

Species diversity versus species composition in relation to climate and habitat variation: a case study on spider assemblages (Aranei) of the East European oak forests.¹

Видовое разнообразие и видовой состав в связи с климатическими и биотопическим факторами: изучение группировок пауков (Aranei) в дубравах Восточно-Европейской равнины.¹

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КЛЮЧЕВЫЕ СЛОВА: пауки подстилки, изменения биоразнообразия, факторы среды, дубравы, Русская равнина.

ABSTRACT: Two groups of parameters derived from both species diversity and species composition of spider assemblages of the East European Plain oak forests were tested in respect to large-scale variation in macroclimatic and habitat factors. The study is based on data equal in sample size and collecting efforts. Various diversity indices were taken as diversity measures. Spatial variation in the species composition was expressed by sample scores on the ordination axes derived from detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA), both based on abundance and presence/absence data. Species composition is found to be a better indicator of spatial variation in macroclimate, giving higher and more stable values of correlation coefficients. Temperature parameters appear to be best explanatory variables for the patterns observed. The diversity measures vary with season and behave often in a different way for the spring, autumn or entire datasets. Only the total abundance shows a clear trend to a northerly and easterly decrease.

РЕЗЮМЕ: Анализ зависимости двух групп параметров, вытекающих из видового разнообразия и видового состава группировок пауков в дубравах Русской равнины, от макрографической изменчивости климатичес-

ких и биотических факторов. Работа основана на данных, полученных по единой методике отбора проб и сбора материала. Для анализа биоразнообразия применялись различные индексы разнообразия. Пространственная изменчивость видового состава оценивалась по характеру расположения учетов обилия и присутствия-отсутствия на ординационных осиях с помощью детрендного корреспондентного анализа (DCA) и канонического корреспондентного анализа (CCA). Отмечено, что видовой состав лучше отражает пространственную изменчивость макроклиматических факторов, обнаруживая более высокие и стабильные показатели коэффициентов корреляции. Температурные параметры оказались переменными, наилучшим образом объясняющие полученные данные. Меры биоразнообразия варьируют по сезонам, часто по разному отражая данные за весну, осень и весь полевой сезон. Лишь общее обилие обнаруживает четкую тенденцию к уменьшению к северу и востоку.

Introduction

The variety of diversity concepts has been divided by Whittaker [1977] into two main groups: (1) inventory diversity, and (2) differentiation

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diversity. In his understanding, inventory diversity is intended to quantitatively describe the diversity of separate biotic assemblages (communities, ecosystems, biomes), while differentiation diversity assumes spatial aspects of variation in the diversity of biotic assemblages along gradients or among regions. In other words, inventory diversity describes the biotic assemblages irrespectively of the identities of the species they are composed of, meaning that two convergent communities situated in different continents may have equal values of various diversity statistics but completely different species listings. In contrast, differentiation diversity will depend on the similarity in the species composition of assemblages to be compared. The inventory diversity concept generally coincides with the landscape-typological approach as commonly termed in the Russian schools of ecology and biogeography, whereas differentiation diversity may be considered as an example of a regional-individualistic approach [see Chernov, 1975, 1984].

The above basic idea of Whittaker can be slightly modified and extended to cover any biotic parameters, be they strict diversity measures or not. Such an extension may be based on the borderline between the individualistic and typological approaches, that is, do the biotic characteristics consider the species composition or do they not. In this respect, two groups of parameters can be distinguished [cf. Hengeveld, 1990, Penev, 1992]:

(1) Parameters dependent on the species composition expressed as species listings, based either on species presence/absence or abundance, frequency, density, biomass and/or other importance measures for each species. From these listings, a good number of structural characteristics can be derived, for example zoogeographical or phenological structures of communities. What is important, two assemblages situated in different faunistic or floristic regions will never be completely identical concerning such parameters.

(2) Parameters independent of the species composition. They are derived irrespectively of species identities and include quantitative characteristics of the assemblage as a whole, such as inventory diversity statistics, total sum of individuals, total biomass, productivity, energy fluxes, etc. However, when based on functional classification principles or biological traits, structural characteristics are also to be grouped here, e.g.

trophic or life-form structures of communities.

Usually papers dealing with spatial variation in diversity treat one of the two groups of parameters outlined above. This paper aims to compare species diversity with species composition in how both reflect large-scale variation of climate and habitat properties. This problem was discussed in an earlier paper based on soil-dwelling wire-worm assemblages (*Coleoptera, Elateridae larvae*) of oak forests along a latitudinal gradient in central Russia [Penev, 1992]. Now we focus on spiders as a taxonomic group different from wire-worms in most biological properties, in particular as inhabiting an overground stratum, the soil litter. Two major gradients will be considered, one latitudinal reflecting trends in nature zonation from north to south, and the other longitudinal due to regional differences as well as to the increasing west-east climate continentality and severity.

Material and methods

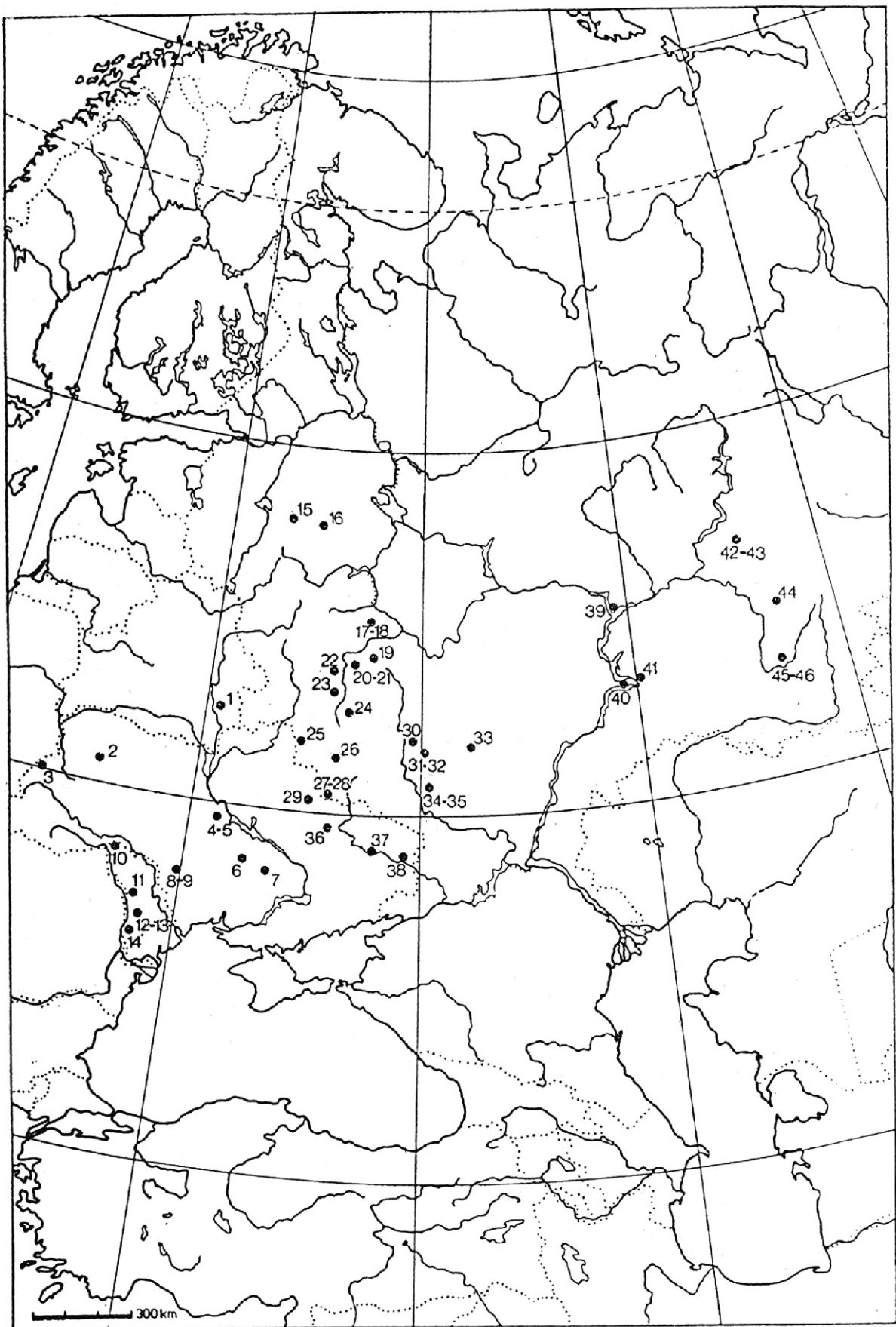
Study area and field procedures

Material was taken during five expeditions over the East European, or Russian, Plain carried out in May-June and from mid-August to early October 1988 to 1990 (Fig. 1, Appendices 1-2). The oak forests were chosen as a model habitat since they represent the climax vegetation type in the central, nemoral regions of European Russia [Razumovsky, 1981], thus being presumably the best indicators of macroclimate-determined spatial variation. The 46 study sites, ranging over a distance of about 1,100 km from north to south, are situated within three nature zones, from mixed coniferous-broadleaved forests to steppes. From west to east, the study area covered a distance of about 2,300 km, ranging from Moldova (= Moldavia) to the Urals.

So many study sites scattered over such vast distances can hardly be expected to be too similar to each other. Indeed, as shown in Appendices 1-2, the oak forests chosen occupy different relief forms, they are supported by a variety of soil types, and they can be represented by various plant associations. Besides, there is no doubt that local habitat conditions do influence large-scale variation in biotic assemblages, modifying the major role of climate. To minimize between-site variation, we stucked to the most mature and well-preserved

Fig. 1. Geographical location of the study sites. Site numbers as in Appendices 1-3. Solid lines show borders between zones, as follows: TAI — taiga, MIX — mixed coniferous-broadleaved forest zone, FST — forest-steppes, STE — steppe zone.

Рис. 1. Географическое местоположение точек сбора материала. Номера точек как в Приложениях 1-3. Сплошные линии показывают границы между зонами: ТАИ - тайги, MIX - смешанных хвойно-широколиственных лесов, FST - лесостепи, STE - степи.



forest patches in each site, representing plant associations most typical for that particular area. In central Russia, for example, zonal oak forests on interfluvial plains are largely *Quercetum aegopodiosum* and *Quercetum aegopodioso-caricosum pilosae* with their variants; in southern Moldavia these are *Quercetum pubescens cotinosum* and *Quercetum pubescens herbosum*; in Cisuralian lowlands they are mainly *Quercetum mixtoherboso-aegopodiosum* [Nikolaeva, 1963; Geideman, 1968, Gorchakovskiy, 1972, Kleopov, 1990]. Apart from this, the sites were chosen so as to avoid marginal variants as regards moisture conditions, that is both too wet or too dry oak forests were not included in the field work.

Twenty soil samples of 25 x 25 cm each were taken at each site. The soil animals were collected from 10 cm thick soil layers on oilskin in the field according to Ghilarov [1975]. The spiders were present only in the litter and were sampled by means of a sieve. The samples were taken along short transects (200-500) m within more or less homogeneous forest patches in consequent series of 3 samples each: the first sample at an oak trunk, the second between trees, and the third in a small forest 'window'. Other details with regard to sampling sites/methods can be derived from Penev [1992].

The environmental data set

There are two major climatic gradients affecting the distribution of oak forests on the Russian Plain. The first one can be called north-southern and it reflects latitudinal changes in thermal conditions and in the radiation balance as a whole [Grigoryev, 1954, Budyko, 1977]. The second gradient is orientated from west to east, being largely due to the increased climatic continentality and severity. To trace these two major trends, we chose climatic parameters (Appendix 3) correlated either with latitude (TANN, TMIN, FRL, PR, WA, CO HUMI, DEFI) or with longitude (TAMP). Most temperature parameters, however, decrease not only from south to north but also in a west-east direction.

Some of the environmental variables were transformed according to the following scales:

- 1) Mean annual precipitation (PR) (mm): **1** – 400-500, **2** – 500-600, **3** – 600-700.
- 2) Precipitation for the warm period (WA): **1** – 250-300, **2** – 300-350, **3** – 350-400, **4** – 400-450, **5** – 450-500, **6** – 500-550.
- 3) Precipitation for the cold period (CO): **1** – 100-125, **2** – 125-150, **3** – 150-175, **4** – 175-200, **5** – 200-225.

4) Mechanical composition of the soil (MECH):

1 – light sandy, sandy loam or loess-like soils, **2** – moderate loam, **3** – heavy loam to clayish; in borderline cases 0.5 is added to the lower value.

5) Thickness of the litter layer (LIT) (cm): **1** – 0-2, **2** – 2-4, **3** – 4-6, **4** – 6-8. The values in Appendix 3 were estimated as an average of the 20 soil samples taken at each site.

6) Humus depth (HUM) (cm): **1** – 0-5, **2** – 5-10, **3** – 10-15, **4** – 15-20, **5** – 20-25, **6** – 25-30, **7** – 30-35, **8** – 35-40, **9** – >40. The values in Appendix 3 represent the averages for each site estimated from the 20 soil samples.

The species data set

The species composition and abundances at each site are given in Appendices 4-5. Out of a total of 452 spider species known from oak forests of the East European Plain in general [Esjunin et al., 1993], 153 species were found in our soil samples. All calculations, however, were carried out considering only adults representing but 124 species, all typical inhabitants of the soil litter stratum. Since we found considerable variation in the samples taken in the spring and in the autumn [Esjunin et al., 1993], the statistical procedures were applied to the whole data set, as well as to subsets including either autumn or spring sites.

