosidae), *Allomengea vidua* (Linyphiidae), *Phrurolithus festivus* (Corinnidae), *Bathyphantes gracilis* (Linyphiidae), *Pardosa lugubris* (Lycosidae), *Bathyphantes parvulus* (Linyphiidae), *Euryopis flavomaculata* (Theridiidae)	*Pisaura mirabilis* (Pisauridae), *Synageles venator* (Salticidae), *Xysticus ulmi* (Thomisidae), *Singa hamata* (Araneidae), *Neoscona adianta* (Araneidae)
Subrecedent species (0.32–1%)		
	Walckenaeria alticeps (Linyphiidae), *Leptorchestes berolinensis* (Salticidae), *Oedothorax* sp. (Linyphiidae), *Erigone arctica* (Linyphiidae)	*Tibellus maritimus* (Philodromidae), *Tetragnatha nigrita* (Tetragnathidae), *Clubiona germanica* (Clubionidae), *Tibellus oblongus* (Philodromidae), *Marpissa radiata* (Salticidae), *Araneus diadematus* (Araneidae), *Araniella cucurbitina* (Araneidae), *Araneus quadratus* (Araneidae), *Cheiracanthium punctorium* (Miturgidae)
Sporadic species (< 0.32%)		
	The remaining 35 species	The remaining seven species

females spend most of their time inside a diving bell and are sit–and–wait ambushers (Schütz & Taborsky, 2003). The exclusion of Cybaeidae from the guild analysis did not affect the results because we caught only two *A. aquatica* individuals. Overall, the analysis of guild composition showed that the spider guild structure in both layers was similar, with the sit–and–wait ambushers being the most numerically dominant guild in both strata, and the web spinners being the most species–rich guild in both strata (figs. 2C–2D).

Effects of vegetation structure

The regression analysis showed that spider abundance, species richness and diversity were significantly affected by plant species richness and plant diversity in the fen (table 2). Overall, the structural parameters of the vegetation were more influential in the grass–dwelling spiders. For example, the analyses showed that plant species richness accounted for 21.7% and 18.1% of the total variation in grass–dwelling spider species rich-

