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

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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

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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 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 m² 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 (χR^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_{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.

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- 418

419

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

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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

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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.).

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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

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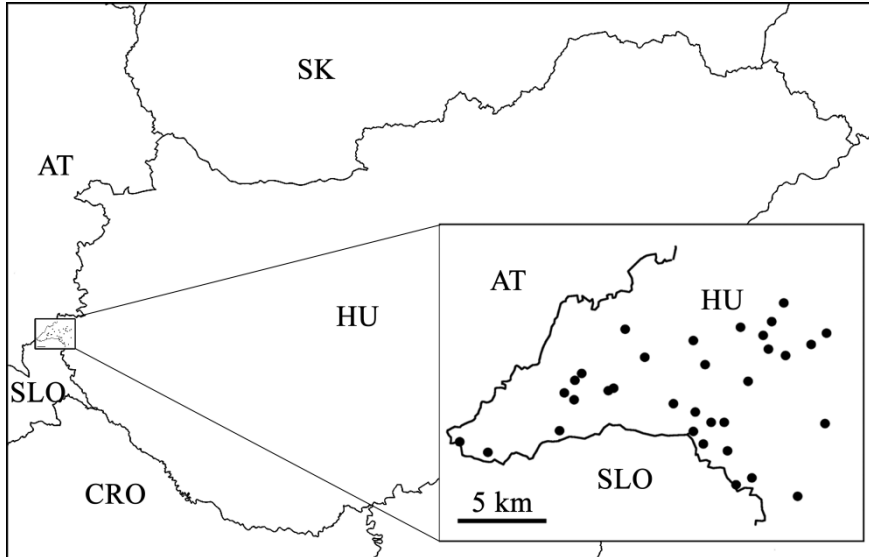
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437 Figure 1.—The study area is the Órség NP in the westernmost part of Hungary. The inset

438 depicts the 35 locations containing the experimental plots.

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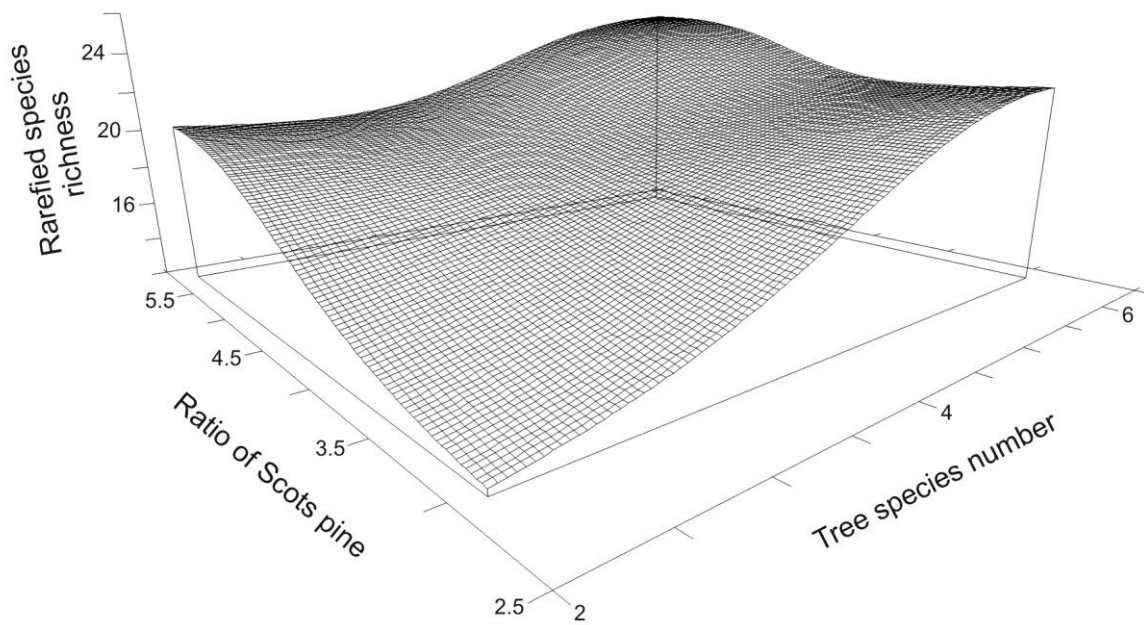
446 Figure 2.—Response surface of the best local mean NPMR model on rarefied species number,
447 depicted for the first two predictor variables (for further explanation see text and Table 2).

