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Coexistence of spiders in floodplain forests as an indicator of ecological stability and landscape sustainability in the inland Danube Delta

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This paper is dedicated to the memory of Ing. Zbyšek Šustek, PhD., who contributed significantly to the development of science and research in zoology, forestry and invertebrate ecology. Through his scientific and publishing activities, he has contributed significantly to the development and knowledge of the order Coleoptera in particular, and the extent of his knowledge has far exceeded this field. Thanks to his human and professional qualities, he was an example, an inspiration, a role model for us. As co-author, he did not live to see the final version. Zbyšek, you left too soon, we miss you, and we will never forget you.

Abstract

The coexistence of spiders in the Central European floodplains of the Danube River was assessed at 18 study sites (more than 43,000 individuals identified). Environmental conditions, i.e. groundwater level, flood regime, vegetation and tree shading, were defined as the main factors. The presence or absence of flooding and the depth of the water table had a significant effect on spider community structure. Based on the evaluation of 281 spider species found at sites in the inland Danube Delta, we conclude that the typical species of floodplain forests are the same, and thus the coexistence of these dominant and frequent species is a fundamental element of epigeic spider communities in floodplain forests in Central Europe (*Piratula hygrophila* Thorell, *Pardosa lugubris* Walckenaer as a leaders; and typical spiders – *Bathyphantes nigrinus* Westring, *Diplocephalus picinus* Blackwall, *Diplostyla concolor* Wider, *Oedothorax retusus* Westring, *Pachygnatha clercki* Sundevall, *Pachygnatha listeri* Sundevall, *Pardosa amentata* Clerck, *Pirata piraticus* Clerck, *Agroeca brunnea* Blackwall, *Liocranoeca striata* Kulczyński, *Ozyptila praticola* C. L. Koch and *Trochosa ruricola* De Geer and two euryhygrophilous species *Centromerus sylvaticus* Blackwall, *Palliduphantes pallidus* O. Pickard-Cambridge). We divided ground-dwelling spiders into four categories by using a simple dominance and frequency index ($DF_{flood} = \Sigma\, D_{hygro} \cdot F_{hygro} \cdot 0.01 / \Sigma\, D_{eury} \cdot F_{eury} \cdot 0.01$), which also characterize floodplain forest microhabitats and reflect their stability. The assessments of the status of floodplain wetland forest biota based on the DF-index values represents not only spatial but also temporal aspects, as well as the possibility of using it to determine the ecological stability of the landscape.

Key words: Araneae; dominance-frequency index; ecological stability; floodplain; species richness

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1. Introduction

The Danube is the second longest river in Europe. Its catchment is made up of a wide range of natural habitats linked to the floodplains of its tributaries. They provide the conditions for a rich and unique biodiversity. Thousands of square kilometres in central Europe belong to the extensive floodplain forest system of the inland Danube delta, which is influenced by the river's specific hydrological regime, characterised by late spring flood-

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ing caused by snowmelt at high altitudes in the Alps. The floodplain forests were declared an internationally important site under the Ramsar Convention on Wetlands in 1993. Europe's floodplain forests are unique areas with a high diversity of plants, animals and habitat types. Although European floodplain forests originally provided high diversity, their richness has declined due to strong human influence (Schindler et al. 2014).

Arthropods are a key group for the high diversity of these landscapes. The Central European floodplains were less investigated concerning the adaptations of arthropods to flood and drought conditions (Marx et al. 2012).

The earliest study of Arthropods and in special of spiders, from Danube delta near Letea in Romania is that by Loksa (1958). The systematic investigation of spiders in different flooded habitats in the Central European floodplains, in particular those of the Danube was in mid-1980s (Fig. 1), Thaler et al. (1984) in Donau Auen (Danubian floodplains) near Stockerau, Thaler & Steiner (1989) near Vienna in Austria and Bauchhenss (1991) five habitats in the Danube floodplain near Dillingen in Germany. In Slovakia, Čarnogurský et al. (1994) compared the soil fauna (including spiders) in forests and adjacent agricultural fields of the Podunajská nížina lowland. Gajdoš et al. (1992) summarised the data on spiders from the Danube lowland. Lisický et al. (1997) evaluated the adaptive changes of invertebrates in the areas influenced by the construction of a power station on the Danube River. Krumpálová (1996, 1997, 1998, 2002, 2005, 2021, 2023 and 2024) analysed the spider assemblages of the study sites before and after putting the Gabčíkovo hydrological structures into operation. She also compared spiders living in the flooded areas with natural flooding regime under the influence of huge hundred year's floods, or the impact of management measures in these sites. Énekesová (2008) investigated spiders in the floodplain forests at the Little Danube near the Vozokany village.

Miller & Obrtel (1975) investigated spiders in the reed stand around the Nesyt fishpond on confluence of six creeks and tributaries of the Dyje river in South Moravia, while Gajdoš (1994) investigated spiders in floodplain of the Morava river. Monitoring of spiders was later continued there by Krumpálová (1999, 2000), Kubcová & Schlaghamerský (2002), or Kalúz et al. (2004).

