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The effect of forest stand characteristics on spider diversity and species composition in deciduous-coniferous mixed forests

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Abstract. We studied how forest stand characteristics influence spider assemblage richness and composition in a forested region of Hungary. Deciduous-coniferous mixed forests dominate in the Őrség National Park. Thirty-five plots were established and sampled for spiders for three years in 70–110 year-old stands with a continuum of tree species composition. Detailed background information was acquired for stand structure, tree species composition, forest-floor-related variables and spatial position of the plots. The effect of variables was analyzed by nonparametric multiplicative regression on rarefied spider species richness and by redundancy analysis on species composition. The relative importance of variable groups was assessed by variation partitioning. Spider species richness was positively and strongly affected by tree species richness, and the species composition of the spider assemblage was influenced by the proportion of the most important tree species. This study established the importance of tree species composition, but variance partitioning analysis also showed that tree species identity and forest floor variables together explain much of the variation. These findings may guide management and conservation efforts to maintain regional diversity of the spider fauna.

Keywords: Araneae, habitat model, species richness, non-parametric multiplicative regression, assemblage composition

Spiders play an important role in forest ecosystems by occupying varied and crucial points in the forest food web and also by significantly contributing to forest biodiversity. In the classic study by Moulder and Reichle (1972) the fate of radioactive ^{137}Cs isotopes was followed through the whole food chain of a *Liriodendron* forest, and spiders proved to be the most important predators of the forest litter community both in numbers and in biomass. Predation by spiders may also initiate cascading effects in the food chain; spiders preying on decomposers will lower the decay rate of plant material (Lawrence & Wise 2000). In removal experiments lack of spiders had a positive effect on populations of both herbivorous prey and smaller predatory arthropods (Clarke & Grant 1968). At the same time, we know that spiders present numerous predatory tactics and fill many different niches (Entling et al. 2007). Therefore, knowledge on species richness and functional diversity (Schuldt et al. 2011) will lead us closer to understanding spiders' roles in different forested habitats.

Spider diversity in forests is influenced by many factors (Larrivee & Buddle 2010), and many studies address a certain set of variables, but many fewer take an integrative approach and compare the relative importance of various environmental factors. Several studies have underlined the importance of local factors (Niemela et al. 1996; Entling et al. 2007). Local variation creates high beta and consequently high gamma diversity (Schuldt et al. 2012) because a considerable proportion of forest spiders are habitat specialists (Floren et al. 2011). However, severe management practices that homogenize forest habitats lead to declines of sensitive species and beta diversity (Niemela 1997).

Beside general patterns in diversity, many studies concentrate on the role of vegetation structure and abiotic factors associated with microhabitats, especially at forest floor level. The species distribution of forest-floor spiders is significantly affected by litter type, structure, ambient light, humidity and temperature parameters (Uetz 1979; Varady-Szabo & Buddle 2006; Ziesche & Roth 2008; Sereda et al. 2012).

Much more controversial than the effect of generally appreciated small-scale structural characteristics is the effect of tree species composition and stand structure on spider assemblages. The spider compositions of deciduous stands in a Canadian boreal forest (aspen and mixed wood) were very similar but distinct from those of spruce stands (Pearce et al. 2004). A study in central European forests found no significant difference in the abundance or species richness of spider assemblages associated with three coniferous species, while such a difference was found across different deciduous species (Korenko et al. 2011). Schuldt et al. (2008) found no general relationship between increasing tree species diversity and patterns of diversity and abundance in the spider communities of deciduous forest stands in Germany. Woody plant diversity affected spider assemblage structure, but not species richness, across 27 study plots in China (Schuldt et al. 2012).

Given the relatively few studies that assess the importance of different groups of variables on forest spider communities, and the existing equivocal results on the role of stand type and tree species diversity, we intended to establish how much spider assemblages differ across different forest stand types with a continuum of tree species composition. We asked how tree species composition, stand structure and forest floor variables affect spider assemblages as well as the respective importance of these factors in determining local species richness and species composition.