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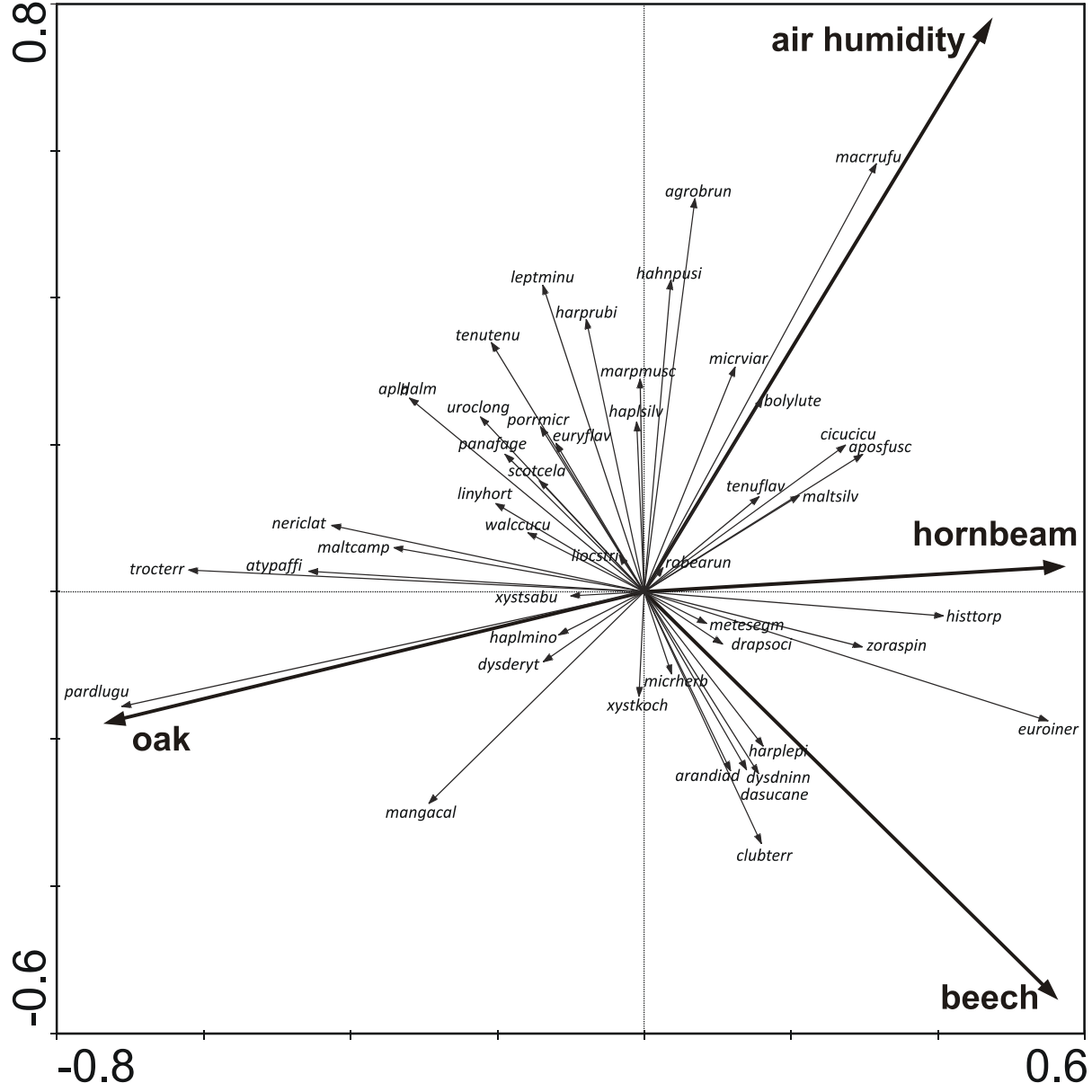
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Figure 3.—RDA ordination diagram of species in relation to environmental variables. Hornbeam, oak, beech: relative volume of the tree species in the stands; air humidity is mean daily air humidity based on 8 measurements. Species abbreviations are composed from the first four letters of the generic and species name of each species (for species list see Supp. Table 2).



