

1 This manuscript contextually identical with this paper:

2 Samu, F., Lengyel, G., Szita, É., Bidló, A., Ódor, P. 2014. The effect of forest stand  
3 characteristics on spider diversity and species composition in deciduous-coniferous mixed  
4 forests. *The Journal of Arachnology* 42: 135-141.

5 The original published paper can be download from the website of the journal:  
6 [http://www.americanarachnology.org/JoA\\_tocs/JOA\\_contents\\_v42n2.html](http://www.americanarachnology.org/JoA_tocs/JOA_contents_v42n2.html)

7

8

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

11

12 Ferenc Samu<sup>1</sup>, Gábor Lengyel<sup>1</sup>, Éva Szita<sup>1</sup>, András Bidló<sup>2</sup> & Péter Ódor<sup>3</sup>

13

14 <sup>1</sup>Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences,  
15 Budapest, Hungary

16 <sup>2</sup>Department of Forest Site Diagnosis and Classification, University of West-Hungary,  
17 Sopron, Hungary

18 <sup>3</sup>Institute of Ecology and Botany, Centre for Ecological Research, Hungarian Academy of  
19 Sciences, Vácrátót, Hungary

20

21

22 **Corresponding author:**

23 Ferenc Samu

24 Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences

25 Postal address: PO. Box 102, Budapest, H-1525 Hungary

26 E-mail: [samu.ferenc@agrar.mta.hu](mailto:samu.ferenc@agrar.mta.hu)

27 Phone: +36 302731986

28 Fax: +36 13918655

29

30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50

**Abstract.** We studied how forest stand characteristics influenced spider assemblage richness and composition in a forested region of Hungary. In the Órség NP deciduous-coniferous mixed forests dominate. In 70-110 years old stands with a continuum of tree species composition 35 plots were established and sampled for spiders for three years. Detailed background information was acquired encompassing stand structure, tree species composition, forest floor related variables and the spatial position of the plots. The effect of variables was analysed by Nonparametric Multiplicative Regression on rarefied spider species richness and by Redundancy Analysis on species composition, relative importance of variable groups was assessed by variation partitioning. Spider species richness was positively and strongly affected by tree species richness, while the species composition of the spider assemblage was influenced by the proportion of the most important tree species. The finding established the importance of tree species composition, but variance partitioning analysis also showed that tree species identity and forest floor variables explain a lot of variation together. 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

## INTRODUCTION

51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65  
66  
67  
68  
69  
70  
71  
72  
73  
74  
75  
76  
77

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  $^{137}\text{Cs}$  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 decaying 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 represent numerous predatory tactics, fill many different niches (Entling et al. 2007). Therefore, knowledge on species richness and functional diversity (Schuldt et al. 2011) will also lead us closer to the understanding of spiders' role in different forested habitats.

Spider diversity in forests is influenced by many factors (Larrivee & Buddle 2010), and there are many studies which address a certain set of variables, but much fewer which take an integrative approach and compare the relative importance of various environmental factors. The importance of local factors in general was underlined in several studies (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). Vice versa, severe management practices that tend to homogenize forest habitats will lead to declines of sensitive species and that of beta diversity (Niemela 1997).

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

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

89 Given the relatively few studies that assess the importance of different variable groups on  
90 forest spider communities, and the existing equivocal results on the role of stand type and tree  
91 species diversity, in the present study we intended to establish how much spider assemblages  
92 are different across different forest stand types with a continuum of tree species composition.  
93 We asked the question how tree species composition, stand structure and forest floor variables  
94 affect spider assemblages and what is the respective importance of these factors in  
95 determining local species richness and species composition.

## 96 MATERIAL AND METHODS

97 **Study area.**—Our study was conducted in forested areas of the Örség National Park (N  
98 46°51'–55' and W 16°07'–23'), close to the borders of Hungary, Slovenia and Austria (Fig. 1).  
99 The elevation is between 250–350 m, the average annual precipitation is 700–800 mm and  
100 average annual temperature is 9.0–9.5 °C (Dövényi 2010).

101 The area of the Örség NP is dominated by beech (*Fagus sylvatica* L.), oak species  
102 (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus*  
103 *sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). The dominant forest types are  
104 sessile oak-hornbeam woodlands, acidofrequent beech woodlands, and acidofrequent mixed  
105 coniferous forests (for more information refer to Ódor et al. 2013).

106 For our survey 35 locations were selected (Fig. 1) in mature stands (age 70-110 yr. old,  
107 size 2-10 ha) of the area by stratified random sampling from the database of the Hungarian  
108 National Forest Service, applying the selection criteria that the topography of the plots is more  
109 or less flat and the top-soil is not influenced by ground-water. Stratification ensured that the  
110 selected locations represented the most common tree species combinations of the region,  
111 including a continuous gradient in the proportion of the main tree species. Within each  
112 location we established a 40 x 40 m plot, where environmental variables were determined.

113 **Variables.**—Within the plots trees were mapped, forest floor vegetation and litter cover  
114 was estimated in quadrates and microclimate measurements were made. The original data  
115 collection resulted in a high number of variables (for more detail on measurements and  
116 methods, see Ódor et al. 2013), for the present study we considered only 21 variables. The  
117 variables represented four categories: (i) tree species composition, which is tree species  
118 richness and the relative representation of main tree species, expressed as percentage relative  
119 tree volume; (ii) stand structural variables (number, size, size variation of trees); (iii) forest  
120 floor variables (coverage of main vegetation elements, litter and bare soil, plus microclimatic  
121 variables) and (iv) spatial component, represented by x, y spatial co-ordinates of plot centre.  
122 These four groups largely cover environmental variables that according to the literature  
123 (detailed in the Introduction) were likely to exert effect on spider distribution in a forest  
124 habitat. The variables are listed, described and categorized in Supplementary Table 1. For  
125 statistical modelling all explanatory variables were standardized (zero mean, one standard  
126 deviation).

127 **Sampling.**—Spiders were collected by pitfall trapping and suction sampling from each plot  
128 during four sampling campaigns in the most species rich periods: summer and autumn. Such a  
129 time limited sampling approach optimised for the most species rich periods is recommended  
130 for the comparison of assemblages at a large number of localities (Jimenez-Valverde & Lobo  
131 2006). Sampling dates and sampling efforts are summarised in Table 1.