Data analysis

Species composition

The sample scores on the first four DCA axes computed with CANOCO [Ter Braak, 1988] were considered as a measure of between-site variation in the species composition. For the same purposes, we also applied a direct gradient analysis technique, i.e. Canonical Correspondence Analysis, CCA [Ter Braak, 1985]. Because of a strong multicollinearity among most of the climatic factors, a forward selection of the environmental variables was carried out before the computation of CCA axes. We chose the variables with the highest values of variance explained and stopped when the Monte Carlo permutation test (99 random permutations) showed no significant additional effect of the variable in question. To better reflect the existing environmental dataset, we also selected some soil variables with rather low values of explained variance. The significance of the correlations between DCA axes and each environmental variable were estimated in all cases by means of transformation of the correlation coefficient to Fisher's z-statistics [Lakin, 1990].

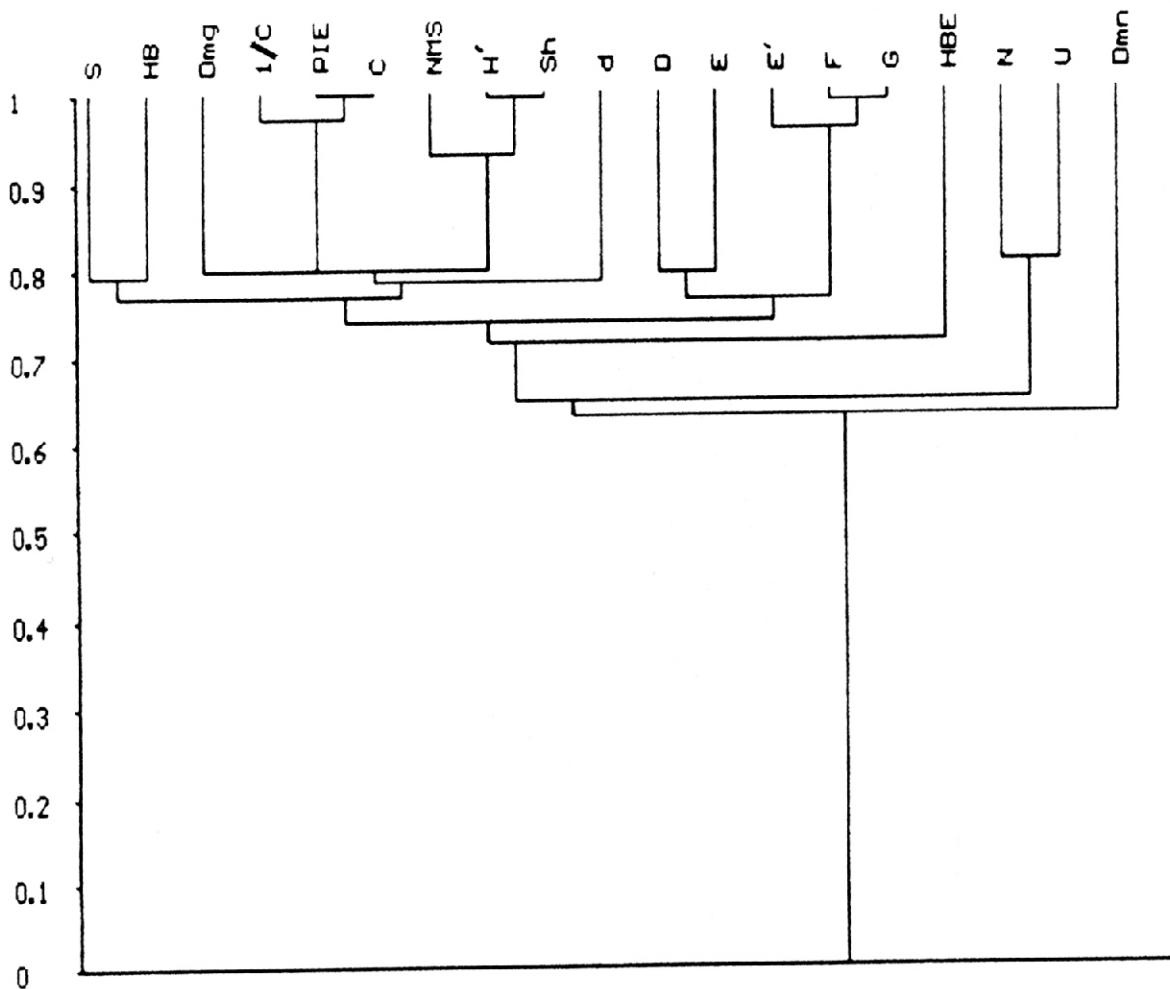


Fig. 2. Single linkage (nearest neighbour) clustering dendrogram of Kendall's rank correlation coefficient between quantitative characteristics of the spider assemblages: S — number of species, N — individuals total, U — McIntosh's diversity measure and D — McIntosh's D index (Magurran, 1988, p. 40), Dmg — Margalef's index, Dmn — Menchini's index, 1/C — reciprocal of Simpson's index (index of 'polydominance') (= Hill's N_2), Sh = exponential Shannon's function (= Hill's N_1), H' — Shannon's index, PIE — 'probability of interspecific encounter', NMS — number of moves per specimen, HB — Brillouin's diversity index, HBE — Brillouin's evenness, E — Pielou's evenness measure, E' — Hill's evenness measure ($= N_{2/N_1}$), F — Alatalo's evenness, G — Molinari's evenness, C — Simpson's index ('concentration of dominance'), d — the Berger-Parker index (= reciprocal of Hill's N). 15

Рис. 2. Кластерная дендрограмма одноразовой связи (ближайшего соседства) коэффициента ранговой корреляции Кендалла для количественных характеристик группировок пауков: S - число видов, N - суммарное число экземпляров, D - коэффициент D Макинтоша [Magurran, 1988: 40], D_{Mg} - индекс Мартгала, D_{Min} - индекс Менхиника, $1/C$ - величина, обратная коэффициенту Симпсона (индекс "полидоминантности") (= индекс N_2 , Хилла), Sh - экспонента коэффициента Шеннона (= индекс N , Хилла), H' - коэффициент Шеннона, PIE - "вероятность межвидовой встречи", NMS - число перемещения на экземпляр, HVE - индекс разнообразия Брийлуэна, HBE - индекс выровненности Брийлуэна, E - индекс выровненности Пайлоу, E' - индекс выровненности Хилла (= $N_{2/M}$), F - индекс выровненности Аллатало, G - индекс выровненности Молинари, C - коэффициент Симпсона ("концентрация доминирования"), d - индекс Бергера-Паркера (= величина, обратная индексу N , Хилла).

Species diversity

The choice of an appropriate index of diversity is a common and not yet fully solved problem in modern ecology. An incredible amount of work, based on both theoretical and empirical evidence, have been devoted to this problem [i.e. Hutheson, 1970; Hurlbert, 1971; Hill, 1973; De Benedictis, 1973; Peet, 1974; Pielou, 1975; Routledge, 1979;

Alatalo, 1980; Pesenko, 1982; Pesenko & Semkin, 1989; Magurran, 1988; Molinari, 1989, etc.]. In any event, we rather prefer to stick to 'pluralistic' views [e.g. Hurlbert, 1971; Pesenko, 1982; Pesenko & Semkin, 1989] and use several indices, although most of them are known to more or less strongly correlate with each other. Our choice of diversity indices was based on the following presumptions:

(1) Theoretical properties of the indices depending on what aspect of diversity they are designed to measure;

(2) Empirical conclusions drawn from a correlation analysis of the various indices based on our field data.

We shall avoid giving here all the formulas of diversity indices, since they are easily available from several recent reviews [e.g. Pesenko, 1982, Magurran, 1988]. Besides, their abbreviations are already commonly used in the modern ecological literature.

As shown by Hill [1973], many diversity indices are members of the equation:

$$N_a = (p_1 + p_2 + p_3 + \dots p_s)^{1/a},$$

where $a \geq 0$. When $a = 0$, $N_a = S$ (number of species); when $a = 1$, $N_a = Sh$ (exponent of the Shannon function); when $a = 2$, $N_a = 1/C$ (inverse of Simpson's 'concentration of dominance' index), etc. Thus, with an increase in a , the dependence on the number of species is decreased. The last member of Hill's series, the reciprocal of the Berger-Parker index d , is completely independent of S [Magurran, 1988]. Hence, we chose both the first three and the last member of Hill's equation. In addition, some other diversity statistics were tested, namely Brillouin's function (HB), Menchini's (Dmn) and Margalef's (Dmg) indices.

Evenness measures have extensively been discussed in several papers [Hill, 1973; Alatalo & Alatalo, 1980; Alatalo, 1981; Molinari, 1989]. Hill's evenness E' ($= N_a/N_s$) has been criticized by Peet [1974] and Molinari [1989], since it may have high values in cases when the real evenness is low. Instead, the measure F has been proposed [Alatalo & Alatalo, 1980; Alatalo, 1981]. However, in its turn, Alatalo's index was criticized by Molinari [1989] who proposed a calibrated variant of this index, called G measure. Based on the above considerations, we selected the indices F , G , as well as Brillouin's evenness HBE .

The dominance measures usually negatively correlate with diversity. However, their use sometimes allows to illustrate cases of high predominance of one or two species. The most popular dominance measure is Simpson's index C . The Berger-Parker index can also be considered as a dominance measure, since it merely expresses the relative abundance of the most abundant species.

The correlation structure of the diversity indices applied is shown in Fig. 2. The nearest-neighbour clustering dendrogram based on Kendall's rank correlation coefficient was used as an additional

criterion for omitting some highly correlated diversity statistics such as the 'number of moves per specimen', NMS [Fager, 1972; Pesenko, 1982], the 'probability of interspecific encounter', PIE , Shannon's and McIntosh's diversity indices, H' and U respectively, Pielou's and Hill's evenness indices, E and E' respectively.

The calculation of all diversity statistics and the cluster analysis were performed with the program BIODIV [Baev & Penev, 1991].

Results

Environmental factors underlying variation in species composition

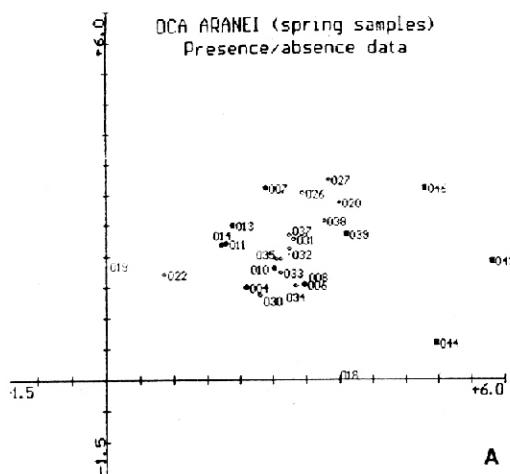
The DCA ordination results are presented in Figs 3a-f, the correlations of the DCA axes with each environmental variable in Tab. 1, the eigenvalues and percentage variances accounted for by the first two axes are given in Tab. 2.

The ordination scattergrams based on the 27 spring sites (Figs 3a, 3b) demonstrate the major role of macroclimatic gradients in compositional variation of the spider assemblages. The distribution of sites on Axis 1 for presence/absence data illustrates an isolated position of the Cisuralian oak forests (sites 42, 44, 46), on the one hand, and of those lying in the central part of the mixed coniferous-broadleaved forest zone (sites 18, 19, 22), on the other. In general, the first DCA axis can hardly be considered as a clear geographical gradient, although it correlates with geographical longitude. Axis 1 shows a relationship to temperature, while Axis 2 to humidity parameters (Tab. 1). The scattergram based on abundance data has a similar structure and correlates with the same factors (Fig. 3b, Tab. 1).

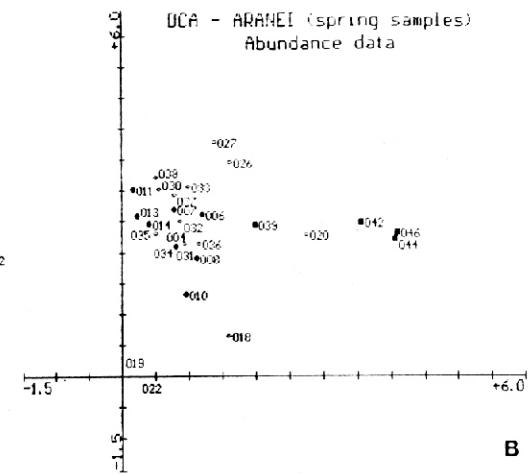
The dominant compositional gradient for the autumn dataset on Axis 1 is orientated latitudinally and correlates positively with the mean annual temperature and the deficit in air humidity (Fig. 3c, Tab. 1). The second axis, in its turn, shows a significant correlation with precipitation parameters. For the abundance data (Fig. 3d), Axis 1 arranges the sites from southwest to northeast and strongly correlates with latitude, longitude, and all temperature parameters as well as with the mechanical composition of the soil. The second axis showed a complicated gradient which correlating with none of the environmental variables.

