

Habitat and landscape attributes influencing spider assemblages at lowland forest river valley (Hungary)

Róbert GALLÉ* and Szabina SCHWÉGER

Department of Ecology, University of Szeged, Középfasor 52, H-6726 Szeged, Hungary;
*Corresponding author, R. Gallé, E-mail: galle.robert@gmail.com

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Abstract. The lower Tisza valley in the Hungarian Great Plain consists mainly of small patches of semi-natural grassland and forest fragments embedded in a matrix of agricultural fields. We tested the effect of landscape and habitat attributes on the structure of spider assemblages. The fieldwork was carried out in nine forest fragments within two regions in the southern part of the Hungarian Great Plain, near the river Tisza. The epigeic spider fauna was collected with pitfall traps. The traps were arranged in three groups of five traps at each fragment. Landscape attributes had the strongest effect on spider species composition at the scales between 250 and 750 m, with a peak at 500 m buffer. Spider species composition differed between regularly flooded and non-flooded fragments. Vegetation cover and the proportion of neighboring forests had significant effect on the rarefaction diversity of spiders. Flooding, soil moisture, vegetation cover, and the proportion of forests within 500 m buffer significantly affected spider assemblages. Our results suggest that both habitat and landscape attributes affected spider species richness and composition in lower Tisza valley. Preserving many forest types is essential to maintain the high number of species in the regional pool.

Key words: Araneae, floodplain, Tisza, Hungarian Great Plain, rarefaction diversity.

Introduction

Most forests have been modified by human activities (Paillet et al. 2009). The most obvious of those changes are in forest structure, through the plantation of commercial trees (Eyre et al. 2010), and removal of non-productive native species, promoting homogenization of forest structure (Horrock et al. 2012). However, the forest epigeic fauna is rich and highly diverse (Schuldt et al. 2008). Floodplain woodlands support a distinctive biota that contributes substantially to regional biodiversity (Sabo et al. 2005). The floodplain of the Hungarian Great Plain was divided by dikes into flooded, non-flooded areas during the river regulation in the 19th century. Regular flooding may alter epigeic species composition, since well-adapted specialists and opportunistic generalists become more abundant (Aakra 2000, Plum 2005).

Spiders play an important role on leaf litter invertebrate assemblages as generalist predators (Wise & Chen 1999, Wise et al. 1993). They exert cascade effects on plants and decomposition process via top down forces and thus maintain the equilibrium of insect communities (Halaj & Wise 2001, Sanders et al. 2008). The strength of these top-down interactions is modified by habitat structural complexity and vegetation height (Sanders et al. 2008). However, spiders can be limited by prey population density (Wise 1999).

In addition to interspecific interactions, the diversity and composition of spider assemblages are influenced by habitat and landscape attributes (Topping 1999, Oxbrough et al. 2005, Herrmann et al. 2010). Spiders are strongly influenced by habitat structure and microclimatic factors (Samu et al. 1999). In the case of forest ecosystems, shading and structure of the forest floor seem to influence spider assemblages (Oxbrough et al. 2005, 2006, Entling et al. 2007). Different litter type and depth may provide different hunting sites, web attachment points, and shelter against predators (Uetz 1979, Bultman & Uetz 1984, Wagner et al. 2003, Pearce & Venier 2006). Accordingly, litter quality might be affected by the composition and diversity of tree species, since decomposition dynamics may differ among tree species (Gartner & Cardon 2004, Schuldt et al. 2008), and according to flooding regime. Habitat requirements are different for every spider species, thus spider species composition may be an indicator of changes in habitat quality (Uetz 1991, Pearce & Venier 2006). At a broader scale, the composition and spatial heterogeneity of the landscape are relevant variables to explain spider assemblages (Turner 2005, Schmidt et al. 2008).

Our study aims to explore the factors influencing the (1) diversity and (2) composition of spider assemblages of flooded and non-flooded forests. We expect the number of species to increase with

higher cover of leaf litter and more structured understory vegetation (Greenstone 1984, Pearce & Venier 2006). Following Entling et al. (2007) and Lambeets et al. (2008, 2009), we expect vegetation structure, shading, and regular flooding to alter species composition of spiders. In terms of landscape attributes, we expect species richness to increase, and the composition of the assemblages to change with the increasing proportion of forests and grasslands. For habitat specialists, habitat patches may function as islands (Schmidt et al. 2008). The increasing proportion of forests results in higher habitat connectivity and greater habitat patches, positively affecting habitat-specialist spiders. Forest patches are usually not hostile, even for grassland specialist species (Lövei et al. 2006, Hartel et al. 2008), thus the inclusion of generalist and grassland spiders in the forest fauna is also feasible (Gallé 2008).