132 Five pitfall traps were deployed in a plot during a campaign: one placed in the centre, the  
133 other four forming a square of c. 15 m sides positioned symmetrically around the centre.

134 Pitfalls were plastic cups of 75 mm upper diameter, filled with 70% ethylene glycol as  
135 preservative with some detergent added (Kádár & Samu 2006). Traps were open for a month;  
136 the catch was sorted, then spiders stored in 70% ethanol until identification. Voucher  
137 specimens were placed in the collection of the Plant Protection Institute, Centre for  
138 Agricultural Research, Hungarian Academy of Sciences.

139 Suction sampling was performed with hand-held motorized suction sampler, fitted with a  
140 0.01 m<sup>2</sup> orifice (Samu & Sároszpataki 1995). With suction sampling we tried to sample all  
141 microhabitats in a forest stand up to 1.5 m height. One sample lasted for c. 60 s, consisting of  
142 several application of the sampler, in a manner that first we sucked from microhabitats that  
143 produced the least debris (e.g. leaves from bushes and lower branches of trees, trunks), then  
144 we continuously sampled other habitats (such as dead wood surface, gravel surfaces, patches  
145 of terricolous mosses), and only for the last couple of applications was litter and soil sampled,  
146 which could potentially congest the apparatus. This way each sample was a cross section of  
147 the microhabitats of a smaller area within the 40x40 m plot. Since the number of specimens  
148 caught had been smaller than our initial expectations, over the campaigns the number of  
149 samples per plot increased (see Table 1). Because of variable catches per samples, all samples  
150 from a plot across methods and dates were lumped, and used that way in data analysis.

151 **Data analysis.**—We estimated spider species richness for the whole area by calculating the  
152 non-parametric species estimator Chao1 (Chao et al. 2005) using the software EstimateS  
153 version 9.0 (Colwell 2013). We also calculated Chao1 estimator separately for each plot and  
154 observed that in 5 plots estimated Chao1 values showed erratic behaviour along the species  
155 accumulation curve, which is a sign that the spider assemblage may have been under sampled  
156 at those plots (Colwell 2013). These plots were excluded from species richness modelling. To  
157 establish plot level species richness estimates for the 30 plots not excluded based on Chao1  
158 behaviour, we used the more conservative rarefaction method. We made estimations of  
159 species richness rarefied to 75 individuals ( $S_{75}$ , mean number of adult individuals caught in  
160 the plots was 74.2) using the individual based abundance model of Colwell et al. (2012) as  
161 implemented in EstimateS (Colwell 2013).

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

181 To study the multivariate response of species to environmental variables Redundancy  
182 Analysis (RDA, carried out by Canoco 4.5 (Ter Braak & Smilauer 2002)) was performed,  
183 supposing approximately linear relationships between species performance and explanatory  
184 variables (Leps & Smilauer 2003). In preliminary Detrended Correspondence Analysis the  
185 gradient lengths of the main axes were short (1.9-2.1 SD units) supporting linear  
186 relationships. Rare species (frequency less than 4) were excluded from the analysis. The same  
187 initial set of explanatory variables was used as for the NPMR model (Sup. Table 1). The  
188 explanatory variables were selected by manual forward selection, their effect and the  
189 significance of the canonical axes was tested by F-statistics via Monte-Carlo simulation (Ter

190 Braak & Smilauer 2002). Because spatial coordinates had a significant effect after model  
191 selection, the analysis was repeated using them as covariates (Ter Braak & Smilauer 2002).  
192 Variation partitioning was carried out to explore the amount of variance in the species  
193 assemblages accounted for by the four categories of explanatory variables (Peres-Neto et al.  
194 2006). All 21 explanatory variables were included in variation partitioning, which was carried  
195 out in R 3.0.2. (R Core Team 2013) using the vegan package (Oksanen et al. 2011).

## 196 RESULTS

197 **Species richness estimation.**—During the study 4567 spiders were caught, distributed  
198 nearly equally among the two sampling methods (suction sampling: 2245, pitfall trapping:  
199 2322 individuals). Out of the total catch 2596 spiders were adults, these represented 91  
200 species (Sup. Table 2).

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

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

209 **Rarefied species number environmental model.**—We applied local Gaussian mean  
210 NPMR to establish which environmental variables are the best in predicting rarefied species  
211 number. The best model (Table 2, Fig. 2) included three explanatory variables: Tree species  
212 richness, Proportion of Scots pine by volume and Shrub density. Spatial variables entered in  
213 the initial model fell out during iterative variable selection. With  $xR^2 = 0.596$ , it explained c.  
214 60% of variance in  $S_{75}$ , and was highly significant ( $P = 0.009$ ) in the randomization test.

215 **Spider assemblage environmental model.**—After the exclusion of rare species, 45 species  
216 were used in RDA. In the final RDA model canonical variables explained 31.2 % of the total  
217 species variance, with the first ( $F=6.22, p=0.002$ ) and all canonical axes ( $F=3.18, p=0.002$ )



218 being significant based on Monte-Carlo simulation. The most important explanatory variables  
219 were the relative volume of oak ( $\lambda_A = 0.10$ ,  $P=0.002$ ), beech ( $\lambda_A = 0.06$ ,  $P=0.004$ ) and  
220 hornbeam ( $\lambda_A = 0.05$ ,  $P=0.004$ ) and air humidity ( $\lambda_A = 0.04$ ,  $P=0.006$ ) (Fig. 3.).