Several ecological and environmental levels need to be considered when assessing spider assemblages in specific habitats and characterizing the state of habitats. Essential, for this purpose, is a sufficient extent of material and a level of knowledge of ecological requirements of individual species. Spiders belong to the most sensitive bio-indicative groups of animals with exhibiting specific requirements to habitat features. Their association and mutual relationships, whether trophic or spatial, have already been evaluated by Hänggi et al. (1995). Coexistence theory informs that stochastic temporal dynamics are responsible to promote species diversity through several fluctuation dependent mechanisms (Chesson 2000; Barabás et al. 2018). Such coexistence arises when species have the same environmental responses and the temporal variation in resource availability and interactions make species to experience both favorable and unfavorable conditions across time, so any species has an opportunity to become dominant (Godoy 2019). The peculiarity is that ecosystems, on average, move from a relatively stable temporal trend to a strong directional change in the environment, often approaching a critical threshold, from which there is no return. Examples of extreme climatic events are beginning to be widely reported in the case of drought, floods and fires (Easterling et al. 2000).

Entling et al. (2007) summarize that spider communities are related to inundated habitat type, and spider community composition is dependent on both shading and habitat moisture, while other environmental conditions are also important for species distribution and abundance. Within niche theory, differences between species and environmental factors determine species distributions and ultimately community composition and diversity (Tokeshi 1999; Entling et al. 2007). Hubbell (1997, 2001, 2005) has the view that niche is of limited relevance for predicting community characteristics. According to Entling et al. (2007), spiders as numerically dominant predators in most terrestrial ecosystems are a species-rich group, in which species occurrence is related to factors such as vegetation structure, soil moisture, disturbance and management regime (Bonte et al. 2002), and thus are an important and valuable animal group. Wise (1993) states that the distribution and abundance of spiders depends on three factors: wind, humidity, and temperature. Hänggi et al. (1995) and Entling et al. (2007) analysed a large dataset of spiders in Central Europe and concluded that there is a strong relationship between community composition and environmental gradients, with two environmental gradients – shading and humidity. Šustek (1994), Lisický et al. (1997) or Krumpálová (2005, 2024) evaluated the adaptive changes of invertebrates and the impact of floods and groundwater level fluctuations on some communities in the Danube floodplain, confirming the strong impact of these factors on other environmental components – vegetation, soil and microclimatic conditions of some habitats.

The aim of this research is to analyse the diverse and divergent responses of epigeic spider assemblages of Central European floodplain forests on the Danube to the diversity of habitat conditions as well as to confirm and clarify the relationships of spiders to the floodplain forest environment in Central Europe. The specific tasks of the study were:

(1) to characterize the spiders of Central European floodplain forests, and their relationship to environmental gradients;
(2) define the importance of spider coexistence in floodplain forests;

(3) use the DF-index, applied to spider communities, to assess ecological stability, environmental quality and sustainability of the floodplain forest ecosystem.

2. Material and methods

2.1. Studied sites

The study sites were located in four countries – eastern Austria, south Moravia, south-western Slovakia, and in southern Germany, in the areas with similar forest vegetation, i.e. in regions (natural landscapes) characterized by uniform climatic and geomorphological patterns. The climate of the forested region of the Pannonian lowlands and hills is Pannonian subcontinental, i.e. a dry warmer climate, winters are moderately colder with little snowfall, and there are long dry periods in summer.

Spiders in the inland Danube Delta and its tributaries were collected by several authors at 18 study sites, most of them in the same time period, but some of them also in different time periods (Table 1, Fig. 1, 2). In the Slovak part of the inland Danube delta, most of the floodplain forests were severely affected by the construction of the Gabčíkovo hydroelectric structures, especially by the diversion of the main river channel into the derivation channel. Nowadays, regular floods are replaced by simulated floods, which are of a different nature and magnitude. The material was collected between the old channel of the Danube River and the derivation channel (Fig. 2).

Table 1. Basic characteristic of the studied floodplain habitats – overview of the studied forest types, authors of the collection (and year of data publication); number of species and specimens; traps were glass jars with a 9 cm diameter; eastern longitude and northern latitude and altitude of the monitored sites are part of the overview.