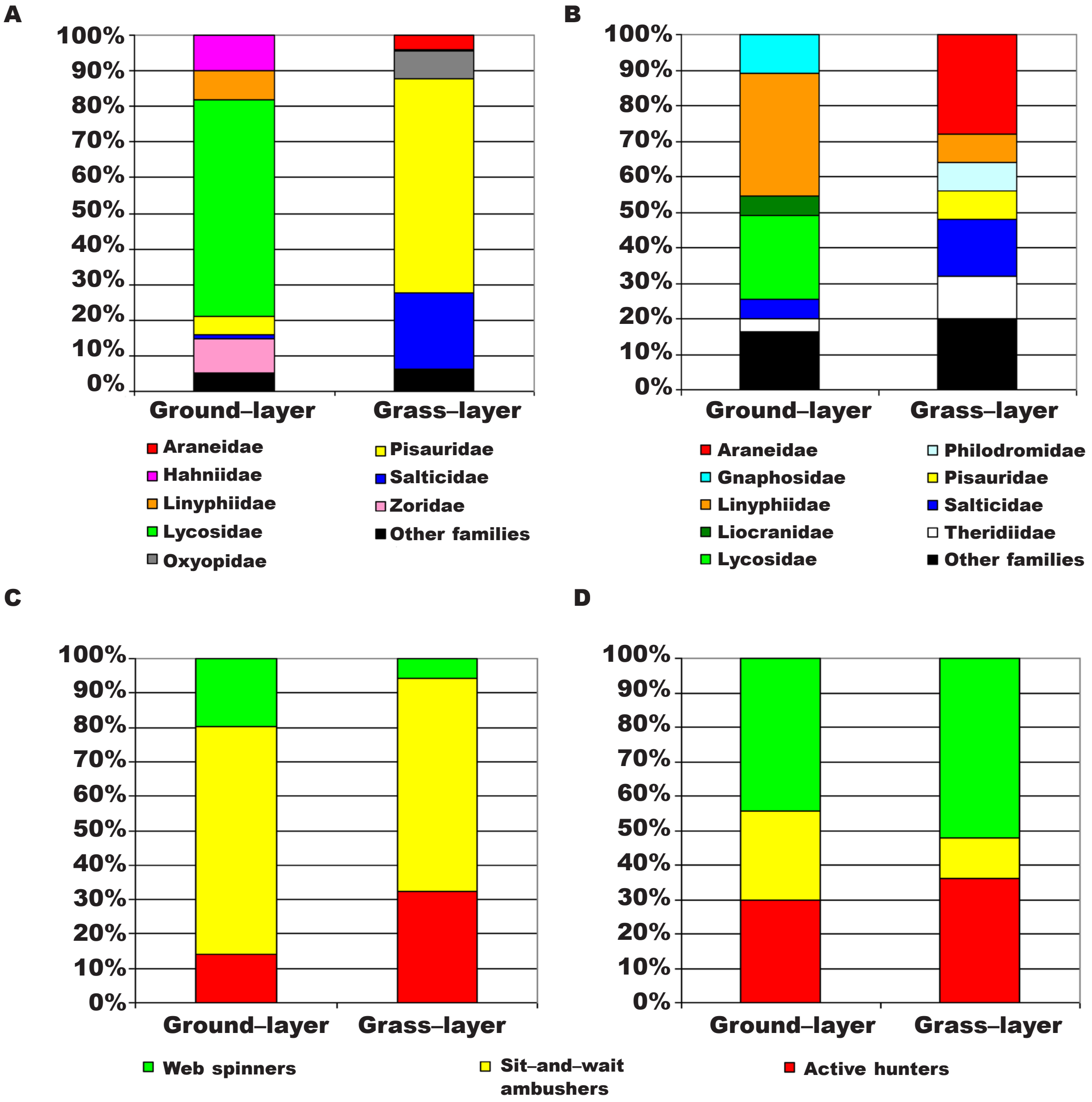

Fig. 2. The dominance structure of spider families and foraging guilds by the number of individuals and by the number of species in the ground–layer and in the grass–layer of the Apšuciems fen: A. The most abundant spider families; B. The most species–rich spider families; C. The most abundant spider foraging guilds; D. The most species–rich spider foraging guilds.

Fig. 2. La estructura de la dominancia de las familias y gremios de alimentación de las arañas según el número de individuos y según el número de especies en el estrato edáfico y en el estrato herbáceo del pantano de Apšuciems: A. Las familias de arañas más abundantes; B. Las familias de arañas con mayor riqueza de especies; C. Los gremios de alimentación de arañas más abundantes; D. Los gremios de alimentación de arañas con mayor riqueza de especies.

ness and abundance, respectively. Meanwhile, a small fraction of the total variance of the ground–dwelling spiders was explained by the vegetation characteristics.

In contrast to the positive relation between spiders and plant diversity, vegetation height negatively affected spider numbers (table 2). The total species richness and diversity of grass–dwellers decreased significantly with increasing height of the vegetation. A correlation analysis between vegetation height and different plant species showed that higher vegetation was positively associated with the presence of *Phragmites australis* (r_S = 0.354; *p*–value < 0.01).

Table 2. Linear regression analysis describing the relationships between the ground–dwelling and the grass–dwelling spiders and the studied vegetation characteristics (N = 57). Statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Tabla 2. Análisis de regresión lineal que describe las relaciones existentes entre las arañas que habitan en el suelo y las que habitan en la hierba y las características estudiadas de la vegetación (N = 57). Significación estadística: * p < *0,05;* ** p < *0,01;* *** p < *0,001.*