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

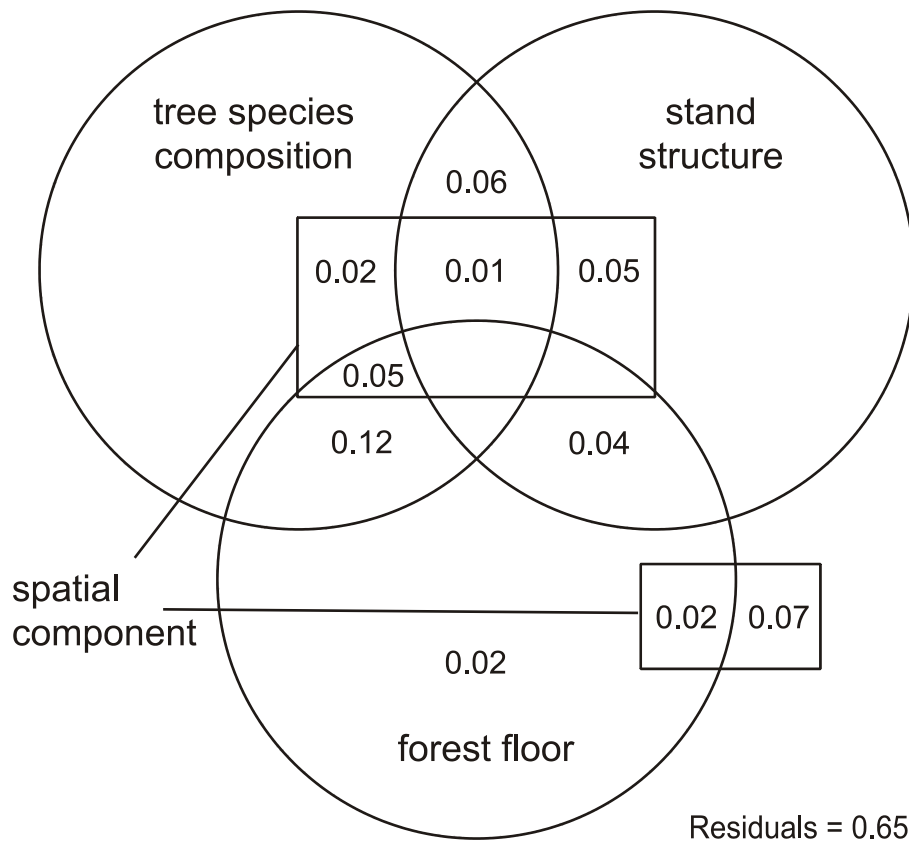
473 Variables in the original analysis were grouped into Tree species composition, Stand

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

475 noted on the Venn diagram.

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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
Tree species composition		
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	%
Stand structure		
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	%
Spatial component		
Longitude coordinate	Longitude coordinate, Hungarian co-ordinate system (EOV)	m
Latitude coordinate	Latitude coordinate, Hungarian co-ordinate system (EOV)	m
Forest floor conditions		
Herbaceous cover	Cover of ground layer (herbs + seedlings) based on 30x30 m plot	m ² /ha
Moss cover	Cover of ground floor bryophytes p	m ² /ha

Dead wood cover	Cover of dead wood	m ² /ha
Litter cover	Cover of litter	m ² /ha
Bare soil cover	Cover of soil	m ² /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	%

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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 caeruleascens</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

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