Material and methods

Study site and sampling

Two regions at the lower reach of the River Tisza were selected for sampling spider assemblages (Fig. 1). The southern region (Vesszős) is near Szeged (46°17'30"N; 20°14'20"E), where the landscape mainly consists of small patches of forest plantations and grasslands embedded in a matrix of arable fields (more than 60%). The Dóc region lies 40 km north of Szeged (46°26'20"N; 20°10' 40"E), which is a relatively low land-use area, with percentages of arable fields less than 50%.



Figure 1. The location of studied regions.

Spider assemblages were studied in a non-flooded poplar plantation, poplar-oak mixed-wood forest, floodplain oak forest, and mixed-wood forest mainly consisting of *Acer negundo* and *Fraxinus pennsylvanica* in the southern region. In the northern region, spiders were collected at a non-flooded poplar plantation, the edge of a poplar forest, non-flooded oak forest, in the floodplain a poplar plantation, and a willow forest.

Pitfall traps were used to sample ground-dwelling spiders. Traps consisted of a plastic cup with 65 mm in diameter. Each trap was filled with antifreeze (ethylene glycol) to a depth of 2 cm to act as a killing and preserving agent (Koivula 2003, Schmidt et al. 2006).

Three lines of traps (sampling plots) were placed at each site, each line consisting of five traps 4 m apart from each other. The data of the five traps were pooled in all analyses. Traps were kept open for four sampling periods in 2007 (27 May–13 June, 30 June–15 July, 16–30 August, 18 September–01 October), which included the activity period of spider species. The data of the four sampling periods were pooled.

To characterize vegetation structure, plant species richness and vegetation cover at the ground level, at 10 cm and 40 cm above ground, and average height of herbaceous vegetation were measured within 1 m² quadrates near traps. Soil samples were taken from the top 10 cm near traps. The percentage of soil water content was measured. Canopy cover was assessed on the basis of digital photographs taken near the ground level at each trap.

To assess landscape attributes, the proportion of land-use types (i.e., grasslands, forests, and arable fields) was measured based on satellite imagery. To identify the scale at which the response of local species composition to landscape composition is the strongest, the landscape attributes was measured at five different scales (i.e., 50 m, 100 m, 250 m, 500 m, and 750 m buffer around each sampling plot).

Data analysis

To identify the scale at which landscape attributes had the strongest effect on spider species composition, a series of Canonical Correspondence Analyses (CCA) was performed using R package *vegan* (Oksanen et al. 2010). Separate CCAs including landscape attributes were performed for each scale. The models were ranked on the basis of the constrained inertia to identify the adequate scale. Species with less than five individuals were excluded from the analyses. Species data were Hellinger transformed prior to analysis (Legendre and Gallagher, 2001). Our statistical approach, i.e., using a series of CCAs to test the species composition–landscape attributes relationship at different spatial scales, followed previous studies (He et al. 2012, Torma & Császár 2013)

Although species richness is one of the simplest measures of diversity (Magurran 2004), it is dependent on sampling efficiency, which is in turn affected by habitat structure (Melbourne 1999). With increasing catch, an increasing number of species is collected (Magurran 2004). Due to variation in the number of recorded individuals, rarefaction diversity was used to standardize the number of species recorded within each sampling plot (Heck et al. 1975, Gotelli & Colwell 2001).

To assess the influence of explanatory variables on rarefaction diversity, habitat and landscape attributes were entered in a linear mixed-effects model with Gaussian error term and nested random effect using R package *nlme* (Pinheiro et al. 2007). Habitat complexes and sampling sites were used as random effects in the model.

Stepwise selection procedure was conducted using R package MASS (Venables & Ripley 2002), with variables being selected according to their Akaike's information criterion (AIC).

The CCA was used to identify explanatory variables that affect species composition. To identify important habitat parameters we applied stepwise selection on the basis of the AIC (Oksanen et al. 2010). The marginal effect of the habitat parameters included in the final CCA was tested with Monte Carlo permutation tests using 5000 permutations.