Predictor (x)			
Response (y)	R^2	*p*–value	Regression equation
Ground–dwelling spiders			
Plant species richness			
Spider abundance	0.07438	0.04012*	y = 8.7995 + 0.8041x
Species richness	0.08362	0.02914*	y = 4.5857 + 0.2632x
Species diversity	0.1376	0.004497**	y = 1.09513 + 0.05695x
Plant diversity			
Spider abundance	0.02047	0.2884	y = 13.035 + 2.895x
Species richness	0.03291	0.1769	y = 5.7055 + 1.1333x
Species diversity	0.08383	0.02892*	y = 1.2514 + 0.3051x
Vegetation height			
Spider abundance	0.001644	0.7646	y = 17.179 + 0.714x
Species richness	0.01304	0.3976	y = 7.3452 – 0.6209x
Species diversity	0.04632	0.1079	y = 1.69339 – 0.19733x
Grass–dwelling spiders			
Plant species richness			
Spider abundance	0.1812	0.0009618***	y = –3.5705 + 1.5505x
Species richness	0.2168	0.0002627***	y = 0.60042 + 0.07585x
Species diversity	0.1216	0.007852**	y = 0.14846 + 0.06674x
Plant diversity			
Spider abundance	0.06134	0.06323	y = 3.721 + 6.191x
Species richness	0.1331	0.005258**	y = 0.8061 + 0.4080x
Species diversity	0.06776	0.05051*	y = 0.354 + 0.342x
Vegetation height			
Spider abundance	0.01234	0.4108	y = 12.660 – 2.416x
Species richness	0.07256	0.04273*	y = 1.39722 – 0.26212x
Species diversity	0.06756	0.05086*	y = 0.85085 – 0.29715x

Spider community patterns

The redundancy analysis (RDA) of the ground–dwelling spider assemblages produced a significant ordination ($p = 0.001$ after 999 permutations; fig. 3A). The numerical output of the RDA showed that the first two canonical axes together accounted for 33.8% of the total variance of the data; the first axis explained 19.8%. Axis 1 correlated strongly with a plant species richness gradient, where plots rich in different plant species were plotted on the left while those with a low number of plant species and a large cover of *Cladium mariscus* were plotted on the right. Axis 2 was associated with the presence/absence of *Scirpus tabernaemontani* and bryophytes, where plots with high coverage of *S. tabernaemontani* and mosses were situated in the lower part of the graph and those with low coverage, in the upper part.