Author / year of publication	Country	Area-site	Forest type / sampling method	Coordinates DMS	Altitude (m a.s.l.)	No. individuals	No. species
DANUBE RIVER							
Bauchhenss (1991)	Germany	Dillingen	softwood pitfall traps	48°34´02˝N 10°27´54˝E	428	1,454	93
Thaler & Steiner (1989)	Austria	Donau-Auen Vienna	softwood pitfall traps	48°07´45˝N 16°39´59˝E	171	6,571	106
Thaler et al. (1984)	Austria	Donau-Auen Stockerau	hardwood pitfall traps	48°22´12˝N 16°11´32˝E	175	3,300	73
Krumpálová (2002, 2021)	Slovakia	Kráľovská lúka	softwood pitfall traps	47°54´16˝N 17°29´24˝E	118	6,818	109
Krumpálová (2005, 2021)	Slovakia	Bodícka Brána	softwood pitfall traps	47°52´22˝N 17°26´54˝E	123	6,290	81
Krumpálová (2005, 2021)	Slovakia	Dobrohošť	softwood pitfall traps	47°59´06˝N 17°20´51´´E	125	8,430	134
Krumpálová (1997)	Slovakia	Hamuliakovo	hardwood pitfall traps	48°01´52˝N 17°15´34˝E	126	262	25
Krumpálová (1997)	Slovakia	Istragov	softwood pitfall traps	47°49´28˝N 17°35´20˝E	119	407	41
Énekesová (2008)	Slovakia	Vozokany	softwood pitfall traps	48°07´00˝N 17°40´19˝E	116	204	23
Krumpálová (1997, 2021)	Slovakia	Kľúčovec	softwood pitfall traps	47°46´26˝N 17°43´57˝E	115	440	25
Krumpálová (1997)	Slovakia	Topoľové hony	hardwood pitfall traps	48°04´04˝N 17°12´37˝E	133	133	21

Author / year of publication	Country	Area-site	Forest type / sampling method	Coordinates DMS	Altitude (m a.s.l.)	No. individuals	No. species
MORAVA RIVER							
Miller & Obrtel (1975)	Czech Republic	Nesyt fishpond	alluvium pitfall traps	48°46´46˝N 16°52´49˝E	189	1,969	38
Gajdoš (1994)	Slovakia	Malé Leváre	softwood sweeping	48°29´49˝N 16°55´35˝E	174	72	22
Gajdoš (1994)	Slovakia	Borová	softwood sweeping	48°38´23˝N 16°58´25˝E	169	243	41
Gajdoš (1994)	Slovakia	Moravský Svätý Ján	softwood sweeping	48°35´13˝N 16°56´34˝E	156	126	24
Krumpálová (2000)	Slovakia	Horniacky Včelín A	softwood pitfall traps	48°18´34˝N 16°53´53˝E	145	2,314	65
Krumpálová (2000)	Slovakia	Horniacky Včelín B	hardwood pitfall traps	48°18´36˝N 16°54´16˝E	147	1,289	63
Krumpálová (1999)	Slovakia	Šrek	meadow pitfall traps	48°15´57˝N 16°57´20˝E	139	2,942	86

Fig. 1. Central Europe – investigated flooded forests in the Danube inland delta (yellow dots) investigated in: A – Donau-Auen (Austria), B – protected area of Dunajské luhy (Slovakia), C – Morava River, Slovak part (Slovakia); D – Morava River, Moravia part; Germany – Dillingen (separate left dot).

Fig. 2. Geographical position of the study sites; a more detailed view of the study areas (yellow dots) in the inland Danube delta.

2.2. Spiders sampling

Spiders in floodplain forests were surveyed between 1975 and 2008, mostly using traps. Traps (glass jars, 0.7 l; 9 cm diameter) were partially filled with 8% formol as a preservative. At each study site, ten traps were set in a line at a typical distance of 5–10 m from each other. Traps were emptied at four-week intervals, mostly from February to November. The trapping period covered most of the growing season as recommended by Riecken (1999). Our sampling in Slovakia was concentrated in the floodplain forests of the inland Danube Delta; where spiders were collected continuously over seven years at three study sites and over two years at six sites. Spiders were also collected in the forests along the tributaries of the Danube and for four years at three sites in the floodplain forests of the Morava River (Fig. 2, Table 1).

2.3. Habitat requirements

For the overall assessment and meta-analysis of the Danube spider fauna, we also used the results of experts from Germany, Austria and Moravia. We evaluated 34,309 individuals from the Danubian and 8,955 individuals from the Moravian forests (Table 1). All adult spiders were identified to species level using the keys for Central European spiders by Heimer & Nentwig (1991) and Nentwig et al. (2021). Nomenclature of spiders follows Platnick (2013) and Nentwig et al. (2021).

For statistical analyses, individual spider species were classified according to their habitat preference using relevant literature data (e.g., Hänggi et al. 1995; Kreuels & Platen 1999; Buchar & Růžička 2002; Matveinen-Huju 2004; Entling et al. 2007) as well as our databases. For the characterization of spiders in terms of their moisture and light requirements, we mainly relied on the works of Miller (1971), Martin (1991), Buchar & Růžička (2002) and Nentwig et al. (2021).

2.4. Environmental variables

Gradient variables were groundwater level (and associated soil moisture), tree shading (percentage of habitat shading), or tree cutting and the influence of vegetation cover (percentage of soil shading). Nominal variables were floods (i.e. periodic annual floods lasting 3–4 weeks; or huge floods, reaching the level of a hundred-year discharge; absence of floods; or simulated floods (Fig. 3) associated with regulation and restoration of river systems.