The first DCA axis generated on the basis of the entire (spring + autumn) dataset can be interpreted as a clear latitudinal gradient for both presence/absence (Fig. 3e) and abundance (Fig. 3f) data. The values of the correlation coefficients (Tab. 1)

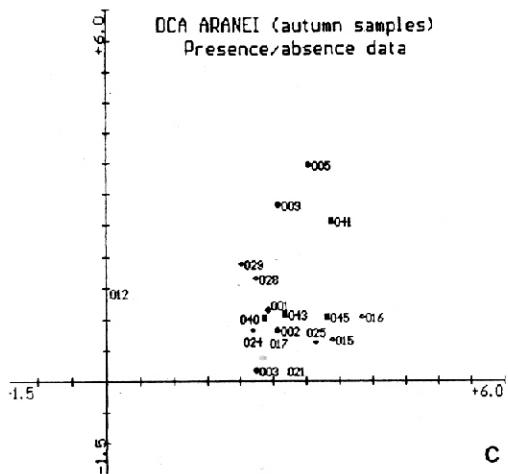
DCA ARANEI (spring samples)
Presence/absence data



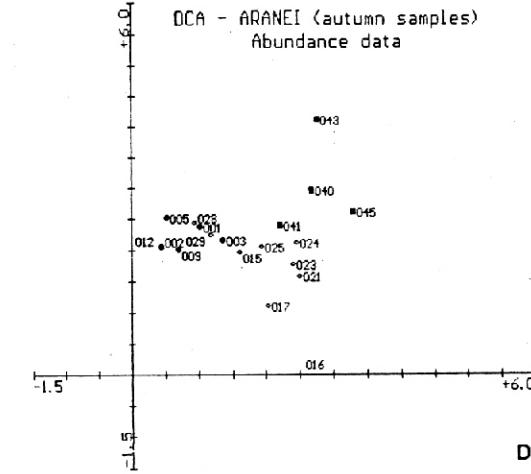
DCA - ARANEI (spring samples)
Abundance data



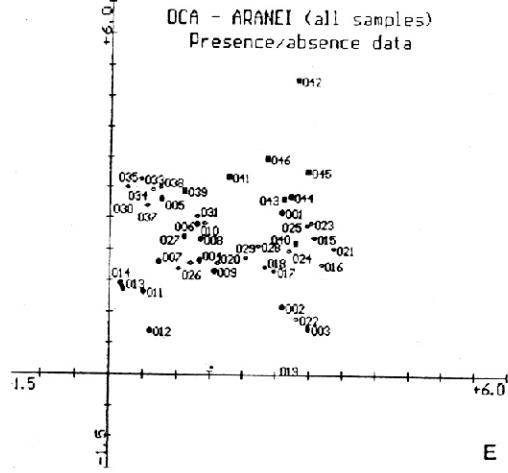
DCA ARANEI (autumn samples)
Presence/absence data



DCA - ARANEI (autumn samples)
Abundance data



DCA - ARANEI (all samples)
Presence/absence data



DCA - ARANEI (all samples)
Abundance data

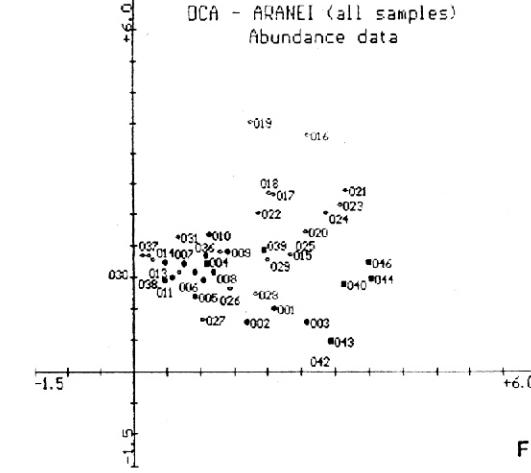


Table 1. Correlations between the assemblage parameters and environmental factors. Abbreviations of environmental variables as in Appendix 2; ‘—’ — not significant, the numbers with an asterisk (*) are significant at $P \leq 0.01$, those with two ones (**) at $P \leq 0.001$, the remaining at $P \leq 0.05$. The assemblage parameters are abbreviated as follows: C — Simpson’s index (‘concentration of dominance’), D — McIntosh’s D index, d — the Berger-Parker index (=Hill’s N_1), DCA1(a) — first DCA axis based on abundance data, DCA1(p) — first DCA axis based on presence/absence data, DCA2 — second DCA axes respectively, Dmg — Margalef’s index, Dmn — Menchinić’s index, F — Alatalo’s evenness, G — Molinari’s evenness, HB — Brillouin’s diversity index, HBE — Brillouin’s evenness, N — individuals total, S — number of species, Sh — exponent of the Shannon’s function (= Hill’s N_1), 1/C — inverse of Simpson’s index (‘polydominance’ index) (= Hill’s N_2).

	LONG	LATI	TANN	TMIN	TAMP	FRL	PR	WA	CO	HUMI	DEFI	MECH	GREY	PODZ	CHER	LIT	HUM	SAND
All samples (n = 46)																		
Spring samples (n = 27)																		
S	-	-	-	-	-	-0.30	-	-	-	-	-	-	-	-	-	-	-	-
N	-0.47**	-0.42**	0.48***	0.51*	-0.52*	0.38	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dmg	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dmn	-	0.33	-0.31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1/C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sh	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HB	-0.31	-	0.33	0.32	-	0.36	-	-	-	-	-	-	-	-	-	-	0.32	-
HBE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34	-
G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.36	-
d	-	-	-	-	-	-	-	-0.30	-	-	-	-	-	-	-	-	-	-
DCA1(p)	-	0.68*	-0.61*	-0.42**	-	-	-	-0.63*	0.43**	0.56*	0.38	0.62*	-0.80*	-	-	-	0.34	-0.49*
DCA2(p)	0.70*	-	-0.49*	-0.62*	0.66*	-0.43*	-0.40*	-0.44**	-	-	-	-	-	-	-	-	-	-
DCA1(a)	0.35	0.65*	-0.68*	-0.53*	-	-0.69*	0.42**	0.43**	-	0.48**	-0.74*	-	-	-	-	-0.48*	-	-0.36*
DCA2(a)	-	-	-	-	-	-	-	-	-	-	-	-	0.58*	-	-	-	-	-

Таблица 1. Корреляции между параметрами группировок и факторами среды. Сокращения переменных окружающей среды как в Приложении 2: '-' — недостоверно; числа, снабженные звездочкой (*), достоверны при $P \leq 0.01$, числа, снабженные двумя звездочками (**), достоверны при $P \leq 0.001$, прочие при $P \leq 0.05$. Параметры группировок сокращены: С — коэффициент Симпсона ("концентрация доминирования"), D — коэффициент D Макинтоша, d — индекс Бергера-Паркера (= индекс N_1 Хилла), DCA1(a) — первая ось дретендного корреспондентного анализа (ДКА) на основе данных по численности, DCA1(p) — первая ось ДКА на основе данных по присутствию/отсутствию, DCA2 — соответственно вторые оси ДКА, Dmg — индекс Маргалефа, Dmp — индекс Менхиника, F — индекс выровненности Алatalо, G — индекс выровненности Молинари, HB — индекс разнообразия Брийлуэна, HVE — индекс выровненности Брийлуэна, N — суммарное число экземпляров, S — число видов, Sh — экспонента коэффициента Шеннона (= индекс N_1 Хилла), 1/C — величина, обратная коэффициенту Симпсона (индекса "полидоминантности") (= индекс N_2 Хилла).

Table 2.
Eigenvalues and percentage variance accounted for by the first two DCA and CCA axes.
Таблица 2
Собственные значения и процент изменчивости за счет первых двух осей дретендного и канонического корреспондентного анализа.

	Eigenvalue		Percentage variance		Eigenvalue		Percentage variance	
	DCA1	DCA2	DCA1	DCA2	CCA1	CCA2	CCA1	CCA2
Spring samples								
Presence/absence	0.57	0.35	8.5	3.8	0.49	0.37	20.0	15.3
Abundance	0.75	0.36	12.2	6.9	0.64	0.37	28.0	15.9
Autumn samples								
Presence/absence	0.53	0.42	12.3	9.7	0.48	0.40	20.9	17.3
Abundance	0.51	0.39	12.5	8.5	0.47	0.37	21.5	17.0
All samples								
Presence/absence	0.54	0.33	13.4	6.1	0.41	0.32	20.2	15.8
Abundance	0.50	0.39	11.0	7.7	0.44	0.37	22.8	18.9

suggest that climate, i.e. primarily temperature, precipitation and air humidity, can be considered as the major factors affecting the large-scale variation in spider assemblages. It is noteworthy that significant correlations of the site scores with the thickness of the litter stratum for both presence/absence and abundance data are also observed (Tab. 1). The arrangement of sites on both second axes reflects a longitudinal variation in climate, expressed by an increasing temperature amplitude and decreasing remaining temperature parameters (presence/absence data). The mechanical composition of the soil and its correspondent variable 'sandy and sandy loam soil' correlated with Axis 2 for abundance data (Tab. 1), suggesting that soil properties may influence species abundances, perhaps indirectly via the plant cover and/or the composition of forest litter.

In most cases, except for the autumn dataset (see Tab. 1), we did not find significant correlations in the third and fourth DCA axes which would add much to the understanding of the observed patterns. The third axis for abundance and, partly, presence/absence data correlated with soil factors, such as the 'mechanical composition of the soil', 'presence of sand', 'podzolized soil type', and 'humus depth'.

In general, the analysis based on all three datasets showed that temperature parameters are the most important determinants of the main trend in the species data, regardless of its latitudinal or longitudinal orientation. Among the temperature measures, the mean annual temperature and the

number of frostless days seem to have the most stable and highest values of the correlation coefficient. The humidity parameters can be judged as being of subordinate importance. The soil properties seem to influence the species abundances by modifying the large-scale variation caused by climate. In both entire and autumn datasets, the species composition based on presence/absence appears to be largely influenced by macro-environmental factors, whereas the species composition combined with abundances reflects local soil conditions as well.

Direct gradient analysis (Figs 4a-f, Table 3) confirms the major role of temperature. In four of the six datasets, the variable with most important contributions to the multiple regression (i.e. with the highest T-value of the canonical coefficient on the first CCA axis) is either the number of frostless days or the mean annual temperature. The most important determinants for the spring dataset are the number of frostless days, the mean annual temperature amplitude, and the thickness of the litter stratum (Figs 4a, b). The relative air humidity correlates with the second CCA axis. The autumn samples (Figs 4c-d) show quite a similar pattern demonstrating the importance of the mean annual temperature (or its exchangeable variable, the number of frostless days), the annual temperature amplitude, the relative air humidity (or its counterpart, the deficit in air humidity). The role of podzolized soil type on both biplots (Figs 4c-d) can be considered as related to the geographical

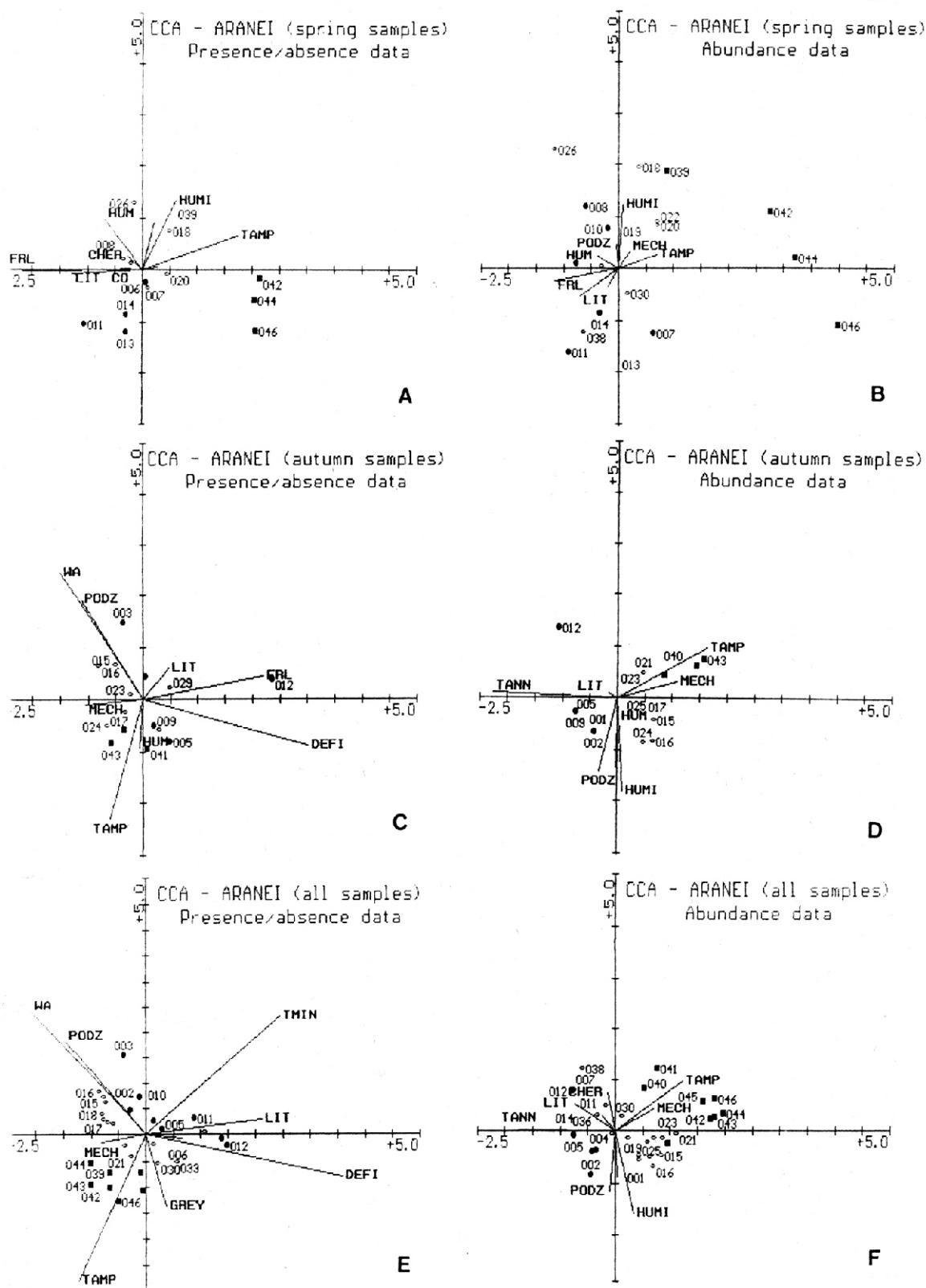


Fig. 4. CCA biplots of sites and environmental variables. Designations as in Fig. 3, variables as in Appendix 2.