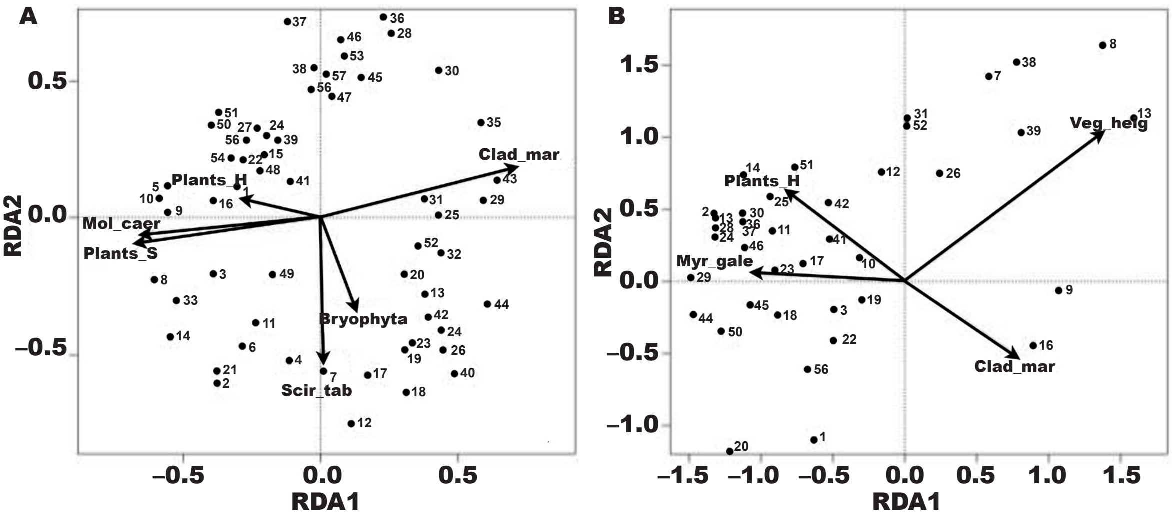

Fig. 3. RDA ordination diagrams showing spider community organization according to vegetation structure, scaling 2. Circles represent sampling plots. Only species with ≥ 4 individuals were included in the analysis, and only the most significant vegetation variables (displayed as arrows) are shown: A. Ordination plot for the ground–dwelling spider assemblages; B. Ordination plot for the grass–dwelling spider assemblages. Abbreviations: Bryophyta. Bryophytes; Clad_mar. *Cladium mariscus*; Mol_caer. *Molinia caerulea*; Myr_gale. *Myrica gale*; Scir_tab. *Scirpus tabernaemontani*; Plants_H. Plant diversity (Shannon index); Plants_S. Plant species richness; Veg_heig. Vegetation height.

Fig. 3. Diagramas de ordenación mediante el análisis de la redundancia (RDA en su sigla en inglés) en los que se muestra la organización de las comunidades de arañas en función de la estructura de la vegetación, escalamiento 2. Los círculos representan las parcelas de muestreo. Solo se incluyeron en el análisis las especies con más de 4 individuos y únicamente se muestran las variables de vegetación más significativas (mostradas como flechas): A. Gráfico de ordenación para los ensamblajes de arañas que habitan en el suelo; B. Gráfico de ordenación para los ensamblajes de arañas que viven en la hierba. Abreviaciones: Bryophyta. Briófitos; Clad_mar. Cladium mariscus*; Mol_caer.* Molinia caerulea*; Myr_gale.* Myrica gale*; Scir_tab.* Scirpus tabernaemontani*; Plantas_H. Diversidad vegetal (índice de Shannon); Plantas_S. Riqueza de especies de plantas; Veg_heig. Altura de la vegetación.*

RDA for the grass–dwelling spider assemblages also produced a significant ordination ($p = 0.003$ after 999 permutations; fig. 3B). The first two axes together explained 42.6% of the total variance, with the first axis alone explaining 39.0%. Similarly, the first axis separated the different plots along a plant diversity gradient. In addition, the vegetation height was a factor that displayed a very long arrow, showing its high importance in structuring grass–dwelling spider assemblages.

Discussion

Spider diversity in the fen

The Shannon index values indicated that spider diversity varied greatly from one fen spot to the other for both the ground–dwelling and the grass–dwelling spiders. The reason for this variability could be related to the fact that the plant species diversity also varied considerably between different parts of the fen. Apšuciems fen is visually a highly heterogeneous habitat that consists of a mosaic of different microhabitats where extremely poor vegetation patches (mainly consisting of *Cladium mariscus*) are scattered within very rich vegetation. Numerous studies have demonstrated that greater structural complexity of vegetation usually results in a higher diversity of spiders (Uetz, 1991; Jeanneret et al., 2003; Langellotto & Denno, 2004; Tews et al., 2004). The Shannon index also indicated that the ground–dwelling spider diversity in the Apšuciems fen was much higher than that of the grass–dwellers. As the Shannon diversity index combines evaluations of both species richness and evenness, such a low value of the Shannon index for the grass–dwelling spiders could be due to the considerably lower species richness of this group of spiders than that of ground–dwellers (only 25 species out of 80 were grass–dwellers), as well as the lower value of the evenness index (J = 0.68 for the grass–dwellers and J = 0.87 for the ground–dwellers). The evenness of the grass–dwelling spiders was low because of the absolute dominance of a single species in the grass–layer —*Dolomedes fimbriatus* (family Pisauridae). Swampy areas are a typical habitat for *D. fimbriatus* (Roberts, 1996), and since it is a large spider (body length of a female can reach 20 mm), it may have a competitive advantage over other spiders that inhabit the same habitat stratum (Harwood et al., 2001). Besides, the differences in body size promote intraguild predation with the larger spider species often being the intraguild predator (Samu et al., 1999; Patrick et al., 2012). Thus, the large body size of *D. fimbriatus* and the suitable conditions for this pisaurid in the fen could be the main reasons why this species has such a high abundance in the studied habitat. On the contrary, in the ground stratum the individuals were more evenly distributed among the different species (table 1). Most of the dominant ground–dwelling species belonged to the family Lycosidae, with the top–scorers being *Trochosa terricola*, *Piratula hygrophilus* and *Hygrolycosa rubrofasciata*. Other researchers that have studied spiders in wetland habitats have also observed that the Lycosidae family usually dominates in this type of habitat (Bultman, 1992; Koponen, 2003; Cummins, 2007). This might be explained by the fact that lycosids, similarly to pisaurids, are also often associated with water (Gertsch, 1979; Foelix, 2011). However, it has been argued that the prevalence of lycosids in the samples is probably because of the collecting method (pitfall traps) used. Pitfall traps are expected to differentially capture spiders with different activity, with the highly active groups (*e.g.*, lycosids) being caught disproportionately more than the others (Bultman, 1992; Mallis & Hurd, 2005; Cummins, 2007). It has been shown that lycosids almost always dominate in the studies where pitfall trapping has been used, and no matter what kind of habitat the study has been carried out in (*e.g.*, Corey et al., 1998; Mallis & Hurd, 2005; Fetykó, 2008; Kowal & Cartar, 2012).

