Epigeic spider (Araneae) assemblages of natural forest edges in the Kiskunság (Hungary)

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Abstract: Natural habitat edges are known to influence the vegetation structure, the microclimate and thereby the invertebrate assemblages. We studied the spiders of two forest edges in the forest-steppe zone of the Great Hungarian Plain (Site 1: a dense juniper shrub – open grassland and Site 2: a juniper and poplar forest – open grassland edge, respectively). The spider assemblages were sampled with pitfall traps arranged in 5×20 grid at the habitat edges. Observed and estimated species richness was higher for the grasslands than for the forests. Rényi's diversity ordering was applied to compare species diversity. The results showed that the grasslands were more diverse in terms of spider species than the forests. The composition of spider assemblages was significantly different between the two habitat types. At Site 2, a higher number forest specialists penetrated into the grassland. Presumably this was due to the shading effect of the nearby poplar trees. Constrained ordinations also revealed a strong influence of the neighbouring poplar trees and vegetation structure on the spider assemblages. No exclusively edge associated species were found on either of the two sharp forest edges.

Abbreviations: N–number of individuals, S–number of species.

Nomenclature: Platnick (2008) for spiders, Simon (2000) for plants.

Introduction

The term edge effect can be used to encompass a wide range of biotic and abiotic trends associated with boundaries between different types of adjacent habitats, whether these are natural or anthropogenic (Murcia 1995, Burgess et al. 2001). Edge effects may influence the behaviour and life cycles (Maelfait and De Keer 1990) of animals, the distribution and abundance of populations (e.g., Molnár et al. 2001, Máthé 2006), the interactions between populations (Murcia 1995, Ferguson 2004) and assemblage structures (Burgess et al. 2001). Edge zones differ both structurally and in species composition from the patch interior (Magura et al. 2002). These edges are essentially characterized by changes in factors such as vegetation structure, plant species richness and microclimate (Zólyomi 1987, Burgess et al. 2001, Dutoit et al. 2007). The distance from the patch interior to a recognizable change in the species composition is taxon–dependent and even sharp edges may appear as broad transition zones for many invertebrate assemblages (Dangerfield et al. 2003).

The present study focused on the little–known effect of naturally occurring sharp edges (Kotze and Samways 2001) on Araneae assemblages. Spiders are suitable objects for such studies as they are one of the most predominant predatory groups in many terrestrial habitats (Samu et al. 1999, 2003). Although they are polyphagous predators, the composition and the structure of the vegetation also exert significant effects on the species composition and diversity of spider assemblages (Ysnel and Canard 2000, Heikkinen and MacMahon 2004).

The aims of the present study were to (1) compare the spider assemblages of the forests and the adjacent grasslands, (2) identify the environmental variables which influence the spider assemblages, and (3) define the width and the position of the edge zone.

Material and methods

Study sites and sampling

The present study was carried out near the village of Bugacpusztaháza (N 46.725^{o}, E 19.654^{o}) in the Kiskunság, in the middle of the Hungarian Great Plain. The mosaic-like landscape structure of the region consists mainly of agricultural fields and forest plantations, but small mosaics of the original forest-steppe are also present.

We studied two forest edges: Juniper shrub vs. open grassland (site 1) and a poplar forest with dense juniper bushes vs. open grassland (site 2). The juniper bushes formed a closed canopy layer, and the ground level was covered with thick leaf litter; accordingly we found only very few herbaceous plants in the forest at the first site, while at site 2, the forest was more open, with the presence of a scarce herbaceous layer. To sample the fauna we employed pitfall traps (diameter 65 mm, filled with ethylene glycol as preservative). At each site 20, groups of pitfall traps arranged in rows parallel with the edge were applied to examine the effects of
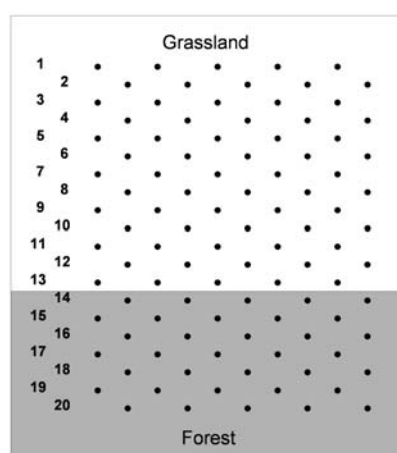
Figure 1. The arrangement of pitfall traps. The numbers indicate the rows of trap.