Рис. 4. Биплоты канонического корреспондентного анализа точек сбора материала и переменных окружающей среды. Обозначения как на Рис. 3, переменные как в Приложении 2.

Table 3. Canonical and correlation coefficient of the CCA axes and environmental variables remained after CANOCO forward selection. The values of the canonical coefficient marked with an asterisk (*) have T-values greater than 2.1 for both spring and whole datasets and 2.23 for autumn samples respectively. The variables not selected for the corresponding dataset are designated with “-”.

Таблица 3. Канонический коэффициент и коэффициент корреляции осей канонического корреспондентного анализа и переменных окружающей среды, оставшиеся после отбора программой CANOCO. Величины канонического коэффициента, отмеченные звездочкой (*), имеют значения Т выше 2,1 как для весенних учетов, так и для всего банка данных, и 2,23 для осенних учетов. Переменные, не отобранные для соответствующего банка данных, обозначены как “-”.

Variable	Presence/absence data				Abundance data			
	Canonical coefficients		Correlation coefficients		Canonical coefficients		Correlation coefficients	
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
Spring samples								
FRL	-0.56*	0.27*	-0.86	-0.01	-1.07*	0.22	-0.81	-0.15
TAMP	0.22*	0.37*	0.68	0.29	-0.11	0.53*	0.49	0.18
HUMI	0.13*	0.46*	0.24	0.59	-0.07	1.01*	0.04	0.87
CO	-0.08	-0.04	-0.16	0.02	-0.24*	-0.01	-0.22	0.01
LIT	0.25*	0.17	-0.50	-0.04	0.14	0.35*	-0.49	-0.37
HUM	-0.39*	0.23*	-0.27	0.43	-0.47*	-0.05	-0.27	0.17
MECH	0.17*	-0.05	0.11	0.02	0.18	0.15	0.13	0.23
PODZ	0.07	0.26*	0.08	0.41	0.03	0.30*	-0.03	0.32
CHER	0.01	0.01	-0.11	0.11	-0.01	-0.08	-0.14	-0.24
Autumn samples								
FRL	-0.12	-0.29*	0.59	0.13	-	-	-	-
TANN	-	-	-	-	-0.65*	-0.03	-0.96	0.05
TAMP	-0.47*	-0.25*	-0.16	-0.68	0.08	-0.05	0.70	0.46
DEFI	0.72*	0.71*	0.81	-0.26	-	-	-	-
HUMI	-	-	-	-	-0.10	-0.45*	0.04	-0.87
WA	-0.18	0.79*	-0.40	0.72	0.20	0.08	-0.01	-0.65
LIT	-0.12*	0.14	0.12	0.17	0.05	-0.01	-0.07	0.05
HUM	-0.25*	0.10	-0.01	-0.27	0.05	-0.26*	0.01	-0.17
MECH	-0.01	0.31*	-0.28	-0.03	-0.03	-0.05	0.47	0.15
PODZ	-0.07	0.19	-0.30	0.56	-0.07	-0.36*	-0.14	-0.68
All samples								
TMIN	-0.02	0.28	0.60	0.64	-	-	-	-
TANN	-	-	-	-	-0.74*	-0.03	-0.90	0.02
TAMP	-0.26	-0.04	-0.30	-0.77	-0.15	0.06	0.63	0.56
DEFI	0.65*	0.02	0.88	-0.22	-	-	-	-
HUMI	-	-	-	-	0.08	-0.48*	0.17	-0.90
WA	-0.06	0.36*	-0.51	0.66	-	-	-	-
CO	-	-	-	-	-0.13*	0.04	0.02	-0.49
LIT	-0.09	0.12*	0.52	0.08	-0.02	-0.01	-0.38	0.30
HUM	-0.06	0.11*	0.16	-0.02	-0.17*	-0.05	-0.12	0.17
MECH	-0.01	0.17*	-0.20	-0.04	0.02	0.04	0.36	0.25
PODZ	0.02	0.16*	-0.36	0.50	-0.19*	-0.12*	-0.05	-0.66
GREY	0.03	-0.04	0.09	-0.38	-	-	-	-
CHER	-	-	-	-	0.05	0.13*	-0.07	0.42

trend in the species data, since this type of soil is characteristic of the northern sites. The whole dataset demonstrates much of the same pattern (Figs 4e, f). Precipitation for the warm period having high importance in Figs 4c and e, we consider this as a result of the influence of a single deviating site (Fig. 1: site 3), the Rostochye Reserve, situated close to the foothills of the Carpathians and characterised by high precipitation rates.

The length of the arrows on the CCA biplots suggests that the species composition expressed in a presence/absence form shows a stronger relation to climatic parameters in comparison to species abundances. The latter seem to be influenced not only by climatic variables but also by factors characterizing the properties of the soil. It is rather possible that some noise in the species abundance data can also be attributed to seasonal variation.

Patterns of variation in species diversity

Similar to the species composition, the species diversity parameters were tested for correlation with environmental variables separately for the three datasets (Tab. 1).

The spring samples demonstrate an increase in the total abundance and diversity (number of species S , indices I/C , Sh , and HB) both from north to south and from west to east. This pattern is illustrated by significant negative correlations of the above parameters with latitude, longitude, annual temperature amplitude as well as with a decrease in the remaining temperature factors. On the contrary, the dominance indices show a reverse pattern meaning that, along with an increase in the climate continentality and severity, the 'concentration of dominance' within the spider assemblages grows, while their diversity becomes lower. Evenness measured with the indices F and G seems to be poorly related to macro-environmental factors and positively correlates solely with the number of frostless days.

The total abundance of the autumn samples correlates in the same way with climate, i.e. it is decreased both eastwards and northwards. The diversity measures, however, show a reverse pattern in comparison to the spring samples (Figs 5a-b), that is they are increased with latitude and longitude. Similarly, the evenness grows northeasterly, being negatively correlated with temperature and positively with the annual temperature amplitude. On the contrary, the more southern spider assemblages demonstrate a higher 'concentration of dominance' in the autumn.

It is noteworthy that the spider assemblages on soils of a heavier mechanical composition have a lower total abundance and a higher evenness as judged from autumn samples. However, this pattern is not observed in the spring dataset. In both autumn and spring samples, both the total abundance and the diversity as measured with Brillouin's index correlate positively with the thickness of the litter, although Brillouin's index in itself is known to be sometimes related to the total abundance [Peet, 1974]. Significant correlations of the evenness with the humus depth is revealed for both spring and whole datasets.

Analysis of the entire dataset confirmed strong negative correlation of the total abundance with an increase in the climate continentality and severity. Diversity measured with Brillouin's function also correlates positively with temperature. In particular, some of the evenness measures (HBE , F) as well as the diversity index D demonstrate a weak but significant relationship with both the mechanical composition of the soil and the humus depth, suggesting that the richer and the heavier the soil, the more diverse the assemblages. Similarly, the sites with a thicker litter show higher diversity as measured with the index HB .

The discriminant abilities of two popular indices, the N^e measure of diversity and the E measure of evenness (Pielou's evenness index), are illustrated in Figs 6a-b. It is evident that the evenness measure fails to reveal any patterns of geographical variation in the assemblages as compared to N^e (see also Fig. 5). The same conclusion can also be drawn for the N^e/N^o measure of evenness and the Shannon function, none indicating a dependence of the spider assemblages on the environmental variables.

Discussion

Species diversity versus species composition as a reflection of large-scale variation in climate and habitats

The above results allow to conclude that the relation of diversity statistics to environmental variation is seasonal. Moreover, although being more or less correlated to each other, most of the diversity measures react differently according to the environmental variables. In the spring and autumn, the diversity is decreased and increased eastwards, respectively. Evenness fails to demonstrate a clear geographical trend in the spring, but in the autumn it is likewise increased to the east. The differences among the indices cannot be considered as pure mathematical artifacts, they may reflect real

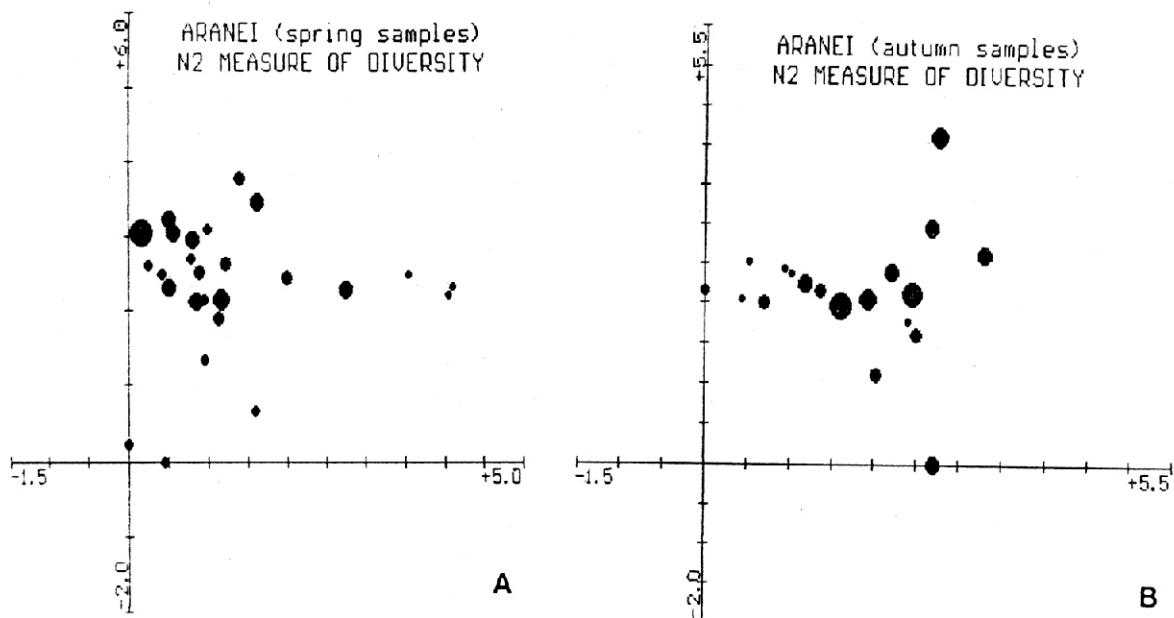


Fig. 5. Scattergrams of the N_2 diversity measure (= reciprocal of Simpson's index) of the spider assemblages. The location of the sites corresponds to the DCA scattergrams in Figs 3b and 2d, respectively.

Рис. 5. Скаттерграммы индекса разнообразия N_2 (= величина, обратная коэффициенту Симпсона) группировок пауков. Расположение точек соответствует скаттерграммамм ДКА соответственно на Рис. 3b и 2d.

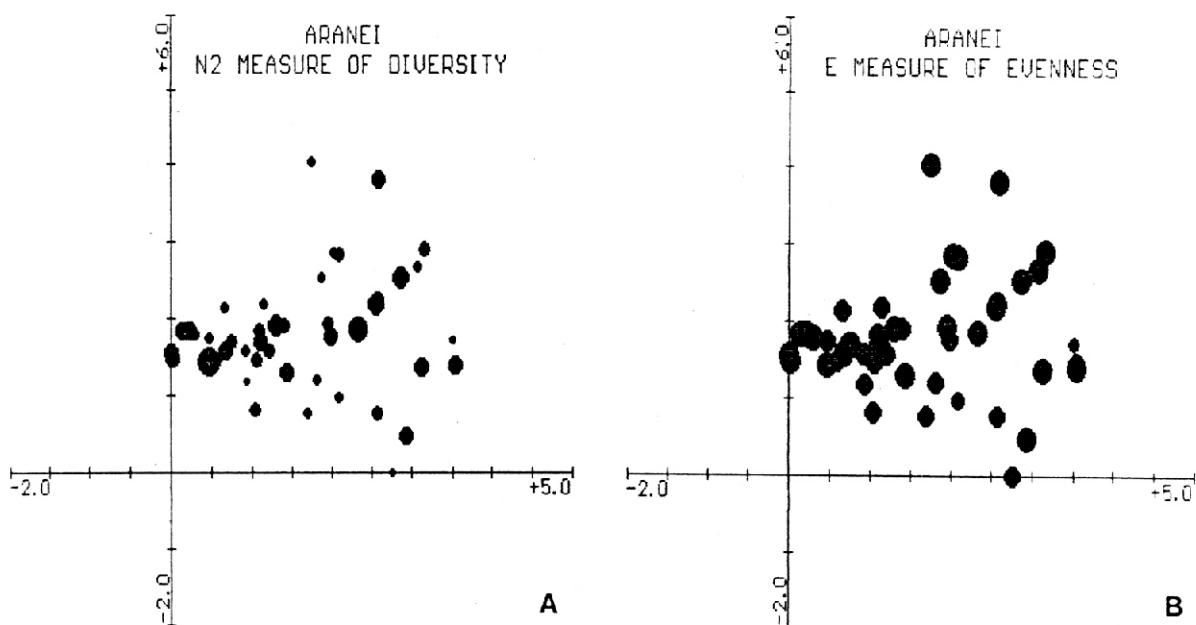


Fig. 6. Discriminant abilities of the N_2 diversity measure (= reciprocal of Simpson's index) and the E evenness measure (= Pielou's index of evenness) based on our filed data. The location of the sites corresponds to the DCA scattergrams in Fig. 3f.