We also found many sporadic spider species in the Apšuciems fen. About 28% of all collected grass–dwelling spiders were represented by less than three individuals, while among the ground–dwelling spiders this number was considerably higher —63% of all ground–dwellers. This phenomenon has two possible, though not mutually exclusive, explanations. The first explanation could be that our results simply confirm the widely observed pattern of spider community organization because many researchers have observed that spider communities characteristically contain comparatively few abundant species, and comparatively many rare species (Sørensen et al., 2002; Hsieh et al., 2003; Pinzon et al., 2012). An alternative explanation for such a large number of rare spider species in the Apšuciems fen might be related to the edge effect. The edge effect is remarkable in the Apšuciems fen because this fen occupies a relatively small area and also because of its close proximity to other habitat types (personal observation). It is known that edge effects in small habitats can alter the spider assemblage dramatically because spiders are known to be relatively effective dispersers. They can easily immigrate in the focal habitat by walking or ballooning (Gertsch, 1979; Bonte et al., 2011). For this reason, it would be valuable to sample the surrounding habitats in the future.

We need to emphasize, however, that any comparisons between the studied strata should be made with caution because we used two different methods to sample spiders —pitfall traps and a sweep net. These methods differ considerably in the overall sampling effort, *i.e.,* pitfall trapping includes continuous sampling, while the duration of sweep–netting is usually much shorter. In the present study, the pitfall traps were operated approximately for a month, whereas the sweep–netting session was performed only once in that period. As local species richness may vary over time (Coddington et al., 1996), sweep netting may not represent the true species richness in the studied habitat. Besides, since the sweep netting in our study was carried out only during the daytime, it was restricted to diurnal spiders only (for example, families Pisauridae, Salticidae and Oxyopidae), while the pitfall traps collected both diurnally active spiders (Lycosidae and Zoridae) as well as nocturnally active ones (Gnaphosidae, Clubionidae and Liocranidae). It is well known that spiders exhibit both diurnal and nocturnal behavior (Canard, 1990; Roberts, 1996) because such differences in diel activity patterns decrease competition (Southwood, 1978; Otronen & Hanski, 1983). In fact, some authors have shown that spiders are generally more active by night than by day (Green, 1999; Cardoso et al., 2008) because predation pressure is lower at night (Coddington et al., 1991, 1996; Mestre et al., 2013), while in daytime, spiders are threatened by many visually hunting predators, especially birds, lizards, wasps and diurnal spiders (Foelix, 2011; Spiller & Schoener, 1998; Jones et al., 2011). This means it would be desirable to collect spiders in both periods, with the night collection perhaps being even more important than daytime collection.