the forest edges on the spider assemblages. Each row of traps contained 5 traps, resulting in a total of 100 traps at each site. The distance between the traps within the rows was 2 m. To obtain a finer resolution, the distance between the rows was 1 m. To maximize the intertrap distance every second row was shifted by 1 m, thus the distance between the traps both within and between the rows was 2 m. When open for a short period, the small intertrap distance does not necessarily influence the independency of traps, and thus the capture rates of ground-dwelling spiders (Muff 2006). Data obtained from pitfalls situated in the same row, at the same distance from the edge were pooled (Fig. 1).

Data obtained from pitfalls situated at the same distance from the edge were pooled; thus we gained data on 20 groups of traps parallel to the edge. The sampling was repeated four times in 2004 and four times in 2005. The pitfall traps were open for two week periods in April, May, July and September. We did not analyze the data of the sampling periods separately, because of the low number of collected individuals and the resulting stochastic variation which may obscure significant patterns in our samples.

To characterize the vegetation structure of the microhabitats, the percent cover of bare soil surface, leaf litter, dicotyledonous, monocotyledonous plants, mosses and lichens was recorded in 1×1 m^2 quadrats which were placed next to the pitfalls along two transects at both sites.

Data analysis

We tested for differences between assemblages of the forests and the grasslands by using non-parametric multivariate ANOVA with 10000 permutations (Anderson 2001). The analyses were run in the PAST program (Hammer et al. 2001). To compare the species richness of the forests and the grasslands, we applied the abundance-based (ACE) estimator on the pooled data of pitfall traps at each habitat. This estimator is likely to be accurate, as it is based on species with less than ten individuals in the samples (Chazdon et al. 1998, Chao et al. 2000).

The choice of different diversity indices may affect the result of the diversity ranking of the communities. A potential solution is to use diversity ordering. As the scale parameter is changed, different diversity indices are obtained, including indices which are sensitive to the rare and the abundant species. Plotting the value of the index against the scale parameter provides the diversity profile of a community. If the curves intersect, the communities are considered to be non-comparable, as there are indices which rank the communities differently (Tóthmérész 1993, 1995). To compare the diversity of the forest and the grassland assemblages we used Rényi's diversity ordering, as this is one of the most useful methods for the comparison of different assemblages (Tóthmérész 1995). We computed the diversity profiles for seven sampling units in all habitats, as seven groups of traps were open at the two forests, respectively. We used the R software (R Development Core Team 2007) with the BiodiversityR Package (Kindt 2008) for the calculations.

To define the width and the position of the edge zone that the spider assemblages may indicate, we calculated the classic Jaccard index and we also stimated Chao's Jaccard-type similarity index based on species abundance data (Chao et al. 2005) using the EstimateS 8.0 software (Colwell 2004). The classic Jaccard index is likely to underestimate the similarity of two assemblages that contain a high proportion of rare species. The Chao's Jaccard-type index is less biased, as the estimated effect of unseen species is taken into account in the index (Chao et al 2005).

We performed constrained ordinations using the Vegan R package (Oksanen et al. 2006) to determine the main environmental parameters affecting the distribution pattern of spider species at the edges. Species represented by less than 18 individuals (one percent) were excluded from the analysis, thus the analysis was completed on 20 species. Abundance data were log-transformed (log(x+1)) prior to analysis to improve the normality of response variables. To gain insight into the existence of distinct assemblages, we applied non-metric multidimensional scaling (NMDS). Similarity matrices were based on Bray–Curtis distance measures. In order to estimate their influence, the environmental parameters of the microhabitats were fitted passively onto the NMDS ordination plot.