METHODS

Study area.—Our study was conducted in forested areas of the Őrség National Park (46°51′55″N, 16°07′23″E), close to the borders of Hungary, Slovenia and Austria (Fig. 1). The

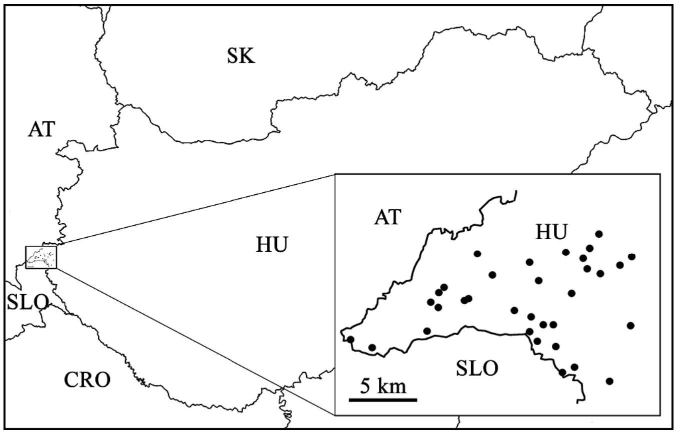

Figure 1.—The study area is Őrség National Park in the westernmost part of Hungary. The inset depicts the 35 locations containing the experimental plots.

elevation is between 250–350 m, the average annual precipitation is 700–800 mm and the average annual temperature is 9.0–9.5 °C (Dövényi 2010).

The Őrség National Park is dominated by beech (*Fagus sylvatica* L.), oak (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst.]. The dominant forest types are sessile oak-hornbeam woodland, acidofrequent beech woodland, and acidofrequent mixed coniferous forest (see Ódor et al. 2013).

We selected 35 locations in mature stands (age 70–110 yr. old, size 2–10 ha) by stratified random sampling of the area (Fig. 1) from the database of the Hungarian National Forest Service, applying the selection criteria that the topography of the plots should be more or less flat and the topsoil should not be influenced by ground water. Stratification ensured that the selected locations represented the most common tree species combinations of the region, including a continuous gradient in the proportion of the main tree species. Within each location we established a 40 × 40 m plot, where environmental variables were determined.

Variables.—Trees were mapped within the plots, forest floor vegetation and litter cover were estimated in quadrats and microclimate measurements were made. The original data collection resulted in a large number of variables (for more detail on measurements and methods, see Ódor et al. 2013), but for the present study we considered only 21 variables. The variables represented four categories: 1) tree species composition, which is tree species richness and the relative representation of main tree species, expressed as percentage relative tree volume; 2) stand structural variables (number, size, size variation of trees); 3) forest floor variables (coverage of main vegetation elements, litter and bare soil, plus microclimatic variables) and 4) spatial component, represented by x, y spatial coordinates of plot center. These four groups largely cover environmental variables that according to the literature (detailed in the Introduction) were likely to exert an effect on spider distribution in a forest habitat. The variables are listed, described and categorized in Supplemental Table 1 (online at http://www.bioone.org/doi/suppl/10.1636/CP13-75).

Table 1.—Sampling dates and sampling efforts in the 35 forested plots of Őrség National Park.

	Suction sampling	Pitfall trapping	
Campaign date	samples/plot	traps/plot	days open
06/07/2009	3	5	31
08/10/2009	5	5	28
01/10/2010	8	5	27
28/05/2012	-	5	30

All explanatory variables were standardized for statistical modelling (zero mean, one standard deviation).

Sampling.—Spiders were collected from each plot by pitfall trapping and suction sampling during four sampling campaigns in the most species-rich periods: summer and autumn. Such a time-limited sampling approach, optimized for the most species rich periods, is recommended for the comparison of assemblages at a large number of localities (Jimenez-Valverde & Lobo 2006). Sampling dates and sampling efforts are summarised in Table 1.

Five pitfall traps were deployed in a plot during a campaign: one placed in the center, the other four forming a square of ca. 15 m sides positioned symmetrically around the center. Pitfalls were plastic cups of 75 mm upper diameter filled with 70% ethylene glycol as preservative, with some detergent added (Kádár & Samu 2006). Traps were open for a month; the catch was sorted and spiders stored in 70% ethanol until identification. Voucher specimens were placed in the collection of the Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences.