Analysis was performed in R (R Development Core Team, 2007) with vegan package (Oksanen et al. 2010).

Results

We collected 3,105 spiders, of which 1,695 were adults and could be identified to species level. Of these, we identified 84 species belonging to 18 families (Supplementary material – available only online). The most abundant species *Ozyptila praticola* (C.L. Koch, 1837), *Pardosa lugubris* (Walckenaer, 1802), and *Trochosa terricola* Thorell, 1856 are known to occur in various forest habitats and edges (Buchar & Ruzicka 2002). Ninety-six out of 103 individuals of the agrobiont species *Oedothorax apicatus* (Blackwall, 1850) occurred in floodplain forest fragments.

Landscape attributes had the strongest effect on spider species composition between 250 m and 750 m, with a peak at the 500 m buffer (Fig. 2). Therefore, we used the proportion of the surrounding grasslands, forests, arable fields in 500 m buffer around the plots for further analyses.

We found a significant effect of vegetation cover, flooding, and proportion of surrounding forest cover on the rarefied species richness (Table 1).

Vegetation cover ($F(1,19)=2.431$; $P<0.001$), plant species richness ($F(1,19)=1.652$; $P=0.002$), tree species richness ($F(1,19)=1.818$, $P<0.001$), flooding ($F(1,19)=2.212$; $P<0.001$), proportion of forests ($F(1,19)=1.740$; $P=0.003$), arable fields ($F(1,19)=2.163$; $P<0.001$) and grasslands ($F(1,19)=1.612$; $P=0.004$) had significant effect on spider species composition (Fig. 3).

Discussion

The high number of the agrobiont spider *O. apicatus* in floodplain forest fragments probably indicates the effect of agricultural matrix on spider assemblages. Their presence in floodplain forest fragments and natural grasslands is presumably

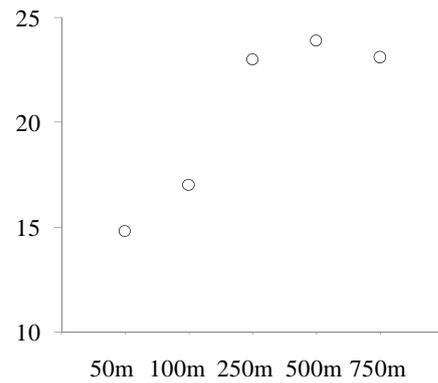


Figure 2. Spider species composition in relation to landscape attributes. Proportion of constrained inertia (%) plotted against the spatial scale (in meters) at which the landscape attributes was calculated.

Table 1. Results of the linear mixed-effects model after stepwise selection. Vegetation cover, flooding, and the proportion of forests in 500 m buffer influenced the rarefaction spider diversity.

	β	t	P
Vegetation cover	-0.021	-2.212	0.042
Flooding	-4.517	-2.854	0.035
Tree species richness	-0.358	-1.430	0.211
Grasslands %	-0.139	-1.742	0.101
Forests %	0.092	2.297	0.036

due to continuous colonization from neighboring habitats. Agrobiont linyphiid spiders have high dispersal ability, due to efficient ballooning mechanism (Duffey 1998, Bonte et al. 2004). Bonte et al. (2004) also found agrobiont linyphiid spiders in natural sand dunes. Moreover, the regular disturbance regime of floodplains due to inundations resembles the disturbance regime of agricultural habitats due to harvesting the crops. Species assemblages of such disturbed habitats are determined by the resistance of species to disturbance (Bonte et al. 2006, Lambrechts et al. 2008). The most of the spider species do not tolerate long submersion during the winter and spring (Pekár 1999). Thus, the majority of spider species migrate from the adjacent non-flooded habitats to habitats with regular flooding, presumably from agricultural fields in the case of the agrobiont *O. apicatus*. Rand et al. (2006) and Opatovsky et al. (2010) also reported the dispersal of agrobiont species to natural habitat patches.

Forest spider species are nonrandomly distributed. The regular flooding events had a significant effect on the rarefaction diversity of spiders.