A preliminary detrended correspondence analysis (DCA) was conducted in order to gain insight into how the species respond to the environmental gradient. The gradient length, a measure of the extent of species turnover, did not exceed three SDs, it indicated a strong linear response of the species variance to the environmental parameters (Leps and Smilauer 2003, Batáry et al. 2008). We performed linear ordination method (RDA, Redundancy analysis). To identify the environmental parameters that explain significant variation, we performed a series of partial canonical redundancy analyses. The marginal and conditional effects of each variable were calculated, followed by Monte-Carlo permutation tests with 1000 permutations. Marginal effect refers to the explained variation by a single variable, whereas conditional
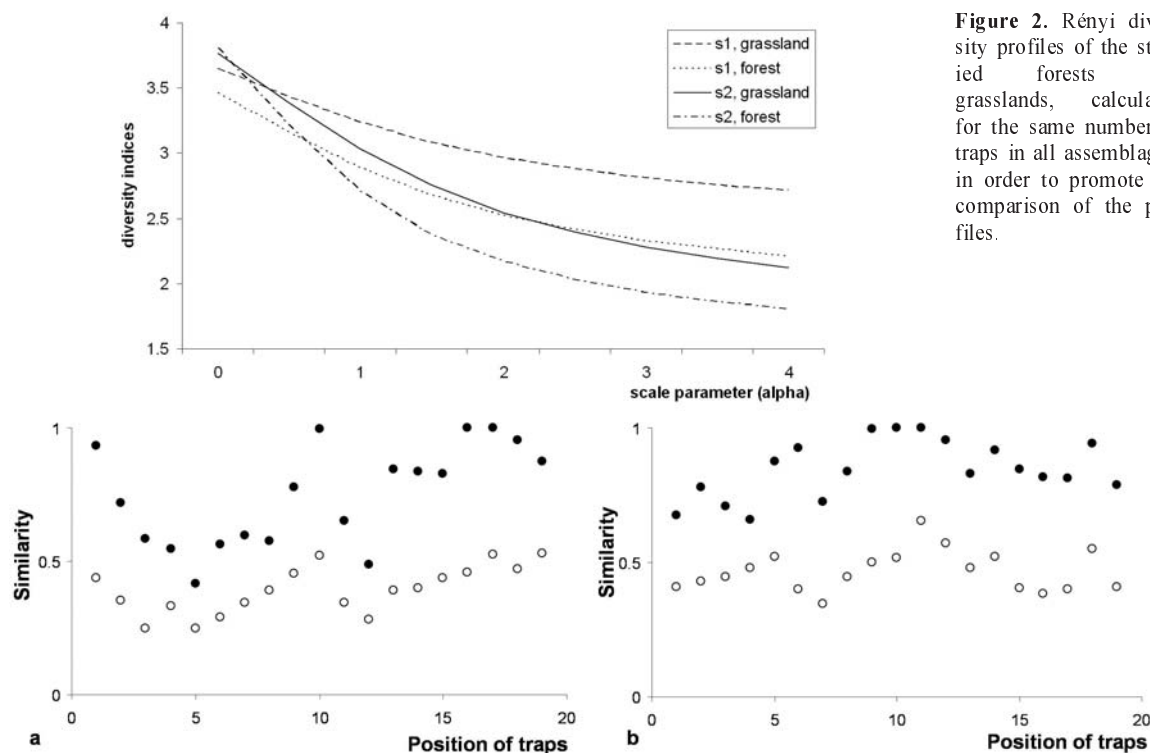
Figure 2. Rényi diversity profiles of the studied forests and grasslands, calculated for the same number of traps in all assemblages, in order to promote the comparison of the profiles.

Figure 3. The Jaccard index and the Chao's Jaccard-type similarity index computed between the subsequent groups of traps. Open circles indicate the classic Jaccard index and filled circles indicate Chao's Jaccard-type similarity index. **a)** site 1; **b)** site 2.

effect refers to the explained variation of the given variable after removing the effect of other variables (Muff et al. 2009).

Results

A total of 1715 adult individuals belonging to 62 spider species were collected during the study. The non-parametric multivariate ANOVA revealed significant differences between the grassland and forest habitat assemblages (for site one: pseudo-F=5.332, p<0.001; for site two: pseudo-F=2.795, p<0.001). The number of observed and the estimated species richness was higher for the grasslands, than for the forests (Appendix).