Suction sampling was performed with a hand-held motorized suction sampler, fitted with a 0.01 m^2 orifice (Samu & Sárospataki 1995). We tried to sample all microhabitats in a forest stand up to 1.5 m height with suction sampling. One sample lasted for ca. 60 s, consisting of several applications of the sampler, in which we first sampled from microhabitats that produced the least debris (e.g., leaves from bushes and lower branches of trees and trunks), then we continuously sampled other habitats (such as dead wood surface, gravel surfaces, patches of terricolous mosses), and only in the last couple of applications was litter and soil sampled, because it could potentially congest the apparatus. This way each sample was a cross section of the microhabitats of a smaller area within the 40×40 m plot. Since the number of specimens caught was smaller than we initially expected, we increased the number of samples per plot over the campaigns (see Table 1). Because of variable catches per sample, all samples from a plot across methods and dates were lumped and used that way in data analysis.

Data analysis.—We estimated spider species richness for the whole area by calculating the non-parametric species estimator Chao1 (Chao et al. 2005) using the software EstimateS version 9.0 (Colwell 2013). We also calculated the Chao1 estimator separately for each plot and observed that in five plots estimated Chao1 values showed erratic behavior along the species accumulation curve, which is a sign that the spider assemblage may have been under sampled at those plots (Colwell 2013). These plots were excluded from species richness modelling. To establish plot level species richness estimates for the 30 plots not excluded based on Chao1 behaviour, we used the more conservative rarefraction method. We made estimations of species richness rarefied to 75 individuals (S_{75}, mean number of adult individuals caught in the plots was 74.2) using the individual-based abundance model of Colwell et al. (2012) as implemented in EstimateS (Colwell 2013).

We explored how species richness is influenced by environmental variables using Nonparametric Multiplicative Regression (NPMR), carried out by Hyperniche 2 (McCune & Mefford 2009). The NPMR method (McCune 2004) predicts a univariate response (e.g., abundance of a species or species richness of a community) at a target locality from other localities that are close to the target locality in the environmental space. The response surface resulting from predictions for each locality can be of any shape and is not determined by a certain function (hence non-parametric). The local mean method, applied here, weights neighboring responses according to vicinity in the environmental space by a Gaussian weighting function. Response from localities where environmental variables have the same values as at the target locality would receive a weight of one; response at less similar localities are weighted decreasingly according to the weighting function. Multivariate weights are gained multiplicatively. The width of the weighting function (standard deviation of the Gaussian function) is termed tolerance and during fitting is optimized for each variable. Variable selection and optimization is done iteratively maximizing the cross-validated coefficient of determination (xR^2, meaning that the observed response at a given point is not included in the estimation of the response), and its significance is tested by Monte-Carlo simulation (McCune 2004). Gaussian local mean NPMR was applied to S_{75} at 30 localities. The method requires positive values, therefore we added a constant ($c = 4$, the smallest natural number that made all values positive) to the values of the standardized explanatory variables.

To study the multivariate response of species to environmental variables, Redundancy Analysis [RDA, carried out by Canoco 4.5 (Ter Braak & Smilauer 2002)] was performed, supposing approximately linear relationships between species performance and explanatory variables (Leps & Smilauer 2003). In preliminary Detrended Correspondence Analysis the gradient lengths of the main axes were short (1.9–2.1 SD units), supporting linear relationships. Rare species (frequency less than 4) were excluded from the analysis. The same initial set of explanatory variables was used as for the NPMR model (Suppl. Table 1). The explanatory variables were selected by manual forward selection, and their effect and the significance of the canonical axes was tested by F-statistics via Monte-Carlo simulation (Ter Braak & Smilauer 2002). Because spatial coordinates had a significant effect after model selection, the analysis was repeated using them as covariates (Ter Braak & Smilauer 2002). Variation partitioning was carried out to explore the amount of variance in the species assemblages accounted for by the four categories of explanatory variables (Peres-Neto et al. 2006). All 21 explanatory variables were included in variation partitioning, which was carried out in R 3.0.2. (R Core Team 2013) using the vegan package (Oksanen et al. 2011).