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

227 RDA ordination indicated that spider species responded to the environmental gradients in  
228 a continuous way, they were rather evenly distributed around the ordination centre (Fig. 3).  
229 Nevertheless, an oak-hornbeam gradient could be discerned along axis 1, with the wolf  
230 spiders *Pardosa lugubris* (Walckenaer, 1802) and *Trochosa terricola* Thorell, 1856 markedly  
231 associated with oak, while *Histoipona torpida* (C. L. Koch, 1834), a funnel web waver species  
232 was strongly associated with hornbeam. Other species such as *Cicurina cicur* (Fabricius,  
233 1793), *Malthonica silvestris* (L. Koch, 1872) had a preference for both hornbeam and  
234 humidity. A number of hunters (*Harpactea lepida* (C. L. Koch, 1838), *Clubiona terrestris*  
235 Westring, 1851, *Dysdera ninnii* Canestrini, 1868) and some linyphiid species (*Drapetisca*  
236 *socialis* (Sundevall, 1833), *Micrargus herbigradus* (Blackwall, 1854)) were associated with  
237 beech. Beech-hornbeam mixed stands occurred in the area, and the amauroboid species  
238 *Eurocoelotes inermis* (L. Koch, 1855) seemed to be strongly associated with this stand type.  
239 Air humidity vs. dryness comprised another significant gradient, with *Macrargus rufus*  
240 (Wider, 1834) associated with humid and *Mangora acalypha* (Walckenaer, 1802) with dry  
241 conditions. Latter orb weaver is mostly known from open grassland habitats. There were,  
242 however, quite a number of species positioned intermediate between oak and humidity (e.g.  
243 *Agroeca brunnea* (Blackwall, 1833), *Lepthyphantes minutus* (Blackwall, 1833) and  
244 *Haplodrassus dalmatensis* (L. Koch, 1866)), which could not be associated with  
245 environmental variables based on the present analysis (Fig. 3).

## DISCUSSION

246  
247 In the present study we explored the basic, but still unresolved problem, how spiders depend  
248 on stand scale vegetation features. In the forested area of the Órség NP, deciduous and mixed  
249 forests show a continuum of tree species composition. By studying spider assemblages in 35  
250 localities, we did not only want to assess regional species richness, but also its variability  
251 depending on an extensive set of variables related to the forest stands. Our sampling efforts  
252 were limited to certain times of the year and certain microhabitats accessible by the sampling  
253 protocol, and were mostly suited to make comparisons across the localities (Jimenez-Valverde  
254 & Lobo 2006). Still, our richness estimate of 95-120 species (with 95% confidence) was very  
255 similar to values reported from temperate forests (Coddington et al. 1996) and approximates  
256 the species number of 149 found in the Uzungwa Mountains of Tanzania (Sorensen 2004).

257 We collected a considerable amount of data about the forest plots, out of which we used  
258 21 variables in four variable groups to explore the dependencies of species richness and  
259 composition. Since sampling resulted in a variable number of individuals, we used individual  
260 based rarefied richness values for comparison. In a Canadian case study rarefied species  
261 richness standardized to the number of individuals enabled the most accurate comparisons,  
262 especially when sampling was limited (Buddle et al. 2005). To analyse the importance of  
263 environmental variables we applied non-parametric method that made no assumption about  
264 species response and used rarefied richness data only from plots where sampling proved to be  
265 adequate.

266 Tree species richness of the forest stands proved to be the most influential factor of spider  
267 species richness. Although intuitively expected, in the light of other studies (De Bakker et al.  
268 2000; Pearce et al. 2004; Ziesche & Roth 2008) this is a notable result, especially because our  
269 survey took into account a spectrum of different environmental variables including micro-  
270 climatic factors, forest floor cover, stand structure and also spatiality. Other studies typically  
271 concentrated on narrower range of explanatory variables. Small scale studies could show the  
272 importance of structural and abiotic features (Varady-Szabo & Buddle 2006; Sereda et al.  
273 2012), while large scale studies showed the negative effects of habitat homogenization and

274 the importance of species pool and connectivity to nearby habitats (Niemela 1997; Floren et  
275 al. 2011). Tree species are in fact connected to all these levels – they have various structural  
276 aspects and also affect forest floor variables. In the present study where variables representing  
277 four different groups were entered into the models, the most influential level of variables was  
278 how variable the tree composition was, i.e. how many tree species were present in a plot.

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

296 We argue, that tree species seem to provide smaller scale environmental features in such  
297 combinations, that – as the present study indicates – tree species composition becomes the  
298 most relevant variable that determines spider assemblage richness and structure. This finding  
299 is important, because highlights the significance of a certain level in abiotic-biotic  
300 organization. Tree species richness is a key factor for many other organism groups like  
301 bryophytes (Király et al. 2013) and forest floor plants (Márialigeti et al. 2009). Present results

302 also underline that conservation oriented forest management should focus on the maintenance  
303 of tree species richness and mixed tree species.

#### 304 ACKNOWLEDGEMENTS

305 We thank András Rákóczi, Kinga Fetykó, László Bodonczai, Gergely Kutszegi, Zsuzsa Mag,  
306 Sára Márialigeti, István Mazál, Ákos Molnár, Balázs Németh and Flóra Tinya for their help in  
307 the field survey, and Erika Botos and Zsuzsanna Benedikty Konczné for help in laboratory  
308 work. The project was funded by Hungarian Science Foundation (OTKA 79158) and the  
309 Órség National Park Directorate. P.Ó. was supported by the Bolyai János Research  
310 Scholarship of the Hungarian Academy of Sciences.

#### 311 LITERATURE CITED

- 312 Buddle, C.M., J. Beguin, E. Bolduc, A. Mercado, T.E. Sackett, R.D. Selby, H. Varady-Szabo  
313 & R.M. Zeran. 2005. The importance and use of taxon sampling curves for comparative  
314 biodiversity research with forest arthropod assemblages. *Canadian Entomologist* 137:120-  
315 127.
- 316 Chao, A., R.L. Chazdon, R.K. Colwell & T.J. Shen. 2005. A new statistical approach for  
317 assessing similarity of species composition with incidence and abundance data. *Ecology*  
318 *Letters* 8:148-159.
- 319 Clarke, R.D. & P.R. Grant. 1968. An experimental study of the role of spiders as predators in  
320 a forest litter community. Part 1. *Ecology* 49:1152-1154.
- 321 Coddington, J.A., L.H. Young & F.A. Coyle. 1996. Estimating spider species richness in a  
322 Southern Appalachian cove hardwood forest. *Journal of Arachnology* 24:111-128.
- 323 Colwell, R.K. 2013. EstimateS: Statistical estimation of species richness and shared species  
324 from samples. Version 9.0. <http://purl.oclc.org/estimates>
- 325 Colwell, R.K., A. Chao, N.J. Gotelli, S.Y. Lin, C.X. Mao, R.L. Chazdon & J.T. Longino.  
326 2012. Models and estimators linking individual-based and sample-based rarefaction,  
327 extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3-21.