Рис. 6. Дискриминантные возможности индекса разнообразия N_2 (= величина, обратная коэффициенту Симпсона) и индекса выровненности E (коэффициента выровненности Пайлоу) на основе наших данных. Расположение точек соответствует скаттерграммамм ДКА на Рис. 3f.

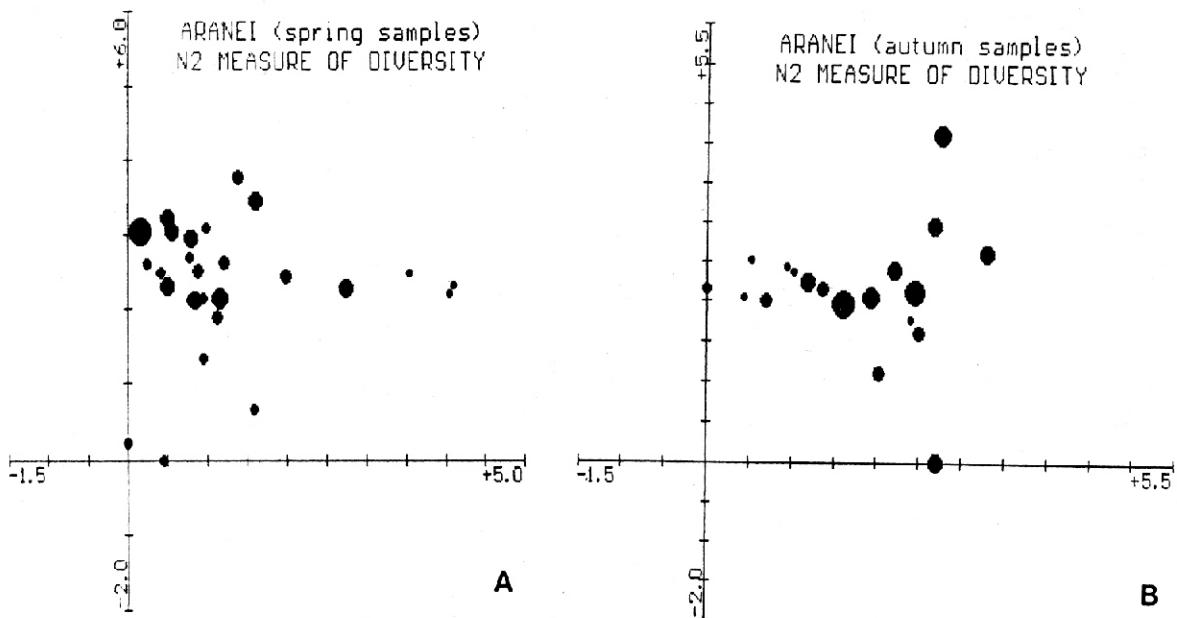


Fig. 5. Scattergrams of the N_2 diversity measure (= reciprocal of Simpson's index) of the spider assemblages. The location of the sites corresponds to the DCA scattergrams in Figs 3b and 2d, respectively.

Рис. 5. Скаттерграммы индекса разнообразия N_2 (= величина, обратная коэффициенту Симпсона) группировок науков. Расположение точек соответствует скаттерграммамм ДКА соответственно на Рис. 3б и 2д.

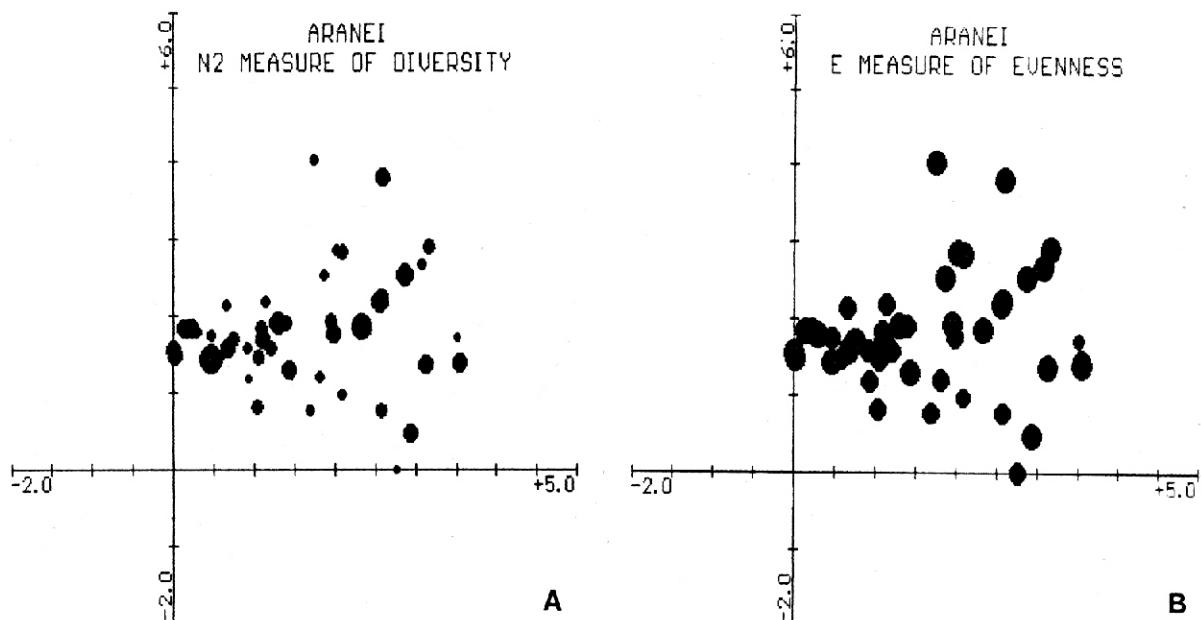


Fig. 6. Discriminant abilities of the N_2 diversity measure (= reciprocal of Simpson's index) and the E evenness measure (= Pielou's index of evenness) based on our field data. The location of the sites corresponds to the DCA scattergrams in Fig. 3f.

Рис. 6. Дискриминантные возможности индекса разнообразия N_2 (= величина, обратная коэффициенту Симпсона) и индекса выровненности Е (коэффициента выровненности Пайлоу) на основе наших данных. Расположение точек соответствует скаттерграммамм ДКА на Рис. 3f.

underlying processes in spider assemblages. For example, the spring samples from the southwestern oak forests are characterised by the highest species richness. In the Moldavian sites (10, 11, 13, 14), 14-21 species per site were found; in the sites of the Dnieper basin (4, 6, 7, 8) 11-26 species per site; in the central Russian oak forests (18, 19, 20) 7-16 species per site; and in the Cisuralian ones (42, 44, 46) 8-12 species per site. The high species richness of the southwestern oak forests is accompanied by codominance of 2-3 or even 4 species: *Microneta viaria*, *Diplocephalus picinus*, rarely *Enoplognatha ovata* (juveniles), *Tapinocyba insecta*, *Diplostyla concolor*, *Lepthyphantes flavipes*, *Hahnia nava*, *Nigma flavescens*. At the same time, solely juveniles of *Helophora insignis* (sites 44, 46) or *Ceratinella brevis* (site 42) dominated the Cisuralian oak forests.

In the autumn, the southwestern oak forests are characterised by a high-level species richness. The diversity, however, is decreased at the expense of the increasing predominance of a single species, *Microneta viaria*, while in the sites located within the zone of mixed coniferous-broadleaved forests (16, 17, 21, 23, 24) no prevailing single-species dominance is observed. In the Cisuralian sites (40, 45), the dominance of *Helophora insignis* revealed in the spring is smoothed in the autumn by its codominance with other species such as *Lepthyphantes mengei*, *L. tenebricola*, *Bolyphantes alticeps*.

The above considerations suggest that species diversity can be regarded as a discrete community parameter influenced by a larger number of stochastic factors than species composition. Variation in diversity among local assemblages depends on climate, habitat peculiarities, species phenology, possible biotic interactions and historical reasons. Although the diversity statistics, primarily the total abundance and the number of species, display some trends in geographical variation, the patterns observed are more irregular in comparison to species composition. Moreover, it is evident that the conclusions made on the basis of one or a few diversity statistics should be interpreted but with caution. Hence, the diversity indices seem to be less suitable as indicators of macro-environmental changes, particularly of climate. This conclusion is further reinforced by evidence recently presented by Heliövaara et al. [1991]: "Species richness decreased northwards, but the relation was not very convincing, suggesting that more specific factors may affect diversity in the Scolytidae" (p. 17).

On the contrary, compositional changes along vast geographical gradients seem to have much in common with the differentiation of biotic assemblages on a local scale. A unimodal response

of a species to environmental factors [Whittaker, Ter Braak, 1990], usually proved for local habitat gradients, may be extended on a far larger geographical scale. Hengeveld [1985] found that the Dutch carabid beetles are normally distributed in relation to climatic variables. Later he proposed the species-surface model [Hengeveld, 1990] which predicts that the abundance of a certain species will gradually decrease from the centre of the range to its margins. Therefore, local species assemblages will be composed of species deriving from different parts of their ranges. Chernov [1989] supposed that continualistic views on spatial variation of a biota should be extended to a zonal scale. Hence, species responses to climate on broader scales will result in continual variation patterns in the assemblage composition, similar to the individualistic concept of Ramensky-Gleason created to explain plant species distributions along local gradients. On the other hand, the climatic parameters also vary continually and therefore should be better indicated by continually varying biotic parameters, such as species composition, rather than discrete ones, such as species diversity. However, the above conclusion presumes that this approach may be applied only within more or less homogeneous faunistic/floristic regions. For example, a continual latitudinal variation in species assemblages along the entire north-south gradient from the European tundra up to the alpine belt of the Caucasus can hardly be expected with respect to climate, since a highly significant faunistic boundary has long been revealed between the Caucasus and Europe at which the fauna drastically changes due to merely historical reasons. In such cases, the second group of parameters (independent of the species composition) provides the only basis for comparisons in assemblages responses to the recent environmental conditions.

Environmental determinants in large-scale variation in species assemblages

The importance of temperature for the distribution of animals has long been known [e.g. Hesse, 1924; Uvarov, 1931]. Over the last few decades, an increased interest has appeared to broad-scale effects of thermal conditions on the distribution of biotic assemblages as well. Latitudinal variation in species richness has been discussed in numerous papers [reviews: Brown & Gibson, 1983; Hengeveld, 1990], being usually attributed to global changes in the radiation balance from the equator to the poles.

It has been shown by many authors that the diversity parameters of spider assemblages on local

scales correlate with the thickness and structure of forest litter [Lowrie, 1948; Huhta, 1971; Uetz, 1976, 1979; Bultman et al., 1982; Leclerc & Blandin, 1990]. Our results demonstrate this relationship on a far broader geographical scale, too.

Conclusions

This study aimed to prove one important methodological problem, namely which species assemblage parameters better reflect large-scale variation in climate. Besides, some patterns in spider assemblage variation with respect to the environment were also discussed. The following conclusions can be drawn as regards both issues:

(1) In studies on the geographic variation in spider assemblages, seasonal changes within them should be accounted for. This results from biological peculiarities of spiders, particularly from their adults often restricted to relatively short time periods. The same conclusion can perhaps be inferred for all soil invertebrate groups which support no more or less constant abundance levels of their populations during the whole year, either separately for imaginal and larval stages or both.

(2) The major variation trend in the species composition can be attributed to temperature, regardless of a latitudinal or a longitudinal arrangement of sampling sites. This conclusion holds for the autumn, spring, and whole datasets as well as for both presence/absence and abundance data. Among the temperature measures, the mean annual temperature and the number of frostless days show the highest values of correlation coefficients. The humidity parameters (precipitation, relative air humidity and its deficit) as well as soil properties (mechanical composition, thickness of litter, humus depth) seem to be of subordinate importance.

(3) North-south trends in the faunal composition can be related to climate, while those from west to east may be considered as a result of the combined effects of both recent ecological conditions (increasing climate continentality and severity) and historical processes (glaciations, influence of two important nemoral refuges, the Carpathian and the Uralian - see Esjunin et al., [1993]).