The diversity profiles of the spider assemblages inhabiting the different habitats are given in Fig. 2. In the case of site 1, the curve for the grasslands was situated above that for the forest and they do not intersect. Thus, the assemblages of the open habitats were more diverse for the whole range of the scale parameter, i.e., for indices sensitive to both the abundant and the rare species. At site 2, the curves intersected at low parameter values (α<0.5), for higher values the curve for the grasslands is situated above that of the forest.

We found fluctuating values of the classic Jaccard index and Chao's Jaccard-type similarity index towards the forest at site 1. Values of the indices indicated smooth transition between grassland and forest assemblages at site 2 (Fig. 3).

The NMDS scatterplot also indicated a smooth transition between the assemblages of the grassland and the forest at

both sites. The spider assemblages of the two sites differed clearly in their species composition. The first axis correlated with the coverage of leaf litter and the proportion of open ground. The second axis correlated with monocotyledonous plants (Fig. 4). RDA revealed that 47.2% of the species variation is due to the constrained components (studied environmental parameters of the microhabitats). The implemented permutation test indicated the significant combined effect of constraints (pseudo-F=6.18, p<0.001, based on 1000 permutations). According to the variance partitioning, the main environmental parameters influencing the spider assemblages were the percent coverage of leaf litter and bare soil surface. More than 25% of the variance was attributed to each of these factors, even though their effect overlapped considerably. These variables are indicators of the ground quality at a given microhabitat (Table 1).

Discussion

In Central Europe forest and open habitats are home to contrasting ground-dwelling spider communities (Entling et al. 2007). Martin and Major (2001) reported that the spider assemblage changed significantly across a forest edge; they found two homogeneous patches on both sides, and the community structure did not vary with the distance from the edge zone. In accordance with the finding in the present study, a number of authors have described that the variation in spider assemblages can be explained by the vegetation structure or succession stage (e.g., Robinson 1981, Raizer and Amaral 2001, Bonte et al. 2002, Asteraki et al. 2004). In some cases,

Table 1. Marginal and conditional contribution of the selected environmental variables in explaining the spider assemblage structure.

	Marginal effect			Conditional effect		
	Constrained variance(%)	Pseudo F	p	Constrained variance(%)	Pseudo F	p
bare soil surface	26.26	13.53	< 0.001	3.27	2.12	0.01
monocots	9.77	4.11	0.003	3.85	2.5	0.001
dicots	23.48	11.66	< 0.001	2.51	1.63	0.046
leaf litter	31.61	17.56	< 0.001	2.92	1.9	0.022
mosses and lichens	23.21	11.48	< 0.001	2.35	1.53	0.104

Figure 4. Non-metric multidimensional scaling (NMDS) of spider assemblages of the two forest edges (sterss: 0.209). The environmental variables are passively included and represented by arrows; their relative effect on the assemblage differentiation is indicated by the length and direction of the arrows. Species with N<17 are shown on the biplot.
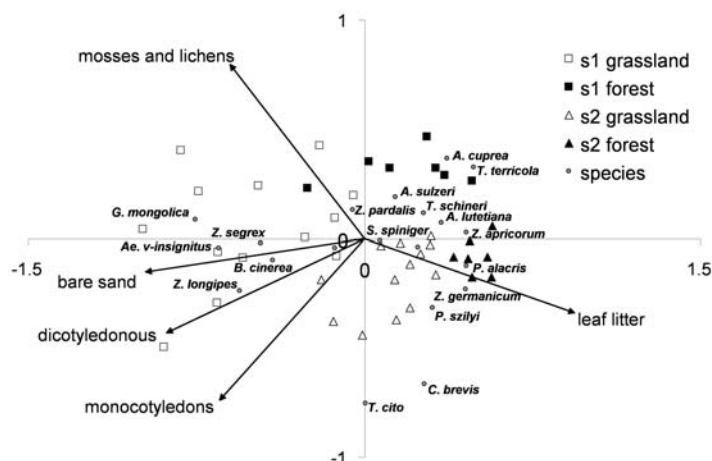
different habitat types exhibited assemblages with similar species richness and diversity, but differed in species composition (Raizer and Amaral 2001). Web-spinners display a strong relationship with the physical structure of the vegetation (Uetz 1991, Baldissera et al. 2004), as they require suitable sites for web building. However, even for non-web-spinners the habitat structure can be important (Bell et al. 2001). In our study, the contrasting structure between the scarce and species-poor litter covered understorey vegetation of the studied forests versus the vegetation structure of the grasslands proved to be very influential factors for the spider assemblages.