328 De Bakker, D., J.P. Maelfait, F. Hendrickx, D. Van Waesberghe, B. De Vos, S. Thys & L. De  
329 Bruyn. 2000. A first analysis on the relationship between forest soil quality and spider  
330 (Araneae) communities of Flemish forest stands. *Ekologia-Bratislava* 19:45-58.

331 Dövényi, Z. 2010. Magyarország kistájainak katasztere [Cadastre of Hungarian regions].  
332 MTA Földrajztudományi Kutatóintézet, Budapest.

333 Entling, W., M.H. Schmidt, S. Bacher, R. Brandl & W. Nentwig. 2007. Niche properties of  
334 Central European spiders: shading, moisture and the evolution of the habitat niche. *Global*  
335 *Ecology and Biogeography* 16:440-448.

336 Floren, A., T. Muller, C. Deeleman-Reinhold & K.E. Linsenmair. 2011. Effects of forest  
337 fragmentation on canopy spider communities in SE-Asian rain forests. *Ecotropica* 17:15-  
338 26.

339 Hänggi, A., E. Stöckli & W. Nentwig. 1995. Habitats of Central European spiders.  
340 *Miscellaneae Faunistica Helveticae* 4:1-460.

341 Hovemeyer, K. & G. Stippich. 2000. Assessing spider community structure in a beech forest:  
342 Effects of sampling method. *European Journal of Entomology* 97:369-375.

343 Jimenez-Valverde, A. & J.M. Lobo. 2006. Establishing reliable spider (Araneae, Araneidae  
344 and Thomisidae) assemblage sampling protocols: estimation of species richness, seasonal  
345 coverage and contribution of juvenile data to species richness and composition. *Acta*  
346 *Oecologica-International Journal of Ecology* 30:21-32.

347 Kádár, F. & F. Samu. 2006. A duplaedényes talajcsapdák használata Magyarországon [On the  
348 use of double-cup pitfalls in Hungary]. *Növényvédelem* 42:305-312.

349 Király, I., J. Nascimbene, F. Tinya & P. Ódor. 2013. Factors influencing epiphytic bryophyte  
350 and lichen species richness at different spatial scales in managed temperate forests.  
351 *Biodiversity and Conservation* 22: 209-223.

352 Korenko, S., E. Kula, V. Simon, V. Michalkova & S. Pekar. 2011. Are arboreal spiders  
353 associated with particular tree canopies? *North-Western Journal of Zoology* 7:261-269.

354 Larrivee, M. & C.M. Buddle. 2010. Scale dependence of tree trunk spider diversity patterns in  
355 vertical and horizontal space. *Ecoscience* 17:400-410.

356 Lawrence, K.L. & D.H. Wise. 2000. Spider predation on forest-floor Collembola and  
357 evidence for indirect effects on decomposition. *Pedobiologia* 44:33-39.

358 Leps, J. & P. Smilauer. 2003. *Multivariate Analysis of Ecological Data using CANOCO*.  
359 Cambridge University Press, Cambridge. pp. 282

360 Márialigeti, S., B. Németh, F. Tinya & P. Ódor. 2009. The effects of stand structure on  
361 ground-floor bryophyte assemblages in temperate mixed forests. *Biodiversity and*  
362 *Conservation* 18: 2223-2241.

363 McCune, B. 2004. *Nonparametric Multiplicative Regression for Habitat Modeling*. Glenden  
364 Beach, Oregon, U.S.A., MjM Software. <http://www.pcord.com/NPMRintro.pdf>

365 McCune, B. & M.J. Mefford. 2009. *HyperNiche*. Version 2.25. Glenden Beach, Oregon,  
366 U.S.A., MjM Software.

367 Moulder, B.C. & D.E. Reichle. 1972. Significance of spider predation in the energy dynamics  
368 of forest-floor arthropod communities. *Ecological Monographs* 42:473-498.

369 Niemela, J. 1997. Invertebrates and boreal forest management. *Conservation Biology* 11:601-  
370 610.

371 Niemela, J., Y. Haila & P. Punttila. 1996. The importance of small-scale heterogeneity in  
372 boreal forests: Variation in diversity in forest-floor invertebrates across the succession  
373 gradient. *Ecography* 19:352-368.

374 Ódor, P., I. Király, F. Tinya, F. Bortignon & J. Nascimbene. 2013. Patterns and drivers of  
375 species composition of epiphytic bryophytes and lichens in managed temperate forests.  
376 *Forest Ecology and Management* 306:256-265.

377 Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, S. G.L., P.  
378 Solymos, M. Henry, H. Stevens & H. Wagner. 2011. *Vegan: Community Ecology*  
379 *Package*. R package version 2.0-1. <http://CRAN.R-project.org/package=vegan>.

380 Oxbrough, A., V. French, S. Irwin, T.C. Kelly, P. Smiddy & J. O'Halloran. 2012. Can mixed  
381 species stands enhance arthropod diversity in plantation forests? *Forest Ecology and*  
382 *Management* 270:11-18.

383 Pearce, J.L., L.A. Venier, G. Eccles, J. Pedlar & D. McKenney. 2004. Influence of habitat and  
384 microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiversity*  
385 *and Conservation* 13:1305-1334.

386 Peres-Neto, P.R., P. Legendre, S. Dray & D. Borcard. 2006. Variation partitioning of species  
387 data matrices: estimation and comparison of fractions. *Ecology* 87:2614-2625.

388 R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna,  
389 Austria, R Foundation for Statistical Computing.

390 Samu, F. & M. Sároszpataki. 1995. Design and use of a hand-hold suction sampler and its  
391 comparison with sweep net and pitfall trap sampling. *Folia Entomologica Hungarica*  
392 56:195-203.