2.5. Data analyses

The assessment of the spider communities was carried out over a long time horizon. We took into account our own and literature data from the Danube area. We analysed the data at the species and community level to see how the epigeic spiders respond to environmental and

Fig. 3. Simulated and coordinated summer flooding replaces natural flooding of Danube forests (Slovakia).

ecological factors. Species dominance and frequency (Balogh 1958), diversity indices and multivariate analyses were calculated using PAST software (Hammer et al. 2001) and CANOCO (Ter Braak & Šmilauer 2002, 2015). Classification of species according to their habitat preferences is common for arthropods, but information on the habitat affinities of spiders is less well known in ecological studies (Matveinen-Huju 2004).

To evaluate the coexistence of epigeic spiders in the Danube River floodplain, we also used DF-index = $\Sigma D \cdot F/100$ (D – dominance, F – frequency of species). We used a combination (ratio) of two indices, one for hygrophilous species and the other for euryhygric species, to determine the stability of the environment. By their ratio, we obtained a number whose value is suitable for determining the originality and conservation of the studied habitat. $DF_{flood} = \Sigma D_{hygro} \cdot F_{hygro} \cdot 0.01 / \Sigma D_{eury} \cdot F_{eury} \cdot 0.01$ [in %], where in our case D_{hygro} is the dominance of the hygrophilous species and F_{hygro} is the frequency of hygrophilous species occurred in the studied habitat (to obtain a real value of the percentage of the species in the coenoses). Similarly, we determined the DF_{eury}, where we took into account the dominance and frequency of euryhygric species. Frequency of occurrence is a little used characteristic in ecology, but it completes the picture of the studied communities, because even species with low abundance have an important and irreplaceable place in them. The DF_{flood}-index thus represents not only a spatial but also a temporal assessment of the coenoses, where, in addition to the percentage of species in the community, information on the frequency of their occurrence in a certain temporal aspect is also taken into account.

We used the sum of the annual dominance of species and their frequency in each plot to assess spider communities using the DF_{flood}-index. For shorter temporal surveys, we recommend using dominance and frequency of occurrence in proportion to the temporal aspect of the survey. The DF_{flood}-index allows us to classify ground-dwelling spiders into several categories that simultaneously reflect the habitat characteristics of the environments surveyed.

3. Results

3.1. Spiders of the floodplains in the Danube, Morava and Dyje rivers

A total of 281 spider taxa were found at 18 sites on the Danube and its major tributaries. Our survey yielded 29,548 individuals; 13,715 spiders were found by other specialists (Table 1). The collected data were analyzed and compared using one-way ANOVA, Levene's test for homogeneity of variance based on means $p \leq 0.0001$, followed by Welch's F test for unequal variances ($F = 11.47$, total df = 709.9, $p = 9.56E-6$) (Hammer et al. 2001). Most spiders were detected in only a small number of individuals. But up to 45 spider species were regularly found at each study site in higher abundance and more frequently (Table 2).

In terms of dominant species, the most active hunting spiders were *Piratula hygrophila* Thorell and *Pardosa lugubris* Walckenaer, which were constantly present at all sites during the investigation. *P. hygrophila* Thorell as a typical wetland-loving spider was regularly present at all study sites in shaded or semi-open habitats of flooded areas with the highest humidity (Table 1, 2). Dominance of *P. hygrophila* Thorell varied from 2.9 to 54%, with an average 23.7%. Generally, in all study sites dominance of *P. hygrophila* Thorell decreased during periods without floods. The presence of floods, including the simulated or huge natural floods, affected its dominance positively; however, its correlation with ground water table was not significant. The second dominant species at the flooded areas was euryhygrophilous spider *P. lugubris* Walckenaer, that occurred at all sites, even in more opened habitats and very quickly invaded habitats with decreased humidity. The dominance of *P. lugubris* Walckenaer varied at studied habitats from 0.4 to 55.0%, in average it amounted 12.7%. The dominance of *P. lugubris* Walckenaer increased especially in years without floods, on altered and drier habitats on the Danube or on the open flooded meadow of the Morava River. In contrast, floods reduced its dominance significantly. The correlation between groundwater tables with its dominance suggests an indirect relation.

Highly dominant spiders with frequent presence included – *Ozyptila praticola* C. L. Koch (98%), its dominance ranged from zero to 23.6, with an average reached 6.4%; *Diplostyla concolor* Wider was frequently present at the study sites (86%), its average dominance of 7.2%. The presence of *Centromerus sylvaticus* Blackwall was 76%, its mean dominance was 8.5%. *Pachygnatha listeri* Sundevall was present frequently at 88% of study sites, its dominance ranged from zero to 17.5% (in average 6.9%) (Table 2).