RESULTS

Species richness estimation.—During the study 4567 spiders were caught, distributed nearly equally among the two sampling methods (suction sampling: 2245, pitfall trapping: 2322 individuals). Out of the total catch 2596 spiders were adults; these represented 91 species (Suppl. Table 2; online at http://www.bioone.org/doi/suppl/10.1636/CP13-75).

Table 2.—Best local mean model of species number rarefied to 75 individuals, fitted by NPMR model (McCune & Mefford 2009) with conservative over-fitting control. The best model based on xR^2 included three variables: tree species richness, relative volume of Scots pine and shrub density. Min. and Max. refer to the minimum and maximum value of the given variable on the standardized scale. Tolerance is one standard deviation of the Gaussian smoothing function by which the optimal model was reached. Tol. % is the percentage of Tolerance to the data range (Max.–Min.).

Variable	Min.	Max.	Tolerance	Tol.%
Tree species richness	2.13	6.25	0.91	22
Scots pine rel. volume	2.95	5.80	0.77	27
Shrub density	3.14	7.41	0.64	15

In species richness estimation of the species pool of forest spiders, we presumed that samples from the 35 localities were representative of the regional forest spider fauna accessible with the given sampling protocol. Chao1 species richness estimator (S_{Chao1}) was calculated along the species accumulation curve. It reached its peak value at 1589 individuals, where it gave an estimate of $S_{Chao1} = 103.4$ species, from where it gradually declined, and at full sample size reached $S_{Chao1} = 100.5$ species with $CI_{95\%} = 94.1–119.9$.

For the 30 plots where the Chao1 estimator was stable, mean species number was 18.2 ($CI_{95\%}=12.5$, 23.8). Chao1 species richness was on average 25.1 ($CI_{95\%}=19.3$, 52.2).

Rarefied species number environmental model.—We applied local Gaussian mean NPMR to establish which environmental variables are the best in predicting rarefied species number. The best model (Table 2, Fig. 2) included three explanatory variables: tree species richness, proportion of Scots pine by volume and shrub density. Spatial variables entered in the initial model fell out during iterative variable selection. With $xR^2 = 0.596$, it explained ca. 60% of variance in S_{75}, and was highly significant ($P = 0.009$) in the randomization test.

Spider assemblage environmental model.—After the exclusion of rare species, 45 species were used in RDA. In the final RDA model canonical variables explained 31.2% of the total species variance, with the first ($F = 6.22$, $P = 0.002$) and all canonical axes ($F = 3.18$, $P = 0.002$) being significant based on Monte-Carlo simulation. The most important explanatory variables were the relative volume of oak ($\lambda_A = 0.10$, $P = 0.002$), beech ($\lambda_A = 0.06$, $P = 0.004$), hornbeam ($\lambda_A = 0.05$, $P = 0.004$) and air humidity ($\lambda_A = 0.04$, $P = 0.006$) (Fig. 3.).

Variation partitioning showed that the four variable groups of the RDA (this time not treating the spatial component as a co-variable) explained 35% of the variation. The most variation was explained by tree species composition (26%) and the least by stand structure (16%) (Fig. 4). However, most of the variation was shared between variable groups. The highest shared variation was between tree species composition and forest floor variables (16%). Spatial component alone was responsible for only 7% of the total variation (Fig. 4).

RDA ordination indicated that spider species responded to the environmental gradients in a continuous way; they were rather evenly distributed around the ordination center