393 Schuldt, A., S. Both, H. Bruelheide, W. Hardtle, B. Schmid, H.Z. Zhou & T. Assmann. 2011.  
394 Predator diversity and abundance provide little support for the enemies hypothesis in  
395 forests of high tree diversity. *Plos One* 6:8.

396 Schuldt, A., H. Bruelheide, W. Hardtle & T. Assmann. 2012. Predator assemblage structure  
397 and temporal variability of species richness and abundance in forests of high tree diversity.  
398 *Biotropica* 44:793-800.

399 Schuldt, A., N. Fahrenholz, M. Brauns, S. Migge-Kleian, C. Platner & M. Schaefer. 2008.  
400 Communities of ground-living spiders in deciduous forests: Does tree species diversity  
401 matter? *Biodiversity and Conservation* 17:1267-1284.

402 Sereda, E., T. Blick, W.H.O. Dorow, V. Wolters & K. Birkhofer. 2012. Spatial distribution of  
403 spiders and epedaphic Collembola in an environmentally heterogeneous forest floor  
404 habitat. *Pedobiologia* 55:241-245.

405 Sorensen, L.L. 2004. Composition and diversity of the spider fauna in the canopy of a  
406 montane forest in Tanzania. *Biodiversity and Conservation* 13:437-452.

407 Ter Braak, C.J.F. & P. Smilauer. 2002. *CANOCO Reference Manual and CanoDraw for*  
408 *Windows User's Guide: Software for Canonical Community Ordination Version 4.5*.  
409 Microcomputer Power, Ithaca, NY.

- 410 Uetz, G.W. 1979. The influence of variation in litter habitats on spider communities.  
411 *Oecologia* 40:29-42.
- 412 Varady-Szabo, H. & C.M. Buddle. 2006. On the relationships between ground-dwelling  
413 spider (Araneae) assemblages and dead wood in a northern sugar maple forest.  
414 *Biodiversity and Conservation* 15:4119-4141.
- 415 Ziesche, T.M. & M. Roth. 2008. Influence of environmental parameters on small-scale  
416 distribution of soil-dwelling spiders in forests: What makes the difference, tree species or  
417 microhabitat? *Forest Ecology and Management* 255:738-752.
- 418



419

420 Table 1.–Sampling dates and sampling efforts in the 35 forested plots of the Órség NP.

421

Campaign date	Suction sampling	Pitfall trapping	
	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

422

423

424

425

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

433

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

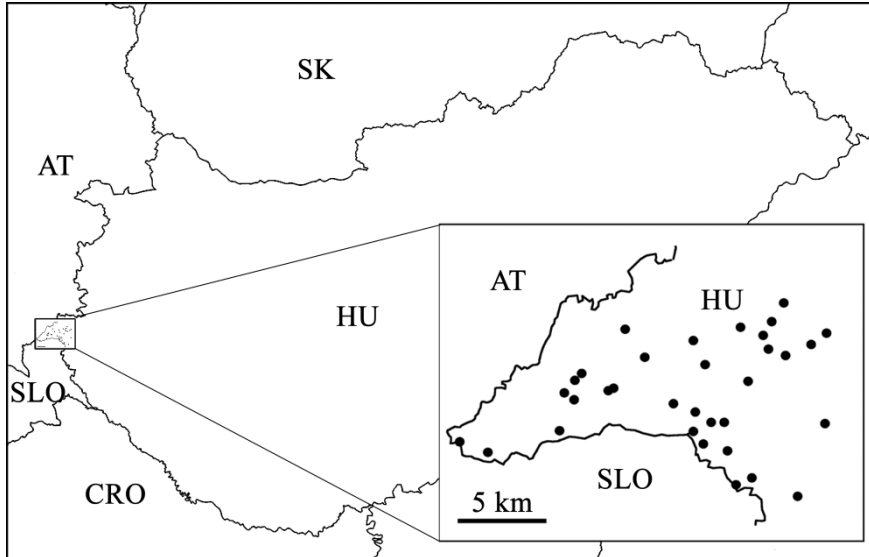
434

435

436

437 Figure 1.—The study area is the Órség NP in the westernmost part of Hungary. The inset  
438 depicts the 35 locations containing the experimental plots.

439



440  
441  
442  
443

444

445

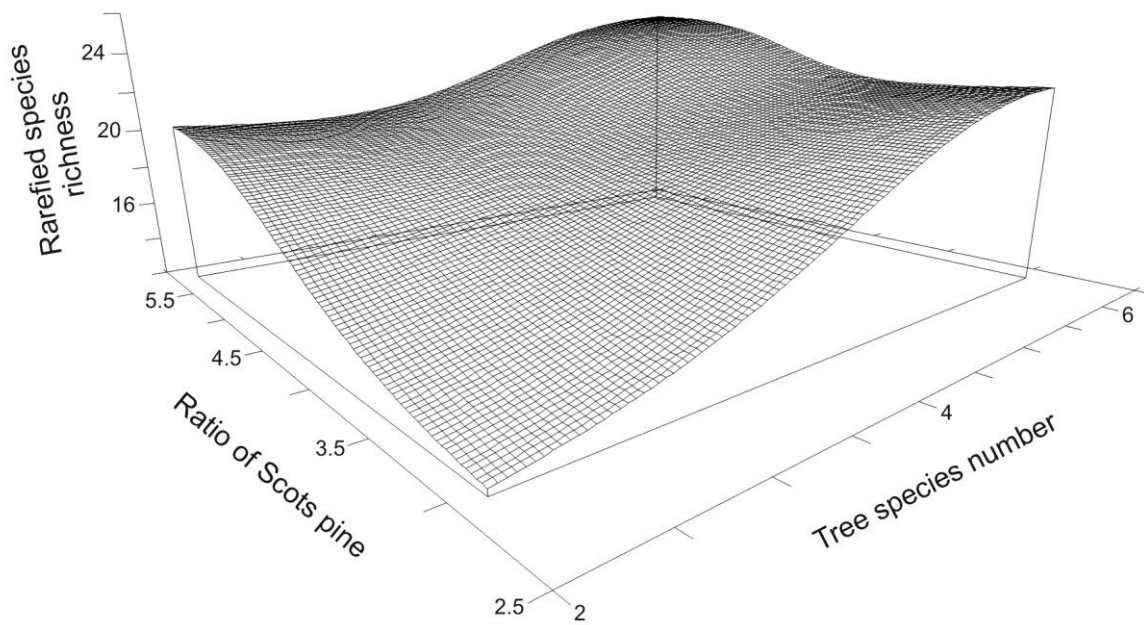
446 Figure 2.—Response surface of the best local mean NPMR model on rarefied species number,  
447 depicted for the first two predictor variables (for further explanation see text and Table 2).