3.2. Spider assemblages in flooded forests – significant relationships to environmental gradients

Regular flooding of the forests and continuous shading by trees created suitable conditions for most of the hygrophilous spiders, in which represented together 80% of individuals with expressive dominance of *P. hygrophila* Thorell. In contrast, at the studied sites with a declining water table with subsequent lack of herbaceous undergrowth, the later extinction of willows and poplars and the absence of flooding, spider communities were characterized by an expansion of *P. lugubris* Walckenaer.

PCA (Fig. 6) (the first axis explained 79.2% of the variability in the data, the second axis 8.9%) confirmed the greatest significance of the two dominant species, *P. hygrophila* Thorell and *P. lugubris* Walckenaer, for structure of the spider assemblages. The absence of floods caused a significant decrease in the dominance of the hygrophilous species and caused an increase in the number of euryhygrophilous species and an enormous increase in the species spectrum (Figs. 4, 6).

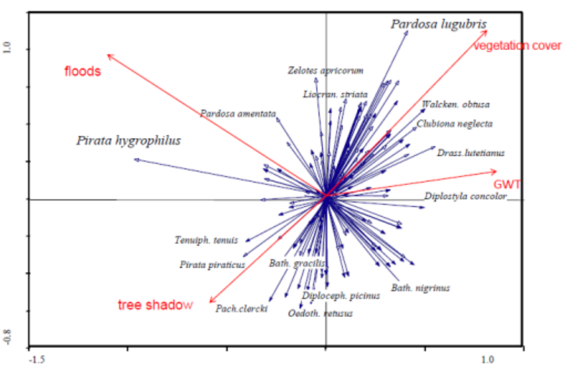

Fig. 4. PCA analysis of spider species spectrum of Central European floodplains. Environmental variables were – vegetation cover – herbaceous undergrowth, ground water table (GWT), tree shading and presence of floods.

The second important ecological variable was groundwater table (GWT), which influenced habitat moisture. Stable GWT (maximum drop to 1 m below ground surface) did not affect herb cover or shading and habitat moisture, all of which ultimately had a positive effect on spider communities (species numbers averaged 35), and the species spectrum did not change much over time. The huge drop in the water table to −5 m resulted in irreversible changes in vegetation and tree cover – the willows lost their leaves; their roots lost their connection to the water table and died very quickly. The study sites were open to the penetration and immigration of new xenocenous spiders with completely different demands on the hydrological regime and light conditions after the groundwater level dropped, which can be compared to the diversity in the open meadow on the Morava River (Fig. 5A). The increase in diversity was associated with an increase in the number of individuals (Fig. 5 B) up to 70 species; and the correlation between the number of species and the water table was −0.89 (significant), the proportion of hygrophilous spiders in the coenoses declined rapidly (Fig. 4). The relationship of the ecological groups of spiders (hygrophilous – euryhygrophilous) and species of the two dominant families (Linyphiidae and Lycosidae) to the gradient of the variables was analyzed using CCA (Fig. 6). CCA showed that the gradient variable, water table level, was significant ($p < 0.0001$, Monte Carlo test with unrestricted permutations), while tree shading and vegetation cover also had a lower p-value. The nominal variable was flooding, its presence or absence. The cumulative variance accounted for 33.46% $[(0.520 / 1.554) \cdot 100]$ of the total variance of the data, with the remaining 66.54% being unexplained variance. Hygrophilous spiders were affected by the presence of flooding, hemi-hygrophilous spiders were affected by groundwater level and tree shading (Fig. 6). Euryhygrophilous species, non-specific or non-typical spiders of flooded areas, were affected by the drop in groundwater level and changes in vegetation cover. Herbaceous undergrowth and humidity had a large effect on wolf spiders (Lycosidae); on the other hand, tree shading and groundwater level affected small linyphiids. The dispersal ability of small linyphiids is usually better than that of lycosids, due to very efficient balloon-like transport.