Vertical distribution patterns of spiders

We compared the family, species and guild composition of spiders in two different habitat strata —the ground–layer and the grass–layer. We found that spiders composition in each strata differed taxonomically. There was a low species and even family (table 1; figs. 2A, 2B) overlap between the ground stratum and the grass stratum. In total, the ground– and the grass–layers shared only eight of 80 spider species. These results are in line with the findings of many other authors who have studied the vertical distribution of spiders and also observed that spiders tend to be stratified in the habitat (*e.g.*, Turnbull, 1960; Culin & Rust, 1980; Stenchly et al., 2012; Pinzon et al., 2013). Moreover, studies indicate that spiders show species–level stratification not only in forested habitats (Brown, 2008; Pinzon et al., 2013) but also in open habitats (Kim et al., 1989; Pekár, 2005) even though these habitat types differ considerably in their vertical stratification. While forest habitats offer many different vertical strata for spiders (*i.e.,* the litter layer, understory, upper canopy, overstory), non–forest habitats exhibit little vertical stratification (Basset et al., 2003). Apparently, different spider species/families are well adapted to living in a particular habitat layer. Horváth et al. (2009), for example, discovered that the large majority of diurnal spiders that hunt on flowers and other upper parts of the plant cannot survive in the lower strata. In contrast, most small spiders (*e.g.*, linyphiids) usually live close to the ground (Balfour & Rypstra, 1998; Foelix, 2011). Such preferences for a certain stratum, however, are not surprising because different strata can provide very different microhabitats for spiders, *i.e.,* each habitat stratum has its characteristic microclimatic conditions, different availability of appropriate substrate for foraging or web–building, and a different spectrum of prey animals (Turnbull, 1960; Abraham, 1983; Foelix, 2011). Studies have shown that spiders are extremely sensitive to the aforementioned factors, possibly explaining why distinctive spider assemblages can establish between vertical strata (Oguri et al., 2014).

Considering how spiders catch their prey, we divided our spider families into three functional groups or guilds: web spinners, sit–and–wait ambushers and active hunters. Our results showed that in spite of the great differences in family and species composition between the ground– and the grass–layer, the proportions of spider functional groups in both habitat layers were similar. In both strata, the sit–and–wait ambushers were the dominant spider guild regarding the number of individuals, while the web spinners dominated in both layers regarding the number of species (figs. 2C, 2D). We should stress, however, that these results could have differed if we had used a different spider guild classification. Spiders can generally be grouped into specific functional groups in many ways. For example, the division can be based on spider foraging strategy, habitat preferences, circadian activity, or prey range (Post & Riechert, 1977; Bultman et al., 1982; Whitmore et al., 2002; Cardoso et al., 2011). As a result, the number of recognized guilds varies. While some authors distinguish only two (Uetz, 1977) or three (Nyffeler, 1982) spider foraging guilds, others subdivide spiders into five (Gertsch, 1979; Young & Edwards, 1990), seven (Canard, 1990), eight (Riechert & Lockley, 1984; Uetz et al., 1999) and even 11 (Post & Riechert, 1977) different foraging guilds. The clearest distinction, however, is between web builders and wandering spiders (Uetz, 1977; Wise, 1995). These two spider guilds are ecologically different. Web builders are sedentary spiders that construct webs and thus feed mainly on moving prey, whereas wandering spiders are non–web–building predators that display a more mobile foraging strategy and thus feed on both moving and motionless prey (Nyffeler, 1999; Cobbold & MacMahon, 2012). We also used this basic and most stable division of spider guilds in the present study, however, we divided the wandering spiders into sit–and–wait ambushers and active hunters. This decision was based on the fact that the foraging strategy of sit–and–wait ambushers lies somewhere in the middle of the two basic guilds. Like active hunters, the sit–and–wait ambushers hunt without using webs, whereas like web builders, they do not actively pursue prey but wait for it to come to them (Wise, 1995). In any case, the results show that each habitat stratum is inhabited by several different guilds and not by a single guild. Such behavior is likely an adaptation to avoid competitive interactions, because since the 'foraging guild' is defined as a group of species using the same class of resources in a similar way, species belonging to the same guild are most likely to be competitors (Polis & McCormick, 1986; Uetz et al., 1999). This hypothesis was supported by Spiller (1984) and Herberstein (1998) who observed that mutually competing web builders construct their webs at different heights when occurring syntopically, but do not do so when one of the compettitors is removed. Similarly, Enders (1974) stated that different orb–weaving spiders can co–exist in the same habitat only if they build their webs at different heights. The same can probably be applied to other (non–web–building) spider foraging guilds (Marc & Canard, 1997; Cardoso et al., 2011).