448

449

450

451



452

453

454

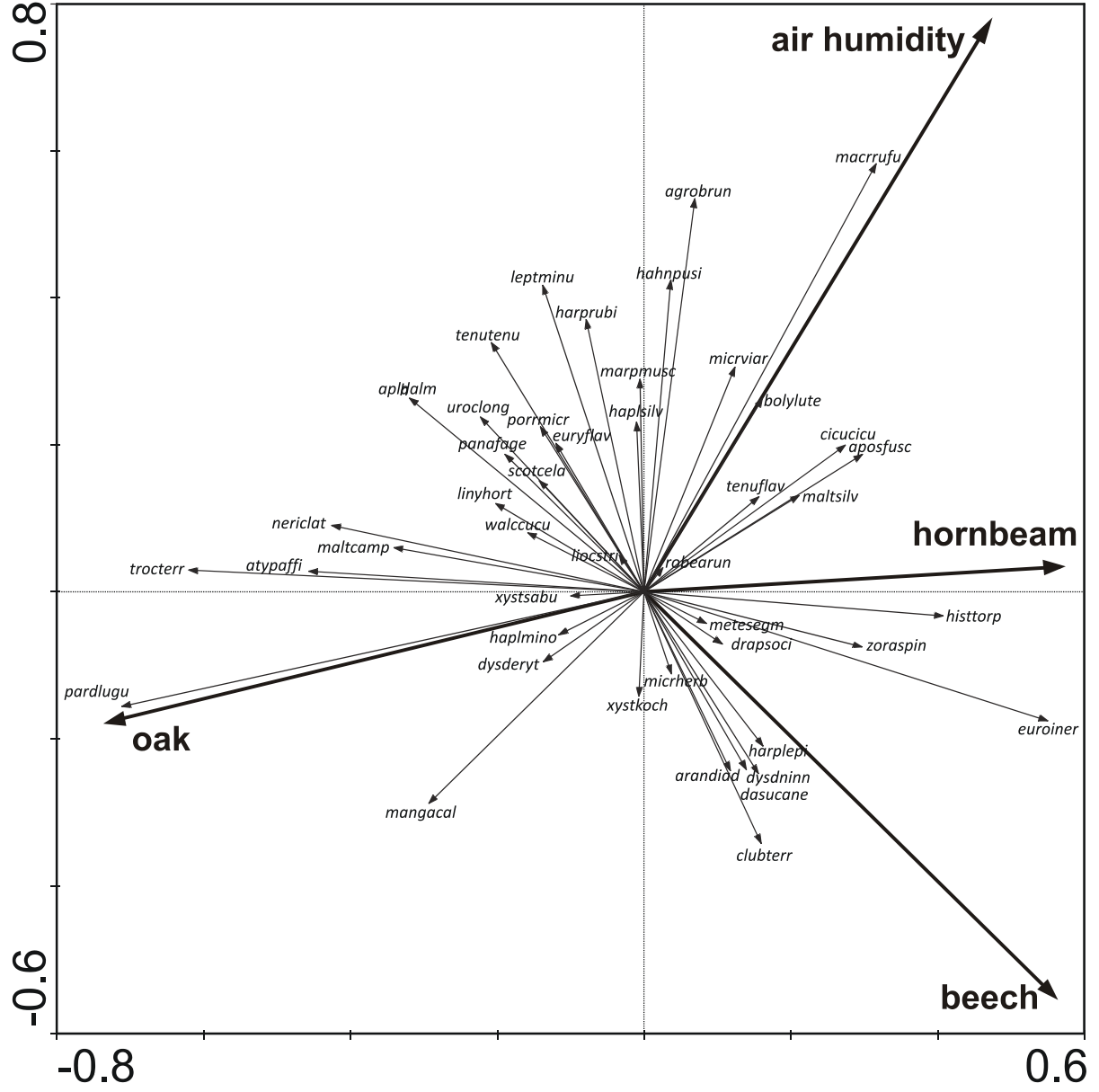
455

456

457

458  
 459  
 460  
 461  
 462  
 463  
 464  
 465  
 466

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 8 measurements. Species abbreviations are composed from the first four letters of the generic and species name of each species (for species list see Supp. Table 2).