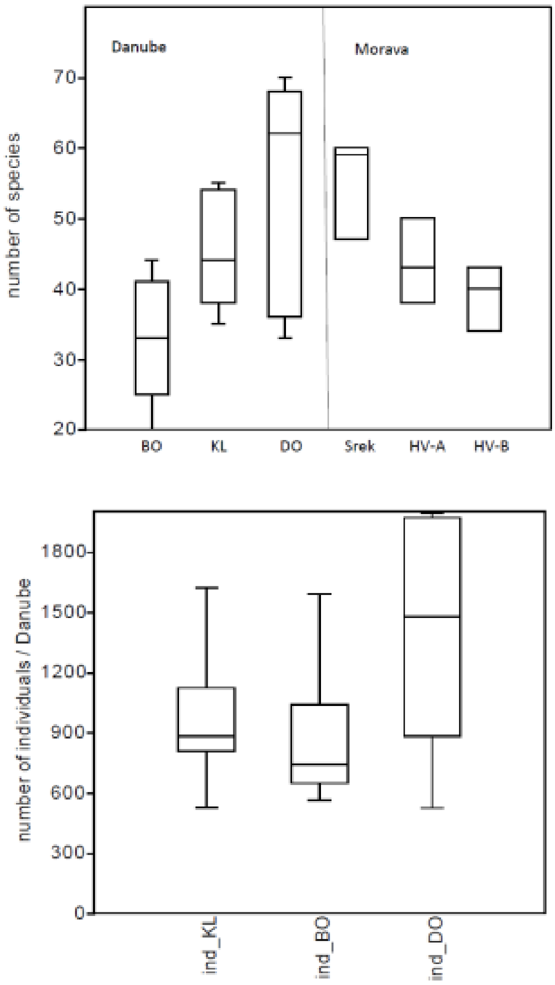

Fig. 5. Box plot (95% interval confidence, interpolation): A – number of spider species of choose study sites – affected coenose in the Danube forest Dobrohošť is very close to the number of species found in open flooded meadow of the Morava river; B – a significant increase in the number of individuals in affected coenose in Danube forest Dobrohošť in comparison with other monitored sites on the Danube, where the number of collected specimens was at a significantly lower level.

Note: Abbreviations Danubian sites: KL = Kráľovská lúka, DO = Dobrohošť, BO = Bodícka Brána. Abbreviations Moravian sites: HV-A = Horniacky včelín A, HV-B = Horniacky včelín B and Šrek.

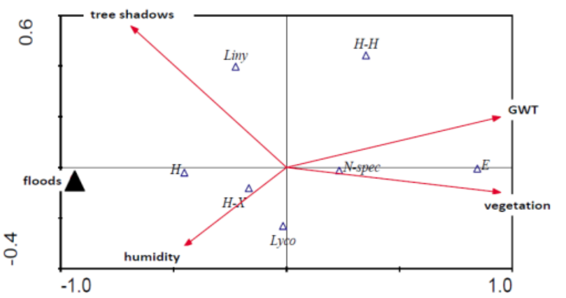

Fig. 6. Analysis of the relationship of spider ecological groups to gradient variables (CCA). Analysis of the influence of these factors showed that the gradient variable, groundwater level, was a significant variable; but shade trees and herbaceous understory had lower p-values; the nominal variable was flooding (its presence or absence).

Note: spider ecological groups (H = hygrophilous, H-H = hemi-hygrophilous, E = euryhygrophilous, H-X = hemixerophilous, Lin = Linyphiidae, Lyc = Lycosidae, N-spec = non-specific spiders), environmental variables (vegetation cover – herbaceous understory, groundwater level, tree shade and humidity), nominal variable – presence or absence of flooding.

3.3. Coexistence of ground dwelling spiders in floodplain forests

All 43 264 individuals belonging to 281 species were considered suitable for evaluation in floodplain forests in the Danube Inland Delta. More than one criterion (higher dominance, frequency, moisture requirements and proportion in the DF_{flood}-index) was fulfilled by 45 of them (Table 2). Based on our results and those of other researchers, we analysed the spiders from all studied sites using statistical methods and categorised them. To assess the coexistence of these species, we determined that the ratio of dominance and frequency ($DF = \Sigma D_h \cdot F_h / \Sigma D_e \cdot F_e$) of hygrophilous (h) and euryhygrophilous (e) spiders had to be greater than 2.5 for a given habitat to be considered a stable wetland (Table 2, Fig. 6).

As a model for the application of the DF-index we used those study areas of the Danube where we have continuously collected spider material for more than three years. During periodic floods and optimal hydrological conditions, DF_{flood}-index values were higher than 2.5 at all study sites in the Danube (Table 3). These sites were assessed as typical floodplain forests in excellent condition. In contrast, after two years without flooding, a reduction in GWT and subsequent changes in herbaceous cover in Danubian study sites, the DF-index value decreased significantly, reflecting real changes in the floodplain forest that caused a significant increase in euryhygrophilous individuals (Table 3).

Similarly, at the studied sites on the Morava River we observed lower values of DF-index, which also corresponded with no flooding period and with the changes in vegetation cover and light conditions of the habitats.

3.4. Categories of spiders to a particular habitat type based on the DF-index and their bioindication value

On the basis of the analysis of all data (Table 2), we created a classification of ground-dwelling spiders in the floodplain forests of Central Europe:

A. Preferentially, floodplain forest spiders are leader species that prefer shaded habitats inside forests as well as forest edges. In Central Europe (Germany, Austria, Moravia, Slovakia, Hungary and Romania) these are two species, *Piratula hygrophila* Thorell and *Pardosa lugubris* Walckenaer, which occurred in high dominance. A higher proportion of *P. lugubris* Walckenaer always indicates that the habitat is becoming drier.