Besides, the greater spatial diversity of the herbaceous vegetation structure, the enhanced prey availability presumably also played an important role in shaping the higher diversity of spider assemblages of the grasslands. Several authors have demonstrated the interaction between the abundances of spiders and herbivorous arthropods, such as Orthoptera, Auchenorrhyncha, Aphididae (Birkhofer et al. 2008, Sanders et al. 2008, Cronin et al. 2004). The high proportion of unconstrained variance (52.8%) may not only represent random noise, but unmeasured variables e.g., prey availability, competition and reproduction (Muff et al. 2009), as well.

Various authors have detected differences between the species composition of different forest types (e.g., Pearce et al. 2004, Finch 2005). The different species composition of the two forests was possibly due to structural differences in the vegetation. Entling et al. (2007) also demonstrated that there was a strong relationship between community composition of ground-dwelling spiders and a shading gradient.

The vegetation of the grasslands, on the other hand, was similar: they were both open sandy grasslands, but the species composition and thus the fine structure of the vegetation differed. Besides the moss and lichens (*Tortula ruralis, Cladonia magyarica, C. foliacea* and *C. rangifera*), which were present in both grasslands, *Stipa borysthenica, Poa bulbosa,* and *Koeleria glauca* were the predominant plant species at site 1 while at site 2 the most abundant herbaceous plant species were *Festuca vaginata* and *Alkanna tinctoria*. The ground-dwelling spider assemblages of structurally different grassland habitats also differed in species composition and dominance structure in an Austrian study (Zulka et al. 1997).

At site two, higher poplar trees were also present in addition to the juniper bushes. At this site a higher number of individuals belonging to forest specialist species were collected in the grassland, e.g., *P. alacris, Z. apicorum*. This shift of the distribution pattern of these species was probably caused by the influence of the higher trees on the microclimate, e.g., the light regime, the temperature, the atmospheric and soil humidity of the adjacent region of the grassland. These factors are known to have strong influence on spider assemblages (Pearce et al. 2004, Entling et al. 2007, Ziesche and Roth, 2007). These factors, together with the vegetation structure, are important assemblage-structuring components (Dennis et al. 2001, Bonte et al. 2002, Gallé and Fehér 2006). Separation of microclimate from habitat structure is complex, as they are often correlated, but partial correlations

have been found between species diversity and temperature in a litter habitat (Uetz 1979). Each species has specific environmental requirements, so small changes in the habitat quality (e.g., microclimate, vegetation and prey availability) result in changes of the spider assemblages (Maelfait et al. 2002).

Previous work has demonstrated that the natural forest-grassland edges possessed distinct invertebrate assemblages which are more diverse than those of the adjacent habitats (Magura and Tóthmérész 1997, 1998, Horváth et al. 2002). The phenomenon was caused by the dense shrub layer at the edge of the forest serving as a separate habitat for many invertebrates. In that case, the edge habitats even had edge-associated spider species, which were the most abundant in the edge zone or lived exclusively there (Horváth et al. 2002). In contrast, both forest edges in this study were sharp, with no distinct vegetation structure. We did not collect any exclusively edge-associated spider species. Gallé and Fehér (2006) reported a similar finding in the case of a sharp edge between a poplar forest and a clearing.

In the case of forests composed of higher trees (site two in the present study) the edge zone was situated on the grassland. Small forest patches with high edge-to-area ratios may constitute appropriate habitats for distinct forest assemblages of spiders (Gallé 2008), despite the fact that this configuration is unsuitable for many vertebrate species (Martin and Major 2001). Accordingly, in the event of forest clearings, the edge effect in small patches can alter the spider assemblage considerably (Bonte et al. 2002), because of the intrusion of typical forest species, due to the high perimeter-area ratio. The small scale assemblage differentiation of spider assemblages found at the forest edges in the present study demonstrates that spiders sensitively indicate changes in the habitat structure.

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Appendix

The observed and estimated number of species, the list of observed species and the number of specimens per group of traps. The file may be downloaded from the web site of the publisher at www.akademiai.com.