467  
 468  
 469  
 470

471

472 Figure 4.—Variation partitioning of species-environmental variables in RDA analysis.

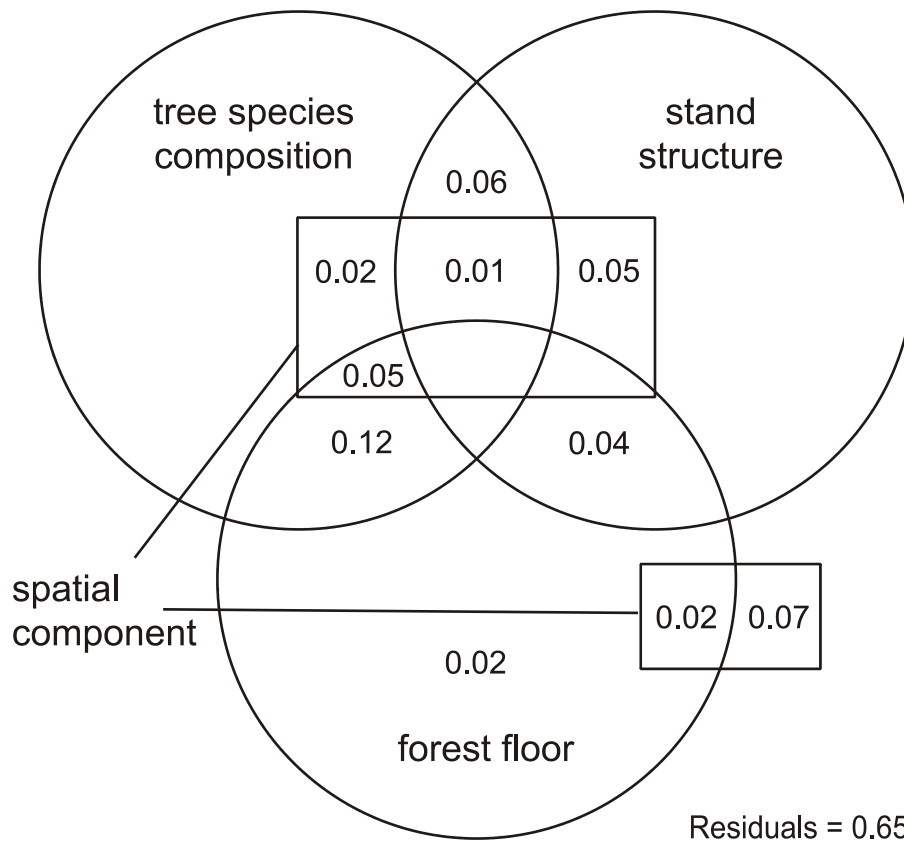
473 Variables in the original analysis were grouped into Tree species composition, Stand

474 structure, Forest floor related variables and Spatial component. Shared variation fractions are

475 noted on the Venn diagram.

476

477



478

479

480

481

482

483

484 Supplementary Table 1.—Explanatory variables of the study, listed by variable groups (bold),  
 485 with brief description and unit. Data collection and detailed descriptions of the explanatory  
 486 variables are detailed in Ódor et al. (2013).  
 487

Explanatory variable	Description	Unit
<b>Tree species composition</b>		
Tree species richness	Species number of mapped trees	count
Proportion of beech	Relative volume of beech	%
Proportion of hornbeam	Relative volume of hornbeam	%
Proportion of Scots pine	Relative volume of Scots pine	%
Proportion of oaks	Relative volume of oaks ( <i>Q. petraea</i> , <i>robur</i> , <i>cerris</i> )	%
Proportion of subordinate trees	Relative volume of other mixing trees	%
<b>Stand structure</b>		
Shrub density	Density of shrubs-trees 0-5 cm DBH	count/ha
Tree density	Density of mapped trees	count/ha
Mean diameter at breast height (DBH)	Mean DBH of mapped (DBH>5cm) trees	cm
Coefficient of variation of DBH	Coefficient of variation of DBH of mapped (DBH>5cm) trees	%
<b>Spatial component</b>		
Longitude coordinate	Longitude coordinate, Hungarian co-ordinate system (EOV)	m
Latitude coordinate	Latitude coordinate, Hungarian co-ordinate system (EOV)	m
<b>Forest floor conditions</b>		
Herbaceous cover	Cover of ground layer (herbs + seedlings) based on 30x30 m plot	m <sup>2</sup> /ha
Moss cover	Cover of ground floor bryophytes p	m <sup>2</sup> /ha

Dead wood cover	Cover of dead wood	m <sup>2</sup> /ha
Litter cover	Cover of litter	m <sup>2</sup> /ha
Bare soil cover	Cover of soil	m <sup>2</sup> /ha
Diffuse light	Mean relative diffuse light, LAI instrument, 36 measurement, 30x30 m	%
Litter weight	Litter weight, from 30x30 cm area	g
Temperature	Mean daily air temperature based on 8 measurements	K
Air humidity	Mean daily air humidity based on 8 measurements	%

---



489  
490  
491

Supplementary Table 2. List of spider species (only adults) caught in the study.

Family	Species	No. of plots	Total catch
Agelenidae	<i>Histoipona torpida</i> (C. L. Koch, 1834)	15	125
Agelenidae	<i>Malthonica campestris</i> (C. L. Koch, 1834)	6	7
Agelenidae	<i>Malthonica ferruginea</i> (Panzer, 1804)	3	3
Agelenidae	<i>Malthonica silvestris</i> (L. Koch, 1872)	5	11
Amaurobiidae	<i>Amaurobius fenestralis</i> (Stroem, 1768)	1	1
Amaurobiidae	<i>Amaurobius ferox</i> (Walckenaer, 1830)	2	2
Amaurobiidae	<i>Eurocoelotes inermis</i> (L. Koch, 1855)	19	210
Amaurobiidae	<i>Urocoras longispinus</i> (Kulczynski, 1897)	17	330
Anyphaenidae	<i>Anyphaena accentuata</i> (Walckenaer, 1802)	2	2
Araneidae	<i>Araneus diadematus</i> Clerck, 1757	4	4
Araneidae	<i>Cercidia prominens</i> (Westring, 1851)	3	4
Araneidae	<i>Mangora acalypha</i> (Walckenaer, 1802)	6	6
Atypidae	<i>Atypus affinis</i> Eichwald, 1830	24	131
Clubionidae	<i>Clubiona caerulescens</i> L. Koch, 1867	2	2
Clubionidae	<i>Clubiona phragmitis</i> C. L. Koch, 1843	1	1
Clubionidae	<i>Clubiona rosserae</i> Locket, 1953	2	2
Clubionidae	<i>Clubiona terrestris</i> Westring, 1851	5	7
Corinnidae	<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	3	6
Dictynidae	<i>Cicurina cicur</i> (Fabricius, 1793)	24	101
Dysderidae	<i>Dasumia canestrinii</i> (L. Koch, 1876)	5	10
Dysderidae	<i>Dysdera erythrina</i> (Walckenaer, 1802)	16	26
Dysderidae	<i>Dysdera longirostris</i> Doblaka, 1853	2	3
Dysderidae	<i>Dysdera ninnii</i> Canestrini, 1868	16	37
Dysderidae	<i>Harpactea lepida</i> (C. L. Koch, 1838)	5	10
Dysderidae	<i>Harpactea rubicunda</i> (C. L. Koch, 1838)	8	14