B. Typical floodplain species are widespread species that often occurred in the floodplain forests of Central Europe (Germany, Austria, Morava, Slovakia, Hungary and Romania), some of them are hygrophilous – *Bathyphantes nigrinus* Westring, *Diplocephalus picinus* Blackwall, *Diplostyla concolor* Wider, *Oedothorax retusus* Westring, *Pachygnatha clercki* Sundevall, *P. listeri* Sundevall, *Pardosa amentata* Clerck, *Pirata piraticus* Clerck, *Agroeca brunnea* Blackwall, *Liocranoeca striata* Kulczyński, *Ozyptila praticola* C. L. Koch and *Trochosa ruricola* De Geer and two are euryhygrophilous *Centromerus sylvaticus* Blackwall, *Palliduphantes pallidus* O. Pickard-Cambridge. These fourteen species with high frequency of occurrence and higher dominance (DF-index ≥ 1) regularly formed the basis of the assemblages.

C. Specific species are characteristic of the floodplain forests of certain landscapes and regions, thus specifying their microclimatic conditions. Many of them are abundant only in a given habitat type.

The following species are typical of the floodplain forests of the inland Danube delta in Slovakia – *Robertus lividus* Blackwall, *Collinsia distincta* Simon, *Ceratinella scabrosa* O. Pickard-Cambridge, *Bathyphantes gracilis* Blackwall, *Hypomma cornutum* Blackwall, *Walckenaeria obtuse* Blackwall, *Ero furcate* Villers, *Neriene clathrate* Sundevall, *Pelecopsis mengei* Simon, *Thyreosthenius parasiticus* Westring, *Clubiona pallidula* Clerck, *Tenuiphantes tenebricola* Wider.

The floodplain forests in Hungary and Romania, according to the excerpted data from cited sources, were no specific spiders; communities were very similar to the Slovakian Danube forests.

In floodplain forests along the Danube in Germany these are typical – *Robertus neglectus* O. Pickard-Cambridge, *Erigonella hiemalis* Blackwall, *Pelecopsis radicicola* L. Koch, *Peponocranium orbiculatum* O. Pickard-Cambridge, *Silometopus bonessi* Casemir, *Trichoncus hackmani* Millidge, *Saaristoa abnormis* Blackwall, *Pirata latitans* Thorell.

Table 2. Characteristic epigeic spiders in forests of Danube inland delta excerpted from 281 find spider species.