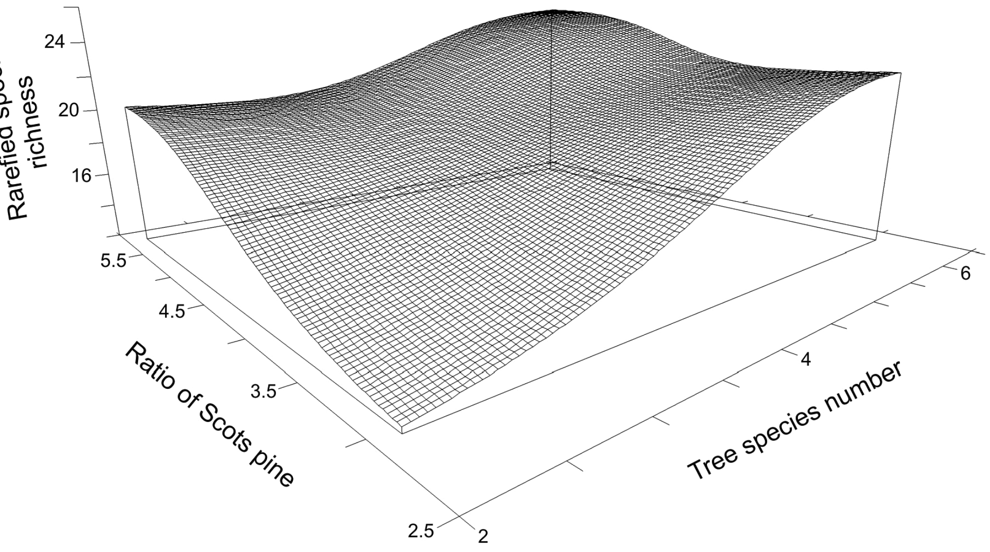

Figure 2.—Response surface of the best local mean NPMR model on rarefied species number, depicted for the first two predictor variables (for further explanation see text and Table 2).

(Fig. 3). Nevertheless, an oak-hornbeam gradient could be discerned along Axis 1, with the wolf spiders *Pardosa lugubris* (Walckenaer 1802) and *Trochosa terricola* Thorell 1856 markedly associated with oak, while *Histopona torpida* (C.L. Koch 1834), a funnel web weaver species, was strongly associated with hornbeam. Other species such as *Cicurina cicur* (Fabricius 1793) and *Malthonica silvestris* (L. Koch 1872) had a preference for both hornbeam and humidity. A number of hunters (*Harpactea lepida* (C. L. Koch 1838), *Clubiona terrestris* Westring 1851, *Dysdera ninnii* Canestrini 1868) and some linyphiid species [*Drapetisca socialis* (Sundevall 1833), *Micrargus herbigradus* (Blackwall 1854)] were associated with beech. Beech-hornbeam mixed stands occurred in the area, and the amauroboid species *Eurocoelotes inermis* (L. Koch 1855) seemed to be strongly associated with this stand type. Air humidity vs. dryness comprised another significant gradient, with *Macrargus rufus* (Wider 1834) associated with humid conditions and *Mangora acalypha* (Walckenaer 1802) with dry conditions. The latter orb weaver is mostly known from open grassland habitats. There were, however, quite a number of species positioned intermediate between oak and humidity [e.g., *Agroeca brunnea* (Blackwall 1833), *Lepthyphantes minutus* (Blackwall 1833) and *Haplodrassus dalmatensis* (L. Koch 1866)] that could not be associated with environmental variables based on the present analysis (Fig. 3).

DISCUSSION

In the present study we explored the basic but still unresolved problem of how spiders depend on stand scale vegetation features. In the forested area of the Őrség National Park, deciduous and mixed forests show a continuum of tree species composition. By studying spider assemblages in 35 localities, we wanted not only to assess regional species richness, but also its variability depending on an extensive set of variables related to the forest stands. Our sampling efforts were limited to certain times of the year and certain microhabitats accessible by the sampling protocol and were mostly suited to make comparisons across the localities (Jimenez-Valverde & Lobo 2006). Still, our richness estimate of 95–120 species (with 95% confidence) was very similar to values reported from temperate forests (Coddington et al. 1996) and approximates the species number of 149 found in the Uzungwa Mountains of Tanzania (Sorensen 2004).

We collected a considerable amount of data about the forest plots, out of which we used 21 variables in four variable groups to explore the dependencies of species richness and composition. Since sampling resulted in a variable number of individuals, we used individual- based rarefied richness values for comparison. In a Canadian case study rarefied species richness standardized to the number of individuals enabled the most accurate comparisons, especially when sampling was limited (Buddle et al. 2005). To analyse the importance of environmental variables we applied non-parametric methods that made no assumptions about species response and used rarefied richness data only from plots where sampling proved to be adequate.