Gnaphosidae	<i>Gnaphosa lucifuga</i> (Walckenaer, 1802)	2	2
Gnaphosidae	<i>Haplodrassus dalmatensis</i> (L. Koch, 1866)	7	16
Gnaphosidae	<i>Haplodrassus minor</i> (O. P.-Cambridge, 1879)	4	8
Gnaphosidae	<i>Haplodrassus silvestris</i> (Blackwall, 1833)	10	17
Gnaphosidae	<i>Zelotes aeneus</i> (Simon, 1878)	1	1
Gnaphosidae	<i>Zelotes electus</i> (C. L. Koch, 1839)	1	1
Hahniidae	<i>Hahnia nava</i> (Blackwall, 1841)	3	5
Hahniidae	<i>Hahnia pusilla</i> C. L. Koch, 1841	5	8
Linyphiidae	<i>Bolyphantes luteolus</i> (Blackwall, 1833)	11	29
Linyphiidae	<i>Centromerus incultus</i> Falconer, 1915	2	2
Linyphiidae	<i>Diplostyla concolor</i> (Wider, 1834)	3	3
Linyphiidae	<i>Drapetisca socialis</i> (Sundevall, 1833)	4	4
Linyphiidae	<i>Erigone dentipalpis</i> (Wider, 1834)	2	2
Linyphiidae	<i>Lepthyphantes minutus</i> (Blackwall, 1833)	15	38
Linyphiidae	<i>Linyphia hortensis</i> Sundevall, 1830	8	13
Linyphiidae	<i>Macrargus rufus</i> (Wider, 1834)	20	56
Linyphiidae	<i>Mecopisthes peusi</i> Wunderlich, 1972	3	5
Linyphiidae	<i>Meioneta rurestris</i> (C. L. Koch, 1836)	2	2
Linyphiidae	<i>Micrargus herbigradus</i> (Blackwall, 1854)	12	21
Linyphiidae	<i>Microlinyphia pusilla</i> (Sundevall, 1830)	1	1
Linyphiidae	<i>Microneta viaria</i> (Blackwall, 1841)	29	138
Linyphiidae	<i>Nerienne clathrata</i> (Sundevall, 1830)	9	12
Linyphiidae	<i>Oedothorax apicatus</i> (Blackwall, 1850)	2	6
Linyphiidae	<i>Panamomops fagei</i> Miller & Kratochvil, 1939	14	27
Linyphiidae	<i>Porrhomma microphthalmum</i> (O. P.-C., 1871)	9	10
Linyphiidae	<i>Tapinocyba insecta</i> (L. Koch, 1869)	1	1
Linyphiidae	<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	14	29
Linyphiidae	<i>Tenuiphantes tenebricola</i> (Wider, 1834)	1	2

Linyphiidae	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	23	40
Linyphiidae	<i>Trichoncus affinis</i> Kulczynski, 1894	2	2
Linyphiidae	<i>Walckenaeria alticeps</i> (Denis, 1952)	1	1
Linyphiidae	<i>Walckenaeria antica</i> (Wider, 1834)	1	2
Linyphiidae	<i>Walckenaeria cucullata</i> (C. L. Koch, 1836)	6	6
Linyphiidae	<i>Walckenaeria mitrata</i> (Menge, 1868)	3	3
Linyphiidae	<i>Walckenaeria simplex</i> Chyzer, 1894	2	3
Liocranidae	<i>Agroeca brunnea</i> (Blackwall, 1833)	22	79
Liocranidae	<i>Agroeca cuprea</i> Menge, 1873	1	1
Liocranidae	<i>Apostenus fuscus</i> Westring, 1851	17	39
Liocranidae	<i>Liocranoeca striata</i> (Kulczynski, 1882)	7	11
Liocranidae	<i>Scotina celans</i> (Blackwall, 1841)	10	21
Lycosidae	<i>Arctosa cinerea</i> (Fabricius, 1777)	1	1
Lycosidae	<i>Aulonia albimana</i> (Walckenaer, 1805)	1	1
Lycosidae	<i>Pardosa lugubris</i> s.str. (Walckenaer, 1802)	31	644
Lycosidae	<i>Trochosa robusta</i> (Simon, 1876)	2	2
Lycosidae	<i>Trochosa ruricola</i> (De Geer, 1778)	1	1
Lycosidae	<i>Trochosa spinipalpis</i> (F.O. P.-Cambridge, 1895)	1	1
Lycosidae	<i>Trochosa terricola</i> Thorell, 1856	28	147
Mimetidae	<i>Ero furcata</i> (Villers, 1789)	2	2
Nemesiidae	<i>Nemesia pannonica</i> (Herman, 1879)	1	1
Pisauridae	<i>Pisaura mirabilis</i> (Clerck, 1757)	2	2
Salticidae	<i>Macaroeris nidicolens</i> (Walckenaer, 1802)	1	1
Salticidae	<i>Marpissa muscosa</i> (Clerck, 1757)	5	5
Salticidae	<i>Salticus scenicus</i> (Clerck, 1757)	1	1
Segestriidae	<i>Segestria bavarica</i> C. L. Koch, 1843	2	2
Tetragnathidae	<i>Metellina merianae</i> (Scopoli, 1763)	1	1
Tetragnathidae	<i>Metellina segmentata</i> (Clerck, 1757)	10	11

Theridiidae	<i>Crustulina guttata</i> (Wider, 1834)	1	1
Theridiidae	<i>Enoplognatha thoracica</i> (Hahn, 1833)	2	2
Theridiidae	<i>Episinus truncatus</i> Latreille, 1809	2	2
Theridiidae	<i>Euryopis flavomaculata</i> (C. L. Koch, 1836)	5	6
Theridiidae	<i>Robertus arundineti</i> (O. P.-Cambridge, 1871)	8	8
Theridiidae	<i>Robertus lividus</i> (Blackwall, 1836)	1	1
Theridiidae	<i>Steatoda bipunctata</i> (Linnaeus, 1758)	1	1
Thomisidae	<i>Xysticus kochi</i> Thorell, 1872	4	5
Thomisidae	<i>Xysticus sabulosus</i> (Hahn, 1832)	9	14
Zoridae	<i>Zora spinimana</i> (Sundevall, 1833)	7	11

492