(4) Species richness is the highest in the southwestern oak forests, decreasing both northerly and easterly. This pattern, however, cannot be regarded as a regular gradient and is not supported by stable significant correlations with environmental variables.

(5) The total abundance of the assemblages decreases significantly north- and eastwards with

the increasing climate continentality and severity.

(6) Numerous alpha-diversity indices also vary in relation to climatic and habitat factors, but in different, sometimes contrary, ways in the spring and in the autumn.

(7) The parameters derived from species composition seem to be better indicators of spatial variation in climate rather than the parameters independent from species identities, e.g. species diversity. Species composition varies continually within relatively homogeneous faunistic regions, thereby reflecting continual variation in climate. Species diversity can be regarded as a discrete and stochastic biotic parameter strongly influenced by a large number of factors.

(8) Species composition based on presence/absence data largely reflects macroclimatic gradients, while species listings combined with abundances demonstrate also a relationship with local habitat conditions, primarily with the mechanical soil composition and litter thickness.

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Appendix 1.

Geographical location and characteristics of 46 study sites (see also Fig. 1). When not stated otherwise, the dominant oak species is *Quercus robur* L. Soil properties in Appendix 2.

Приложение 1.

Географическое местоположение и характеристика 46 точек сбора (см. также Рис. 1). Где не указано иначе, доминирующей породой дуба выступает вид *Quercus robur* L. Свойства почв приведены в Приложении 2.

No	Site	Province	Date	Forest type	Forest age (yr)
1	Struki 12 km NE Buda-Koshelevo	Gomel	7-9.09.1989	interfluve Querceto-Carpinetum nudum	120-130
2	Derno 30 km E Lutsk	Volyn	12-14.09.1989	interfluve Querceto-Carpinetum nudum	100-150
3	Rostochye Reserve ca. 40 km WNW Lvov	Lvov	16-20.09.1989	upland Quercetum nudum	80-120
4	Peruny nr. Mikhaylovka 10 km S Kanev	Cherkassy	28-29.05.1988	Quercetum aegopodiosum on fluvial terrace	80-120
5	Peruny nr. Mikhaylovka 10 km S Kanev	Cherkassy	28-29.09.1990	Quercetum aegopodiosum on fluvial terrace	100-120
6	Chernyi Les nr. Znamenka	Kirovograd	20-22.05.1988	interfluve Fraxineto-Quercetum aegopodiosum	100-200
7	Komissarovski Les 12 km W Volnogorsk	Dnepropetrovsk	19-21.05.1990	interfluve Querceto-Fraxinetum mixtoherboso-urticosum in ravine	80-120
8	Savranksi Les nr. Polyanetsko	Odessa	31.05-2.06.1988	interfluve Quercetum mixtoherboso-aegopodiosum	120-200
9	Savranksi Les nr. Polyanetsko	Odessa	4-7.10.1989	interfluve Quercetum mixtoherboso-aegopodiosum	120-200
10	Rossoshanskii Les 3 km N Briceani	Moldova	29-31.05.1990	interfluve Quercetum mixtoherboso-urticosum	70-120
11	Kodry Reserve nr. Lozova	Moldova	7-9.06.1988	upland Quercetum petraeae aegopodiosum	80-100
12	Kotovskii Les nr. Kotovsk	Moldova	26-29.09.1989	upland Quercetum pubescens cotinosum	40-70
13	Kotovskii Les nr. Kotovsk	Moldova	1-2.06.1990	upland Quercetum pubescens cotinosum	40-70
14	Tigechskii Les 5 km S Tigecei	Moldova	5-6.06.1990	upland Quercetum nudum	70-150
15	Sokolovo 15 km E Dubniki	Novgorod	31.08-3.09.1989	interfluve Quercetum mixtoherboso-oxalidosum	200-220
16	Dubniki 16 km NNE Udomlya	Tver (=Kalinin)	4-6.09.1990	floodland Quercetum caricosum	150-250
17	Sharapovo 50 km SW Moscow	Moscow	9-10.09.1990	interfluve Quercetum aegopodioso-caricosum pilosae	120-150
18	Sharapovo 50 km SW Moscow	Moscow	23-24.05.1991	interfluve Quercetum aegopodioso-caricosum pilosae	120-150
19	Vasilevskii 10 km N Venev	Tula	7-10.05.1988	interfluve Querceto-Tilietum equisetosum	50-70
20	Tulskiye Zaseki nr. Krapivna	Tula	3-7.05.1989	interfluve Querceto-Tilietum aegopodiosum	200-300
21	Tulskiye Zaseki nr. Krapivna	Tula	12-13.09.1990	interfluve Querceto-Tilietum aegopodiosum	200-300
22	Chernysheno ca. 30 km WSW Kozelsk	Kaluga	28.04-1.05.89	interfluve Quercetum aegopodioso-alliosum	-100-150
23	Trud ca. 20 km SE Ulyanovo	Kaluga	18-22.08.1991	interfluve Quercetum aegopodioso-galeobdolosum	150-400
24	Setukha 50 km E Orel	Orel	15-16.09.1990	interfluve Quercetum mixtoherbosum in ravine	100-120
25	Khinel 25 km SW Sevsk	Bryansk	18-19.09.1990	Quercetum caricoso-aegopodiosum on fluvial terrace	100-170
26	Kazatskii Les 25 km SW Kursk	Kursk	5-9.05.1990	interfluve Quercetum aegopodioso-convallariosum	50-100
27	Les-na-Vorskle Reserve	Belgorod	15-20.05.1988	upland Quercetum aegopodioso-caricosum pilosae	200-300

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Appendix 1.

Geographical location and characteristics of 46 study sites (see also Fig. 1). When not stated otherwise, the dominant oak species is *Quercus robur* L. Soil properties in Appendix 2.

Приложение 1.

Географическое местоположение и характеристика 46 точек сбора (см. также Рис. 1). Где не указано иначе, доминирующей породой дуба выступает вид *Quercus robur* L. Свойства почв приведены в Приложении 2.

No	Site	Province	Date	Forest type	Forest age (yr)
1	Struki 12 km NE Buda-Koshelevo	Gomel	7-9.09.1989	interfluve Querceto-Carpinetum nudum	120-130
2	Derno 30 km E Lutsk	Volyn	12-14.09.1989	interfluve Querceto-Carpinetum nudum	100-150
3	Rostochye Reserve ca. 40 km WNW Lvov	Lvov	16-20.09.1989	upland Quercetum nudum	80-120
4	Peruny nr. Mikhaylovka 10 km S Kanev	Cherkassy	28-29.05.1988	Quercetum aegopodiosum on fluvial terrace	80-120
5	Peruny nr. Mikhaylovka 10 km S Kanev	Cherkassy	28-29.09.1990	Quercetum aegopodiosum on fluvial terrace	100-120
6	Chernyi Les nr. Znamenka	Kirovograd	20-22.05.1988	interfluve Fraxineto-Quercetum aegopodiosum	100-200
7	Komissarovski Les 12 km W Volnogorsk	Dnepropetrovsk	19-21.05.1990	interfluve Querceto-Fraxinetum mixtoherboso-urticosum in ravine	80-120
8	Savranski Les nr. Polyanetsko	Odessa	31.05-2.06.1988	interfluve Quercetum mixtoherboso-aegopodiosum	120-200
9	Savranski Les nr. Polyanetsko	Odessa	4-7.10.1989	interfluve Quercetum mixtoherboso-aegopodiosum	120-200
10	Rossoshanskii Les 3 km N Briceani	Moldova	29-31.05.1990	interfluve Quercetum mixtoherboso-urticosum	70-120
11	Kodry Reserve nr. Lozova	Moldova	7-9.06.1988	upland Quercetum petraeae aegopodiosum	80-100
12	Kotovskii Les nr. Kotovsk	Moldova	26-29.09.1989	upland Quercetum pubescens cotinosum	40-70
13	Kotovskii Les nr. Kotovsk	Moldova	1-2.06.1990	upland Quercetum pubescens cotinosum	40-70
14	Tigechskii Les 5 km S Tigecei	Moldova	5-6.06.1990	upland Quercetum nudum	70-150
15	Sokolovo 15 km E Dubniki	Novgorod	31.08-3.09.1989	interfluve Quercetum mixtoherboso-oxalidiosum	200-220
16	Dubniki 16 km NNE Udomlya (=Kalinin)	Tver	4-6.09.1990	floodland Quercetum caricosum	150-250
17	Sharapovo 50 km SW Moscow	Moscow	9-10.09.1990	interfluve Quercetum aegopodioso-caricosum pilosae	120-150
18	Sharapovo 50 km SW Moscow	Moscow	23-24.05.1991	interfluve Quercetum aegopodioso-caricosum pilosae	120-150
19	Vasilevskii 10 km N Venev	Tula	7-10.05.1988	interfluve Querceto-Tiliatum equisetosum	50-70
20	Tulskiye Zaseki nr. Krapivna	Tula	3-7.05.1989	interfluve Querceto-Tiliatum aegopodiosum	200-300
21	Tulskiye Zaseki nr. Krapivna	Tula	12-13.09.1990	interfluve Querceto-Tiliatum aegopodiosum	200-300
22	Chernysheno ca. 30 km WSW Kozelsk	Kaluga	28.04-1.05.89	interfluve Quercetum aegopodioso-alliosum	-100-150
23	Trud ca. 20 km SE Ulyanovo	Kaluga	18-22.08.1991	interfluve Quercetum aegopodioso-galeobdolosum	150-400
24	Setukha 50 km E Orel	Orel	15-16.09.1990	interfluve Quercetum mixtoherbosum in ravine	100-120
25	Khinel 25 km SW Sevsk	Bryansk	18-19.09.1990	Quercetum caricoso-aegopodiosum on fluvial terrace	100-170
26	Kazatskii Les 25 km SW Kursk	Kursk	5-9.05.1990	interfluve Quercetum aegopodioso-convallariosum	50-100
27	Les-na-Vorskla Reserve	Belgorod	15-20.05.1988	upland Quercetum aegopodioso-caricosum pilosae	200-300

Appendix 1. (Continued)
Приложение 1. (Продолжение)

No	Site	Province	Date	Forest type	Forest age (yr)
28	Les-na-Vorskla Reserve	Belgorod	24-26.09.1990	upland Quercetum aegopodioso-caricosum pilosae	100-300
29	10 km SW Trostyanets	Sumy	21-23.09.1990	interfluve Quercetum aegopodiosum	100-150
30	Venevitinovo 33 km NE Voronezh	Voronezh	29-30.05.1989	Querceto-Pinetum aegopodioso- caricosum(pilosae) on fluvial terrace	70-80
31	Voronezh Reserve	Voronezh	31.05-1.06.1989	Quercetum aegopodioso-caricosum pilosae on fluvial terrace	60-80
32	Voronezh Reserve	Voronezh	2-3.06.1989	Quercetum aegopodioso-caricosum pilosae on fluvial terrace	70-100
33	Tellerman Forestry nr. Borisoglebsk	Voronezh	20-24.05.1989	interfluve Quercetum aegopodioso-caricosum pilosae	100-150
34	Shipov Les nr. Vorontsevka	Voronezh	5-6.06.1989	upland Quercetum aegopodioso-caricosum pilosae	80-130
35	Shipov Les nr. Vorontsevka	Voronezh	7-8.06.1989	upland Quercetum aegopodioso-caricosum pilosae	80-150
36	Gaidary S Gotvald	Kharkov	12-13.05.1990	interfluve Quercetum aegopodiosum	120-150
37	Serebryanskoye Forestry nr. Kremennaya	Lugansk	15-17.05.1990	floodland Quercetum caricoso-aegopodioso-convallariosum	80-150
38	Stanichno-Luganski Reserve nr. Lugansk	Lugansk	11-13.06.1989	floodland Quercetum convallarioso-aristolochiosum	70-90
39	Volga-Kama Reserve ca. 50 km S Kazan	Tatar	9-10.06.1991	floodland Quercetum mixtoherboso-aegopodiosum	70-120
40	Zhilgi Reserve, nr. Bakhilovo	Samara	23-26.08.1988	upland Quercetum mixtoherboso-aegopodiosum	80-100
41	Novosemekino ca. 15 km NW Samara	Samara	18-22.08.1988	interfluve Quercetum convallariosum	60-80
42	Sarashi 20 km S of Barda	Perm	25-26.06.1991	upland Quercetum aegopodioso-graminosum	60-120
43	Sarashi 20 km S of Barda	Perm	4-5.09.1991	upland Quercetum aegopodioso-graminosum	60-120
44	Vilyai 20 km S Asha	Chelyabinsk	15.06.1991	interfluve Quercetum mixtoherboso-aegopodiosum	60-80
45	Shulgan-Tash Reserve	Bashkiria	12-15.08.1988	upland Quercetum mixtoherboso-aegopodiosum	100-200
46	Shulgan-Tash Reserve	Bashkiria	17.06.1991	upland Quercetum mixtoherboso-aegopodiosum	100-200

Appendix 2. Soil properties (see Appendix 1).
Приложение 2. Свойства почвы (см. Приложение 1).