Tree species richness of the forest stands proved to be the most influential factor of spider species richness. Although intuitively expected in the light of other studies (De Bakker et al. 2000; Pearce et al. 2004; Ziesche & Roth 2008), this is a notable result, especially because our survey took into account a spectrum of different environmental variables including microclimatic factors, forest floor cover, stand structure and spatiality. Other studies have typically concentrated on a narrower range of explanatory variables. Small-scale studies could show the importance of structural and abiotic features (Varady-Szabo & Buddle 2006; Sereda et al. 2012), while large-scale studies showed the negative effects of habitat homogenization and the importance of species pool and connectivity to nearby habitats (Niemela 1997; Floren et al. 2011). Tree species are in fact connected to all these levels – they have various structural aspects and also affect forest floor variables. In the present study where variables representing four different groups were entered into the models, the most influential level of variables was how variable the tree composition was; i.e., how many tree species were present in a plot.

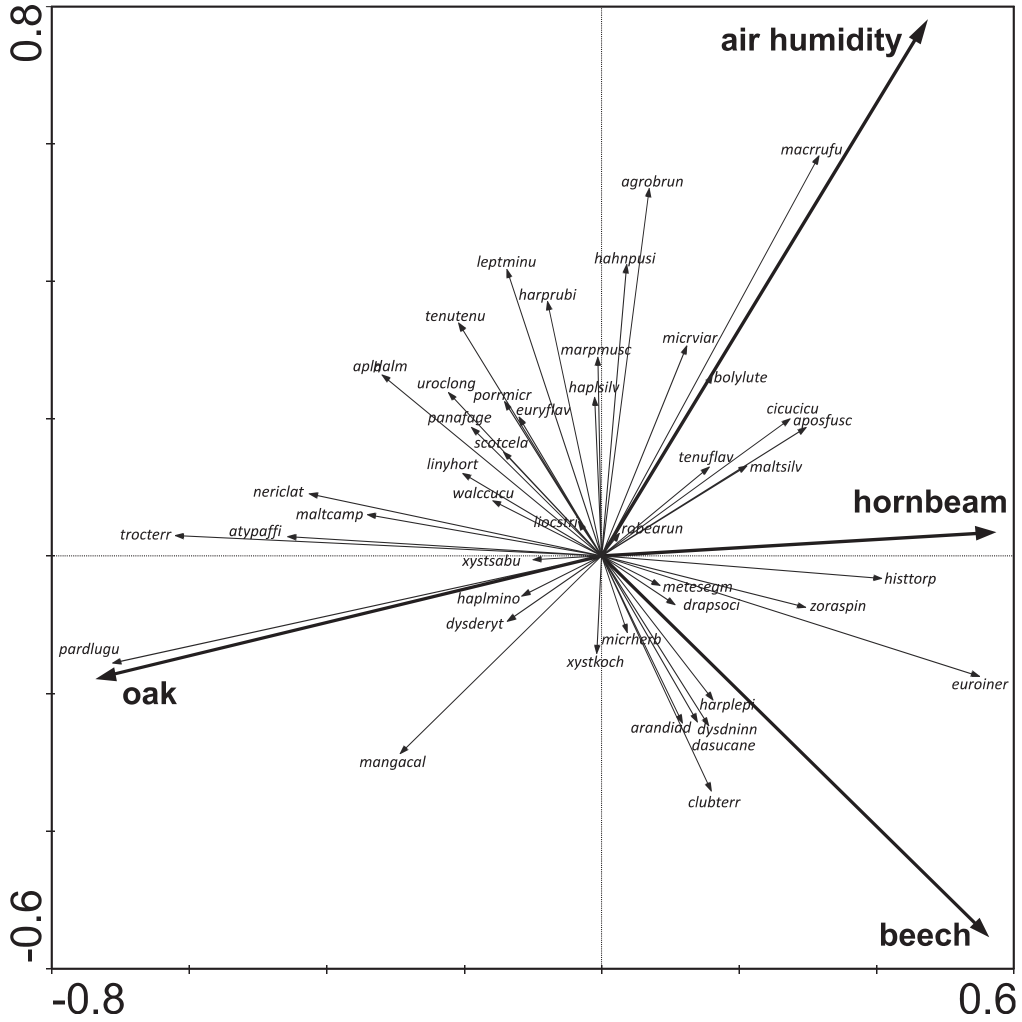

Figure 3.—RDA ordination diagram of species in relation to environmental variables. Hornbeam, oak, beech: relative volume of the tree species in the stands; air humidity is mean daily air humidity based on eight measurements. Species abbreviations are composed from the first four letters of the generic and species name of each species (for species list see Suppl. Table 2; online at http://www.bioone.org/doi/suppl/10.1636/CP13-75).

Although it is only logical that if the number of tree species influences spider richness, then spider species composition should be influenced by tree species composition, not all previous studies warrant this outcome (Pearce et al. 2004; Oxbrough et al. 2012). In a study where association between spider species in different tree species was investigated, the outcome was different between deciduous and pine trees (Korenko et al. 2011). The physiognomy