Spider response to differences in vegetation structure

In our study, spider abundance and species richness was positively associated with the plant species richness and plant diversity in the fen. Many other researchers have also observed that greater habitat complexity results in a higher abundance and diversity of spiders, because structurally more diverse habitats allow a greater niche diversification and coexistence of more spider species (Greenstone, 1984; Rypstra, 1986; Uetz, 1991; Langellotto & Denno, 2004). Overall, complex vegetation is beneficial for spiders in many ways. For example, one of the factors that explains spider distribution in the habitat is microclimate (Turnbull, 1973; Tolbert, 1979), and since it is known that microclimate often correlates with the architecture of plants (Geiger, 1965; Hore & Uniyal, 2008), then there will be a greater variety of different microclimates if the habitat is more complex (Buchholz, 2009). Moreover, the structural complexity within the habitat also provides a greater diversity of sites which can be used by spiders for resting, basking, sexual display, finding food, ovipositon or overwintering, and as an additional refuge from intraguild predation (Lawton, 1983; Halaj et al., 1998). And finally, the structural heterogeneity may also influence spider community structure indirectly via its influence on prey abundance and diversity, because typical prey species (such as herbivorous invertebrates) benefit from the greater variety of food resources available in more structurally diverse habitats (Nentwig, 1980; Siira–Pietikäinen et al., 2003).

In contrast, vegetation height negatively influenced spider species richness and diversity. We also observed this in our previous research where we studied grass–dwelling spiders in several calcareous fens of the Coastal Lowland and concluded that higher vegetation has a significant negative effect on this group of spiders (Štokmane & Spuņģis, 2014). Again, we should emphasize that this is inconsistent with the findings of other authors who have shown that the number of spider species, as well as spider diversity, usually increase in accordance with the height of the herbaceous vegetation because higher vegetation is usually also more structured vertically (Greenstone, 1984; Mrzljak & Wiegleb, 2000; Harris et al., 2003).

We think that one reason for this discrepancy could be related to the structural features of our studied fen habitats —the correlation analysis showed that fen places which were associated with taller vegetation were also associated with *Phragmites australis* (Štokmane & Spuņģis, 2014 and this study). *P. australis* is a typical expansive plant species which spreads very rapidly and forms monodominant stands, thereby simplifying the vegetation structure of the habitat (Auniņš et al., 2013). As a result, due to the lack of architectural diversity, spider species richness and diversity might also be low. Besides, *P. australis* creates shading, and thus the proportion of the photophilous spider species (*e.g.*, *Pirata uliginosus, Bathyphantes parvulus*) can decrease (Štambuk & Erben, 2002). In their study, Buchholz & Schröder (2013) also found that spider assemblages of *P. australis* belts were less diverse than those of all other habitat types. They wrote that these outcomes can be related to fewer available niches (as a result of homogeneous reed belts) or to temporal flooding (which is common in reed belts).