Site No	Soil type	Mechanical composition	Humus depth
1	Soddy podzolic	Sandy to sandy loam	8-13
2	Soddy podzolic	Sandy loam	15-30
3	Soddy podzolic to carbonatic	Sandy and loess-like loam to gravel	8-25
4	Soddy podzolic	Sandy loam to sandy	3-12
5	Soddy podzolic	Sandy loam to sandy	12-30
6	Grey forest	Moderate loam	10-20
7	Chernozem	Loess-like to moderate loam	30-40*
8	Grey forest	Moderate loam	15-35
9	Grey forest	Moderate loam	8-35
10	Grey forest	Moderate loam	30-40*
11	Brown forest	Moderate loam	10-30
12	Grey forest	Loess-like loam	5-15
13	Grey forest	Loess-like loam	3-12
14	Brown forest	Sandy & loess to heavy loam	2-20
15	Soddy podzol gleyed	Clayish	5-15
16	Soddy podzolic gleyed	Heavy loam	10-20
17	Soddy podzol	Moderate loam	8-12
18	Soddy podzol	Moderate loam	10-25
19	Grey forest	Moderate to heavy loam	20-30
20	Grey forest	Moderate to heavy loam	10-25
21	Grey forest	Moderate to heavy loam	10-25
22	Grey forest, partly gleyed	Moderate to heavy loam	10-20
23	Grey forest	Heavy loam	5-15
24	Chernozem	Moderate loam	10-50*
25	Grey forest	Sandy loam	15-20
26	Chernozem	Moderate loam	20-40*
27	Grey forest	Loess-like to heavy loam	10-40*
28	Grey forest	Loess-like to moderate loam	10-40*
29	Grey forest	Moderate loam	15-30*
30	Grey forest podzolized	Sandy loam	3-20
31	Grey forest	Moderate to sandy loam	8-40*
32	Grey forest	Silty to sandy loam	5-40*
33	Grey forest	Moderate to heavy loam	25-40*
34	Grey forest	Moderate to heavy loam	22-40*
35	Grey forest	Moderate to heavy loam	7-40*
36	Grey forest	Moderate loam	8-30*
37	Meadow chernozem-like	Moderate to heavy loam	20-40*
38	Meadow chernozem-like podzolized	Loess-like to moderate loam	10-40*
39	Soddy podzolic	Moderate to sandy loam	8-30
40	Brown forest	Moderate loam, gravel	5-40*
41	Chernozem	Moderate loam	15-40*
42	Grey forest	Gravel	3-20*
43	Grey forest	Gravel	1-20
44	Grey forest	Moderate loam, gravel	5-20
45	Grey forest	Moderate loam, gravel	10-40
46	Grey forest	Moderate loam, gravel	7-20

Variation in oakwood spider assemblages of the Russian Plain

Appendix 3.

BROW — brown forest soil, CHER — chernozem (black soil), CO — precipitation for the cold period, DEFI — mean annual humidity deficit (mmB), FRL — number of frostless days, GREY — grey forest soil, HUM — mean depth of the humus layer (A1 + A1AZ horizons), HUMI — mean annual relative humidity of the air (%), LATI — latitude, LIT — mean depth of the litter, LONG — longitude, MECH — mechanical composition of soil, PODZ — podzolized soil, PR — mean annual precipitation, SAND — sandy soils, TAMP — annual temperature amplitude (the difference between the mean temperatures of the warmest and coldest months), TANN — mean annual temperature ($^{\circ}\text{C}$), TJAN — mean temperature of the coldest month (January), WR — precipitation for the warm period. Number of sites as in Appendices 1, 2 and in Fig. 1.

Site	LONG	LATI	TANN	TMIN	TAMP	FRL	PR	WA	CO	HUMI	DEFI	SAND	MECH	GREY	PODZ	CHER	BROW	LIT	HUM
1	30°30'	52°43'	6.0	13.1	25.3	17	2	4	3	79	3.3	1	1.0	0	1	0	0	2.7	2.1
2	25°05'	50°45'	7.2	15.1	23.5	16	2	4	3	78	3.4	1	1.0	0	1	0	0	2.3	4.7
3	23°45'	49°50'	7.0	16.1	21.5	17	3	6	5	80	3.0	1	1.0	0	1	0	0	3.3	3.2
4	31°25'	49°45'	8.0	15.0	25.4	20	2	3	2	74	3.8	1	1.0	0	1	0	0	2.9	1.3
5	31°25'	49°45'	8.0	15.0	25.4	20	2	3	2	74	3.8	1	1.0	0	1	0	0	0.1	4.3
6	32°30'	48°45'	7.3	13.9	26.3	18	1	2	2	75	4.5	0	2.0	1	0	0	0	3.6	3.2
7	34°05'	48°45'	7.8	14.4	26.8	15	1	2	2	73	5.1	0	1.5	0	0	1	0	4.3	7.1
8	30°00'	48°05'	8.2	15.0	26.0	19	1	2	1	77	4.0	0	2.0	1	0	0	0	3.5	5.4
9	30°00'	48°05'	8.2	15.0	26.0	19	1	2	1	77	4.0	0	2.0	1	0	0	0	3.7	6.1
10	27°05'	48°20'	7.8	14.7	24.4	17	3	4	2	77	3.9	0	2.0	1	0	0	0	4.2	7.2
11	28°00'	47°00'	8.7	15.6	24.6	19	2	3	3	73	4.7	0	2.0	0	0	0	1	2.2	4.0
12	28°25'	46°55'	9.3	16.3	25.3	19	1	2	2	71	5.4	0	1.5	1	0	0	0	2.7	2.6
13	28°25'	46°55'	9.3	16.3	25.3	19	1	2	2	71	5.4	0	1.5	1	0	0	0	4.3	1.8
14	28°20'	46°30'	9.6	16.6	24.9	19	1	2	3	73	5.2	0	2.0	0	0	0	1	4.1	2.5
15	33°15'	58°00'	3.6	10.5	26.9	13	2	4	4	78	2.8	0	3.0	0	1	0	0	1.7	2.4
16	35°10'	57°50'	3.7	10.4	27.0	14	3	4	4	79	2.8	0	3.0	0	1	0	0	1.9	4.0
17	37°15'	55°10'	4.1	9.7	28.0	15	3	4	4	78	2.9	0	2.0	0	1	0	0	0.8	2.0
18	37°15'	55°10'	4.1	9.7	28.0	15	3	4	4	78	2.9	0	2.0	0	1	0	0	1.3	3.9

Приложение 3.

Географическое местоположение и характеристика точек сбора. BROW — бурая лесная почва, CHER — чернозем, CO — осадки за холодный период, DEF1 — среднегодовая амплитуда увлажнения (мВ), FRL — число безморозных дней, HUMI — средняя толщина гумусового горизонта ($A_1 + A_2$), HUMII — среднегодовая относительная влажность воздуха (%), LATI — широта местности, LIT — средняя толщина пластики, LONG — долгота местности, MECH — механический состав почвы, GREY — серая лесная почва, PODZ — сподзеленная почва, PR — среднегодовая сумма осадков, SAND — песчаные почвы, TAMP — среднегодовая температура ($^{\circ}\text{C}$), TANN — среднегодовая температура ($^{\circ}\text{C}$), WR — средняя температура за самый холодный месяц (январь), WR — осадки за теплый период. Номера точек как в Приложениях 1, 2 и Рис. 1.

Site	LONG	LATI	TANN	TMIN	TAMP	FRL	PR	WA	CO	HUMI	DEF1	SAND	MECH	GREY	PODZ	CHER	BROW	LIT	HUM
19	38° 12'	54° 28'	4.2	9.9	28.5	1.5	2	4	3	77	3.1	0	2.5	1	0	0	0	1.3	7.5
20	37° 10'	53° 55'	4.2	9.9	28.5	1.5	2	3	3	77	3.4	0	2.5	1	0	0	0	1.4	4.5
21	37° 10'	53° 55'	4.2	9.9	28.5	1.5	2	3	3	77	3.4	0	2.5	1	0	0	0	0.7	2.0
22	35° 15'	53° 48'	4.6	10.9	28.5	1.5	2	4	3	77	3.1	0	2.5	1	0	0	0	1.6	4.6
23	35° 50'	53° 38'	4.6	10.9	28.5	1.5	2	4	3	77	3.1	0	3.0	1	0	0	0	1.0	2.1
24	36° 47'	52° 55'	4.6	10.8	28.0	1.5	2	3	3	79	3.3	0	2.0	0	0	1	0	0.8	8.3
25	34° 10'	52° 00'	5.5	11.9	27.2	1.5	2	4	3	78	3.3	1	1.0	1	0	0	0	2.2	4.5
26	36° 18'	51° 32'	5.3	11.0	27.7	1.7	2	4	4	79	3.4	0	2.0	0	0	1	0	4.2	7.5
27	36° 00'	50° 50'	6.0	12.1	28.0	1.6	2	3	3	76	4.1	0	2.0	1	0	0	0	2.7	6.2
28	36° 00'	50° 50'	6.0	12.1	28.0	1.6	2	3	3	76	4.1	0	1.5	1	0	0	0	1.8	5.9
29	34° 50'	50° 30'	6.5	12.8	27.3	1.6	2	3	3	76	4.1	0	2.0	1	0	0	0	1.8	5.4
30	39° 40'	51° 52'	5.1	10.1	29.2	1.6	2	3	3	74	4.3	1	1.0	1	0	0	0	2.7	3.1
31	39° 40'	51° 52'	5.1	10.1	29.2	1.6	2	3	3	74	4.3	1	1.5	1	0	0	0	3.5	6.7
32	39° 40'	51° 52'	5.1	10.1	29.2	1.6	2	3	3	74	4.3	1	1.0	1	0	0	0	4.0	6.2
33	42° 05'	51° 20'	5.6	10.1	30.9	1.6	2	1	2	73	5.0	0	2.5	1	0	0	0	2.8	8.4
34	40° 20'	50° 32'	5.8	10.6	29.9	1.7	2	2	2	73	5.0	0	2.5	1	0	0	0	3.7	7.9
35	40° 20'	50° 32'	5.8	10.6	29.9	1.7	2	2	2	73	5.0	0	2.5	1	0	0	0	3.5	8.3
36	36° 20'	49° 35'	6.6	12.4	28.2	1.8	2	2	3	74	4.7	0	2.0	1	0	0	0	4.2	6.1
37	38° 15'	49° 00'	7.6	13.3	28.5	1.7	1	2	2	74	5.0	0	2.5	0	0	1	0	3.0	6.7
38	39° 25'	48° 30'	7.6	13.3	28.8	1.8	1	2	2	71	5.7	0	1.5	0	0	1	0	5.1	6.6
39	49° 10'	55° 20'	2.8	6.5	32.5	1.5	2	2	1	76	3.4	1	1.5	0	1	0	0	1.3	4.4
40	49° 45'	53° 25'	3.8	6.2	34.5	1.6	1	2	2	72	4.6	0	2.0	0	0	1	0	3.2	5.3
41	50° 20'	53° 25'	3.8	6.2	34.5	1.6	1	1	1	72	4.6	0	2.0	0	0	1	0	3.0	6.0
42	55° 45'	56° 44'	1.5	4.4	33.6	1.1	2	3	3	76	3.1	0	2.0	1	0	0	0	1.6	2.2
43	55° 45'	56° 44'	1.5	4.4	33.6	1.1	2	3	3	76	3.1	0	2.0	1	0	0	0	2.0	1.4
44	57° 15'	54° 48'	1.4	5.0	32.0	1.1	2	4	2	75	3.0	0	2.0	1	0	0	0	1.6	2.2
45	57° 00'	53° 10'	2.0	4.0	31.0	1.0	2	2	1	73	3.4	0	2.0	1	0	0	0	3.0	4.8
46	57° 00'	53° 10'	2.0	4.0	31.0	1.0	2	2	1	73	3.4	0	2.0	1	0	0	0	1.7	2.9

Variation in oakwood spider assemblages of the Russian Plain

Appendix 4.
Species composition, abundance (individuals per 1.25 m²) and diversity statistics of the spring spider assemblages. Site numbers as in Appendices 1-2 and Fig. 1, statistics abbreviations as in Tab. 1.

Приложение 4.
Биологический состав, численность (экз./1,25 м²) и меры разнообразия весенних группировок пауков. Номера точек как в Приложениях 1-2 и Рис. 1, сокращения индексов как в Табл. 1.