of forest stands characterized by certain tree species also determines abiotic factors, such as microclimate and litter characteristics, and also determines the quality of undergrowth. Our variation partitioning showed that this is indeed the case. Tree species composition and forest floor characteristics together explain the most variation in spider species distribution, but if single variables are considered, then the complexity of many environmental factors seems to be united (and most easily measured) in tree species. Associations, such as the correlation of wolf spiders with higher preferences for open habitats (Hänggi et al. 1995) with oak, are likely to have a complex explanation including litter type and microclimatic conditions, which are all related to the dominant tree species. We can see examples of other associations that may be determined by the specific microhabitats certain tree species provide – for instance the occurrence of *Drapetisca* spp. on smooth bark surfaces, which are provided by beech (Hovemeyer & Stippich 2000; Larrivee & Buddle 2010).

We argue that tree species seem to provide smaller-scale environmental features in such combinations, that—as the present study indicates—tree species composition becomes the most relevant variable determining spider assemblage richness and structure. This finding is important, because it highlights the significance of a certain level of abiotic-biotic organization. Tree species richness is a key factor for many other organism groups like bryophytes (Király et al. 2013) and forest floor plants (Márialigeti et al. 2009). The present results also emphasize that conservation-oriented forest management should focus on the maintenance of tree species richness and mixed tree species.

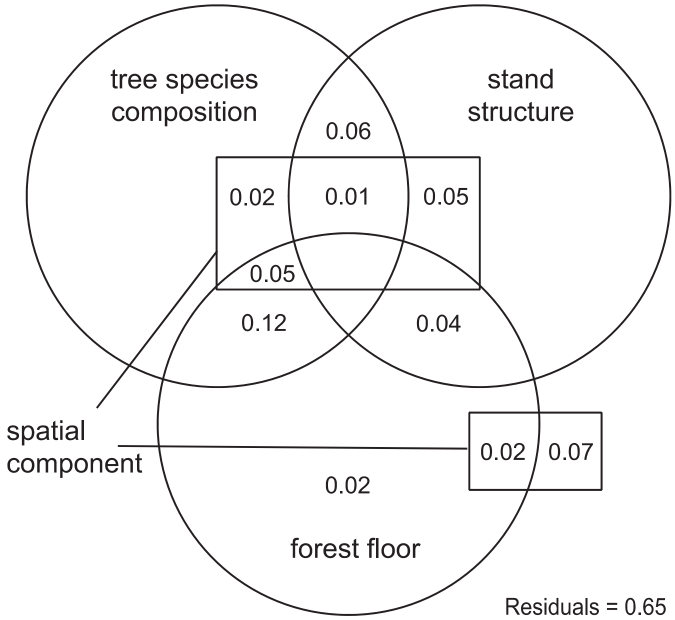

Figure 4.—Variation partitioning of species-environmental variables in RDA analysis. Variables in the original analysis were grouped into tree species composition, stand structure, forest floor related variables and spatial component. Shared variation fractions are noted on the Venn diagram.

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