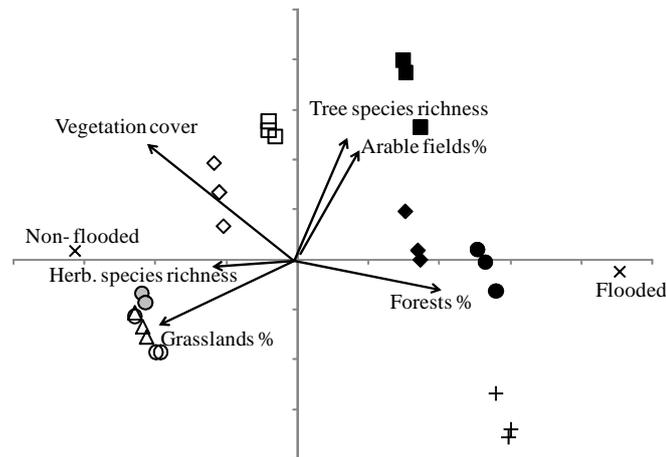


Figure 3. Ordination plot of the canonical correspondence analysis. Factors with significant effect are represented with (X). Filled symbols represent floodplain forests, open symbols represent non-flooded forests. Diamonds - poplar forests (S) circles - poplar forests (N), grey circle - poplar forest near the edge (N), squares - oak, and mixed oak forests (S), triangles - oak forest (N), crosses - willow forest (N); N - northern habitat complex, S - southern habitat complex.

This is in concordance with Sabo et al. (2005) and Lambeets et al. (2009), as they also demonstrated that riparian habitats do not necessarily harbor more species than other habitat types, despite the high local variation in habitat parameters. Regular flooding events determine species composition of the vegetation and habitat structure, which in turn influence spider species composition (Duffey 1968, Scheidler 1990, Ballinger et al. 2005, Plum 2005, Petillon et al. 2008, Gallé et al. 2011). Gravesen (2000) and Lambeets et al. (2006) also demonstrated that flooding intensity and vegetation structure influence spider species composition in wetlands.

The present study confirmed the direct effect of tree and herbaceous species richness on spiders. Several studies also demonstrated the effect of plant diversity on habitat structure and microclimatic characteristics (Bell et al. 2001, Schuldt et al. 2008). Tree species richness plays a prominent role in determining canopy cover. Shading is important because it affects microclimatic conditions of the forest floor (McIver et al. 1992).

Recent studies have shown that landscape attributes influence spider species composition (e.g., Öberg et al. 2007, Batáry et al. 2008, Schmidt et al. 2008). However, it is difficult to generalize the effect of landscape attributes. The response of local abundance of spiders to landscape attributes varies between families and species (Burel & Baudry 1995, Jeanneret et al. 2003), depending on the degree of habitat specialization of species (Haila 2002).

In accordance with our results, several studies suggest that landscape attributes at scales of ~ 500 m buffer affect spider diversity and composition

(Clough et al. 2005, Schmidt & Tschardtke, 2005, Schmidt et al. 2005). Various species react differently to the scale of the landscape attributes, depending on dispersal abilities (Schmidt et al. 2008).

Several studies also found that a higher proportion of natural and semi-natural habitats in the surrounding landscape is associated with a higher number of spider species, since these patches may serve as source habitat for spiders (e.g., Jeanneret et al. 2003, Öberg et al. 2007, Drapela et al. 2008). Our results confirmed the influence of the surrounding grasslands on spider diversity and composition. This is presumably due to the penetration of grassland specialist species into forest fragments. However even at a distance of a few meters, the movement of some open-area species into the forest fragments is limited (Downie et al. 1996, Oxbrough et al. 2006, Gallé & Torma 2009). Generalist and grassland-specialist species penetrate into the forest interior only if the canopy is not closed (Gallé 2008).

Barbaro et al. (2005) also concluded that, besides landscape heterogeneity, the shape and proportion of deciduous forest fragments in the surrounding landscape had positive influence on pine forest spiders. The size and connectivity of forest fragments strongly influence on the species composition if it is less than several hectares (Pajunen et al. 1995, Pearce et al. 2005). Smaller patches, with a high edge-to-area ratio, act as edge habitat and thus could be inhabited by grassland-specialist spiders (Gallé 2008).

In consequence of the river regulation, floodplain forests along the river Tisza decreased drastically and the remnants of the original habitats are invaded by numerous non-native plant spe-

cies. The studied fragments harbor different spider species. Thus, besides conserving the remaining semi-natural floodplain forest fragments, maintaining the diversity of non-flooded forests will result in higher number of species in the regional species pool.

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(List of the collected species. Abbreviations: (N)= northern habitat complex, (S)= southern habitat complex.)