	4	6	7	8	10	11	13	14	18	19	20	22	26	27	30	31	32	33	34	35	36	37	38	39	42	44	46
S	19	26	11	16	12	21	12	11	12	7	14	6	10	15	13	10	14	9	12	12	18	11	16	14	7	8	10
N	63	137	28	77	54	42	59	45	23	12	26	8	17	34	26	37	39	29	21	29	34	34	74	33	13	18	31
D	0.72	0.69	0.68	0.69	0.64	0.87	0.67	0.68	0.73	0.79	0.83	0.88	0.86	0.72	0.81	0.62	0.74	0.66	0.84	0.80	0.86	0.79	0.74	0.78	0.59	0.55	0.38
Dmg	4.34	5.08	3.00	3.45	2.76	5.35	2.70	2.63	3.51	2.41	3.99	2.40	3.18	3.97	3.68	2.49	3.55	2.38	3.61	3.27	4.82	2.84	3.49	3.72	2.34	2.42	2.62
Dmn	2.39	2.22	2.08	1.82	1.63	3.24	1.56	1.64	2.50	2.02	2.75	2.12	2.43	2.57	2.55	1.64	2.24	1.67	2.62	2.23	3.09	1.89	1.86	2.44	1.94	1.89	1.80
1/C	7.26	7.42	5.03	6.48	5.10	14.00	5.72	5.55	5.69	5.14	8.89	5.33	8.26	6.22	8.24	4.26	7.01	4.75	8.32	8.16	11.80	8.38	8.42	7.95	3.07	2.95	2.12
Sh	10.27	13.06	7.44	9.56	6.68	16.97	7.87	7.29	8.26	6.00	11.09	5.66	9.03	9.37	10.22	6.32	9.41	6.29	9.91	9.60	14.92	9.46	10.31	10.39	4.56	4.64	3.77
HB	2.03	2.31	1.60	1.99	1.64	2.29	1.80	1.70	1.61	1.29	1.87	1.15	1.64	1.79	1.82	1.54	1.85	1.50	1.74	1.82	2.14	1.86	2.06	1.89	1.08	1.14	1.03
HBE	0.77	0.76	0.73	0.70	0.93	0.73	0.82	0.73	0.77	0.80	0.87	0.83	0.79	0.90	0.70	0.74	0.79	0.81	0.84	0.83	0.94	0.77	0.83	0.64	0.67	0.54	
F	0.64	0.53	0.63	0.64	0.72	0.81	0.69	0.72	0.65	0.83	0.78	0.93	0.90	0.62	0.79	0.61	0.71	0.71	0.82	0.83	0.78	0.87	0.80	0.74	0.58	0.53	0.41
G	0.26	0.15	0.24	0.26	0.37	0.49	0.32	0.37	0.27	0.52	0.45	0.71	0.65	0.24	0.45	0.23	0.36	0.36	0.50	0.52	0.44	0.59	0.47	0.39	0.20	0.15	0.07
C	0.14	0.13	0.20	0.15	0.20	0.07	0.17	0.18	0.18	0.19	0.11	0.19	0.12	0.16	0.12	0.23	0.14	0.21	0.12	0.12	0.08	0.12	0.12	0.13	0.33	0.34	0.47
d	0.25	0.31	0.39	0.31	0.30	0.14	0.34	0.31	0.35	0.33	0.19	0.25	0.18	0.29	0.23	0.43	0.26	0.38	0.19	0.21	0.21	0.19	0.24	0.54	0.56	0.68	

	4	6	7	8	10	11	13	14	18	19	20	22	26	27	30	31	32	33	34	35	36	37	38	39	42	44	46
<i>Dicymbium nigrum</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>Diplocephalus latifrons</i> (O.P.-Cambr.)	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>D. picius</i> (Blackw.)	13	15	2	10	16	3	2	10	4	-	1	2	-	-	3	16	8	5	4	4	2	4	-	2	-	2	
<i>Entelecara acuminata</i> (Wider)	-	1	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	-	-	-	-	-	-	
<i>Erigone atra</i> Blackw.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
<i>E. dentipalpis</i> (Wider)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>Erigonella biemialis</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
<i>Glyphestis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	
<i>Gongyliellum latebricola</i> (O.P.-Cambr.)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
<i>Gongyliellum rufipes</i> (L.)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	3	-	-	
<i>Maso sundevallii</i> (Westr.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	1	-	
<i>Micrargus herbigradus</i> (Blackw.)	-	1	-	4	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Moebelia penicillata</i> (Westr.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
<i>Panamomops mengui</i> Simon	-	13	-	1	-	-	-	-	-	-	-	-	-	-	1	6	3	10	11	1	-	5	11	-	1	1	-
<i>Tapinocyba bispinosa</i> (O.P.-Cambr.)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. insecta</i> (L.Koch)	2	3	-	24	1	-	1	-	-	-	-	-	-	-	1	-	1	4	4	2	-	-	-	-	-	-	-
<i>Thyreosthenius biovatus</i> (O.P.-Cambr.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>T. parasiticus</i> (Westr.)	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Trematocephalus cristatus</i> (Wider)	-	-	-	-	-	-	-	-	1	-	3	-	-	1	-	-	3	-	-	3	-	-	-	-	-	-	-

Appendix 5. Species composition, abundance (individuals per 1.25 m^2) and diversity statistics of the autumn spider assemblages. Site numbers as in Appendices 1-2 and Fig. 1, statistics abbreviations as in Tab. 1.

Быловой состав, численность ($\text{экз.}/1,25 \text{ м}^2$) и меры разнообразия осенних группировок птиц. Номера точек как в Приложениях 1-2 и Рис. 1, сокращения имен птиц как в Табл. 1.

	1	2	3	5	9	12	15	16	17	21	23	24	25	28	29	40	41	43	45
Fam. Atypidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Atypus piceus</i> (Sulz.)	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Fam. Dysderidae	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Harpactea saeva</i> (Herm.)	-	-	-	-	-	1	-	-	-	-	1	-	2	1	-	-	-	-	-
Fam. Mimetidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ero furcata</i> (Villers)	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
Fam. Theridiidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Crustulina guttata</i> (Widér)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Robertus insignis</i> O.P.-Cambr.	-	-	-	-	-	-	2	6	3	9	3	1	10	-	3	2	2	2	1
<i>R. lividus</i> (Blackw.)	4	2	5	-	-	-	-	-	-	-	-	1	-	-	-	2	2	1	3
<i>R. neglectus</i> (O.P.-Cambr.)	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
<i>Iberidion pallens</i> Blackw.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Fam. Linyphiidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Agyrta nurestris</i> (C.L.Koch)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Allomengea vidua</i> (L.Koch)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bathyphantes gracilis</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
<i>B. nigritus</i> (Westr.)	-	3	-	-	-	-	-	-	-	-	1	1	3	-	2	-	-	-	-
<i>Polyphantes alticeps</i> (Sund.)	-	-	-	-	-	-	-	-	-	-	1	1	1	-	2	1	1	1	8
<i>B. crucifer</i> (Menge)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	4

	1	2	3	5	9	12	15	16	17	21	23	24	25	28	29	40	41	43	45
<i>Centromerus aequalis</i> (C.L.Koch)	9	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
<i>C. arcarius</i> (O.P.-Cambr.)	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. sellarius</i> (Simon)	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. serratus</i> (O.P.-Cambr.)	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. syriaticus</i> (Blackw.)	5	4	-	-	-	5	3	-	4	1	3	3	3	8	7	1	-	-	5
<i>Diplostyla concolor</i> (Wider)	-	1	12	-	18	13	-	1	3	4	3	-	-	2	11	1	-	1	-
<i>Floronia bucculenta</i> (Clerck)	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Helopora insignis</i> (Blackw.)	4	-	-	-	-	4	-	-	3	2	1	3	3	6	16	1	-	7	-
<i>Leptophantes angulipalpis</i> (Westr.)	1	-	-	2	-	-	-	-	-	-	-	3	7	7	-	1	1	-	-
<i>L. cristatus</i> (Menge)	-	-	1	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-
<i>L. flavipes</i> (Blackw.)	-	-	-	9	11	14	-	-	-	-	-	-	12	7	-	-	-	-	-
<i>L. mansuetus</i> (Thorell)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>L. mengei</i> Kulcz.	-	-	3	-	-	1	-	-	-	-	-	1	-	-	3	-	1	11	-
<i>L. minutus</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>L. nigritiventris</i> (L.Koch)	-	-	-	-	-	1	-	1	-	4	-	1	-	-	3	-	1	1	3
<i>L. pallidus</i> (O.P.-Cambr.)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>L. tenebricola</i> (Wider)	2	2	16	-	-	-	-	-	-	-	-	-	-	-	4	-	-	6	-
<i>Macrargus multesimus</i> (O.P.-Cambr.)	24	-	-	-	-	2	-	-	-	-	-	2	3	2	-	-	1	-	-
<i>M. rufus</i> (Wider)	14	21	28	-	4	1	2	-	1	-	-	1	14	5	-	-	1	-	-

	1	2	3	5	9	12	15	16	17	21	23	24	25	28	29	40	41	43	45
<i>Microneta viaria</i> (Blackw.)	50	58	13	32	8	39	11	-	1	-	2	1	8	57	20	7	5	1	-
<i>Porrhomma pallidum</i> Jack.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. pygmaeum</i> (Blackw.)	-	-	-	-	3	-	-	5	-	-	-	-	-	-	-	-	-	-	-
<i>Tapinopa longidens</i> (Wider)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	1	-
<i>Abacoproces saltuum</i> (L.Koch)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Asthenargus paganus</i> (Simon)	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ceratinella brevis</i> (Wider)	-	-	-	-	6	-	1	-	-	-	-	-	1	7	-	1	1	6	2
<i>Dicymbium nigrum</i> (Blackw.)	-	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. tibiale</i> (Blackw.)	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplocephalus latifrons</i> (O.P.-Cambr.)	-	42	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. picinus</i> (Blackw.)	-	5	-	-	2	-	1	4	5	-	-	-	-	1	-	4	-	-	-
<i>Erigone dentipalpis</i> (Wider)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	4
<i>Glyphaesia</i> sp.	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gonatium rubellum</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gongylidium rufipes</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	3	3	-	-	-	-	-
<i>Maso sundevallii</i> (Westr.)	-	-	1	-	-	2	-	-	-	-	-	-	1	-	-	3	-	-	-
<i>Micrargus herbigradus</i> (Blackw.)	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mioxena blanda</i> (Simon)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Panamomops mengui</i> Simon	-	-	1	-	-	1	-	-	-	-	-	-	-	-	4	7	-	-	-

	1	2	3	5	9	12	15	16	17	21	23	24	25	28	29	30	40	41	43	45
<i>H. ononidum</i> Simon	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	4	-	2	
<i>H. pustula</i> C.L.Koch	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-	3	-	-	-	
Fam. Dictynidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Bromella falcigera</i> (Balogh)	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Nigma flavescens</i> (Walck.)	-	2	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Fam. Amaurobiidae	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Amaurobius pallidus</i> L.Koch	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	1	-	
Fam. Liocranidae	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	
<i>Agroeca bramea</i> (Blackw.)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
Fam. Clubionidae	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	4	-	
<i>Clubiona caerulescens</i> L.Koch	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. comta</i> C.L.Koch	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. germanica</i> Thorell	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
<i>C. terrestris</i> Westr.	-	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Fam. Gnaphosidae	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
<i>Haplodrassus silvestris</i> (Blackw.)	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
<i>Zelotes subterraneus</i> (C.L.Koch)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Fam. Zoridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Zora armillata</i> Simon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Z. nemoralis</i> (Blackw.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Fam. Philodromidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Thanatus sibiricus</i> (Menge)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Fam. Thomisidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Oxyptila praticola</i> (C.L.Koch)	-	-	1	-	-	3	-	-	-	-	-	-	-	-	1	2	-	-	-	
Fam. Salticidae	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	1	-	1	
<i>Ballus depresso</i> (Walck.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Euophrys erratica</i> (Walck.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Marpissa muscosa</i> (Clerck)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	

Appendix 5. (Continued)
Приложение 5. (Окончание)

	1	2	3	5	9	12	15	16	17	21	23	24	25	28	29	40	41	43	45
S	14	15	21	11	17	17	24	15	11	9	7	14	18	21	20	17	15	17	16
N	119	163	99	60	101	117	60	41	20	21	24	21	40	130	80	58	35	27	55
D	0.56	0.57	0.69	0.5	0.7	0.65	0.82	0.79	0.81	0.8	0.64	0.9	0.83	0.58	0.74	0.75	0.81	0.85	0.77
Dmg	2.72	2.75	4.35	2.44	3.47	3.36	5.62	3.77	3.34	2.63	1.89	4.27	4.61	4.11	4.34	3.94	3.94	4.85	3.74
Dmn	1.28	1.17	2.11	1.42	1.69	1.57	3.1	2.34	2.46	1.96	1.43	3.06	2.85	1.84	2.24	2.23	2.54	3.27	2.16
1/C	4.14	4.51	6.84	3.1	7.34	5.96	12.5	9.09	7.41	7.23	4.11	11.31	10.81	4.45	8.49	8.29	9.35	9.99	9.14
Sh	6.26	6.46	10.27	5.06	10.33	8.71	17.24	11.34	8.98	7.93	5.23	12.59	13.81	8.41	12.04	11.88	11.54	13.32	11.48
HB	1.67	1.73	2.07	1.4	2.1	1.97	2.38	2.01	1.66	1.62	1.34	1.89	2.13	1.92	2.18	2.11	1.98	1.98	2.08
HBE	0.65	0.64	0.7	0.62	0.74	0.7	0.83	0.8	0.79	0.9	0.76	0.88	0.87	0.68	0.83	0.82	0.86	0.84	0.82
F	0.6	0.64	0.63	0.52	0.68	0.64	0.71	0.78	0.8	0.9	0.74	0.89	0.77	0.47	0.68	0.67	0.79	0.73	0.78
G	0.21	0.27	0.25	0.14	0.31	0.27	0.35	0.45	0.48	0.64	0.39	0.62	0.43	0.1	0.31	0.3	0.46	0.38	0.44
C	0.24	0.22	0.15	0.32	0.14	0.17	0.08	0.11	0.14	0.14	0.24	0.09	0.09	0.22	0.12	0.12	0.11	0.1	0.11
d	0.42	0.36	0.28	0.53	0.27	0.33	0.18	0.22	0.25	0.19	0.42	0.14	0.2	0.44	0.25	0.28	0.2	0.22	0.2