Our results showed that grass–dwelling spiders were generally more affected by the vegetation characteristics than ground–dwellers. We think that this could be explained by the fact that grass–dwelling spiders depend on vegetation to a larger degree than the ground–dwellers do. This is especially true when speaking about grass–dwellers that build webs (or so–called aerial web spinners, *e.g.*, Araneidae, Theridiidae) because vegetation is their main substrate for web building (Whitmore et al., 2002), and a richly structured vegetation often ensures that a greater range of sizes and types of webs can be built (Greenstone, 1984; Uetz, 1991; Rypstra et al., 1999). Meanwhile, in contrast to aerial web spinners, web–spiders that generally live close to the ground (the so–called ground level web builders, *e.g.*, Agelenidae, Linyphiidae, Hahniidae) use not only the vegetation as the web support structure but also several other structural aspects of the habitat, such as ground litter, dirt or stones (Roberts, 1996; Balfour & Rypstra, 1998; Oxbrough et al., 2005).

Distribution patterns of spider assemblages

We described the patterns in spider species composition across the fen using a redundancy analysis (RDA). The RDA showed that spider assemblages have a tendency to arrange in the ordination space according to habitat type. The differentiation of both the ground– and the grass–layer spider assemblage structure was determined mainly by the plant diversity gradient. Spider composition was highly dissimilar between the fen places with low plant species diversity and those places with high plant diversity. This corroborates the findings of many other authors who have also found that the type of vegetation has a great influence on the composition of spider assemblages, with different plant communities harbouring different associations of spiders (Muma, 1973; Gertsch & Riechert, 1976; Uetz, 1991; Buchholz, 2010; Torma et al., 2014). Thus, these results indicate that it is very important to maintain a variety of habitat types within the focal habitat in order to enhance the spider biodiversity.

The ordination analysis also revealed that while plant species richness and diversity appear to be a very important influencing factor for both ground–dwelling and grass–dwelling spider assemblages, some vegetation variables affected exclusively one or the other spider group. For instance, the variation in the ground–dwelling spider assemblage structure also seemed to be determined by the presence (or absence) of *Scirpus tabernaemontani* and the cover of mosses. These two factors were highly correlated with each other. It is therefore hard to say which of the two is more important for the ground–dwelling spiders in this study. However, the literature emphasizes the importance of mosses for some spider groups of the ground–layer, because mosses might serve as a refuge for particular ground–dwellers and they are also an important web attachment substrate for small web builders (*e.g.*, Linyphiidae, Hahniidae) (Roberts, 1996; Harvey et al., 2002a; Jonsson, 2005). Meanwhile, an important factor that determined the structure of the grass–dwelling spider assemblages was vegetation height. We think that this outcome may be related to the differing biology of spider species, since different species need specific vegetation heights. For instance, many of our collected grass–dwelling spiders (*Evarcha arcuata*, *Oxyopes ramosus*, *Pachygnatha clercki*, *Sibianor aurocinctus*) are usually associated with low vegetation (Locket & Millidge, 1951, 1953; Roberts, 1996; Harvey et al., 2002a, 2002b), while, for example, *Araneus diadematus*, which spins large orb webs, needs tall vegetation (Harvey et al., 2002b). Thereby, our results suggest that it would be advisable to maintain a mosaic of different vegetation heights in a habitat to ensure that the ecological needs of certain species are met and thus that the overall diversity of spiders is maximized.

The main conclusions

In conclusion, our findings show that the habitat separation of spiders in the Apšuciems fen seems to occur both vertically and horizontally. In our study, the spider assemblages of the ground–layer and the grass–layer were characterized by little similarity in species (and even family) composition. Apparently, most spider species are well adapted for a specific habitat stratum. In addition, our study showed that an important determinant of spider species richness and diversity in the fen was habitat diversity. The data indicated that structurally more diverse vegetation supports a higher number of spider species, which could be explained by a greater variety of available niches within a more complex vegetation. Overall, our results showed that since vegetation differed from one fen spot to the other, the spider composition was also highly dissimilar in different fen parts. Our results thus emphasize the importance of maintaining a mosaic–like pattern in the habitat, because different vegetation patches (*e.g.*, a rich/poor vegetation, a tall/short vegetation) can provide habitat for very different spider assemblages and thus enhance the overall spider diversity.

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