Taxa	hum	light	Morava		Danube		D (%)	F	DF index
			D (%) min	D (%) max	D (%) min	D (%) max	average	(%)	(%)
Piratula hygrophila Thorell, 1872	h	p-sh, sh	2.9	22	1.2	54	23.16	100	23.16
Ozyptila praticola (C. L. Koch, 1837)	h-h	p-sh, sh	0	23.6	0	15.7	6.41	98	6.26
Diplostyla concolor (Wider, 1834)	h-h	p-sh, sh	0	33.4	0	28.9	7.20	86	6.17
Pachygnatha listeri Sundeval, 1830	h	p-sh, sh	0	17.5	0	17.2	6.94	88	6.11
Agroeca brunnea (Blackwall, 1833)	h-h	sh	0	7	0	19.3	2.62	81	2.12
Pardosa amentata (Clerck, 1757)	h	s-o	0	3.6	0	13.5	3.19	60	1.9
Diplocephalus picinus (Blackwall, 1841)	h-h	p-sh, sh	0.3	7.8	0	17.1	1.92	95	1.83
Liocranoeca striata (Kulczyński, 1882)	h	o, sh	0.3	7	0	7.5	2.55	64	1.63
Oedothorax retusus (Westring, 1851)	h-h	s-o	0	1.2	0	17.9	3.75	40	1.52
Trochosa ruricola (De Geer, 1778)	h-h	o	0	2.6	0	12.8	2.19	67	1.46
Bathyphantes nigrinus (Westring, 1851)	h	p-sh, sh	0	4	0	8.6	2.27	64	1.46
Pirata piraticus (Clerck, 1757)	h	o, s-o	0	3.2	0	12.7	2.59	48	1.24
Pachygnatha clercki Sundeval, 1823	h	o, s-o	0	2.1	0	7.6	2.66	45	1.2
Diplocephalus latifrons (O. P. Cambr., 1863)	h-h	s-o, sh	0	0.2	0	15	1.59	48	0.76
Bathyphantes gracilis (Blackwall, 1841)	h	s-o, p-sh	0	0.3	0	6.3	1.47	45	0.67
Robertus lividus (Blackwall, 1836)	h-h	p-sh, sh	0	4.2	0	1.6	0.82	69	0.56
Ceratinella scabrosa (O. P. Cambr., 1871)	h-h	sh	0.3	2.4	0	1.8	0.87	55	0.48
Neriene clathrata (Sundevall, 1830)	h-h	p-sh, sh	0	1.8	0	1.3	0.70	64	0.45
Walckenaeria obtusa Blackwall, 1836	h	sh	0	2.7	0	3.5	0.83	52	0.44
Trochosa spinipalpis (F. O. P. Cambr., 1895)	h	s-o, p-sh	0	2.8	0	0.6	1.49	29	0.43
Dicymbium nigrum (Blackwall, 1834)	h	o, s-o	0	2.8	0	0.7	1.48	24	0.5
Gongylidium rufipes (Linnaeus, 1758)	h	p-sh, sh	0	1.6	0	3.2	0.78	38	0.3
Walckenaeria nudipalpis (Westring, 1851)	h	p-sh, sh	0	1.2	0	1.7	0.62	45	0.28
Neriene montana (Clerck, 1757)	h-h	p-sh, sh	0	2.8	0	1	0.54	38	0.21
Clubiona lutescens Westring, 1851	h-h	s-o, p-sh	0	1.4	0	1.3	0.34	43	0.15
Ero furcata (Villers, 1789)	h-h	p-sh, sh	0	0.4	0	0.6	0.26	40	0.11
Clubiona pallidula (Clerck, 1757)	h-h	sh	0	0.4	0	0.4	0.28	33	0.09
Drassyllus lutetianus (L. Koch, 1866)	h	p-sh, sh	0	0.9	0	0.5	0.27	24	0.06
Allagelena gracilens C. L. Koch, 1841	h-h	p-sh	0	0.2	0	0.4	0.20	24	0.05
DF Σ hygrophilous and hemi-hygrophilous									61.46
Tenuiphantes flavipes (Blackwall, 1854)	h-x	p-sh, sh	0	8.7	0	7.8	1.12	38	0.43
Zelotes subterraneus (C. L. Koch, 1833)	h-x	o, p-sh	0	0.4	0	1.4	0.53	36	0.19
Clubiona neglecta O. P. Cambridge, 1862	h-x	o, s-o	0	0.3	0	0.7	0.26	26	0.07
Araneus marmoreus Clerck, 1757	h-x	s-o, p-sh	0	0	0	0.4	0.17	26	0.04
Alopecosa aculeata (Clerck,1757)	x	p-sh	0	0.1	0	3.6	0.79	19	0.15
DF Σ hemixerophilous and xerophilous									1.51
Pardosa lugubris (Walckenaer, 1820)	e	p-sh	0.4	38	0.8	55.3	12.75	100	12.75
Centromerus sylvaticus (Blackwall, 1841)	e	o, sh	0	50	0	20	8.46	76	6.45
Palliduphantes pallidus (O. P. Cambr., 1871)	e	p-sh, sh	0	1.1	0	7.7	1.61	55	0.88
Oedothorax apicatus (Blackwall, 1850)	e	o	0	19	0	1.3	3.56	24	0.85
Tenuiphantes mengei (Kulczyński, 1887)	e	s-o, p-sh	0	0.4	0	6.2	1.77	33	0.59
Walckenaeria antica (Wider, 1834)	e	o, s-o	0	1.7	0	1.2	0.87	60	0.52
Pisaura mirabilis (Clerck, 1757)	e	o, s-o	0	0.3	0	4.2	0.67	55	0.37
Zora spinimana (Sundevall, 1833)	e	o, s-o	0	2.4	0	1.3	0.69	24	0.16
Metellina segmentata (Clerck, 1757)	e	o, sh	0	0	0	0.7	0.37	33	0.12
Linyphia triangularis (Clerck,1757)	e	s-o, p-sh	0	0.3	0	0.6	0.22	31	0.07
Trachyzelotes pedestris (C. L. Koch, 1837)	e	o, p-sh	0	0.3	0	0.7	0.29	24	0.07
DF Σ euryhygrophilous									23.27
$DF_{flood} = \Sigma D_{hygro} \cdot F_{hygro} \cdot 0.01 / \Sigma D_{eury} \cdot F_{eury} \cdot 0.01$									2.64

Note: The first column characterizes the spider's requirements on habitat humidity condition: h = hygrophilous, h-h = hemihygrophilous, e = euryhygrophilous, h-x = hemixerophilous, x = xerophilous; the second column describes their light requirements to vegetation cover density: sh = shaded by trees, p-sh = partially shaded, o = open, s-o = semi open [to characterize of spiders in terms of their moisture and light requirements we used the works of Buchar & Růžička (2002), Entling et al. (2007) and Nentwig et al. (2021); D = dominance, F = frequency, DF_{flood}-index.

The Danubian floodplain forests in Austria are specific by – *Collinsia distincta* Simon, *Dismodicus bifrons* Blackwall, *Kaesteria pullata* O. P. Cambridge, *Entelecara erythropus* Westring, *Tricca lutetiana* Simon, *Philodromus dispar* Walckenaer, *Dysdera hungarica* Kulczyński, *Centromerus leruthi* Fage and *Porrhomma microps* Roewer.

The floodplain areas of the Morava River (Slovakia and Moravia) are specified by – *Ero cambridgei* Kulczyński, *Abacoproeces saltuum* L. Koch, *Dismodicus bifrons* Blackwall, *Erigonella ignobilis* O. P. Cambridge, *Pelecopsis mengei* Simon, *Tapinocyba insect* L. Koch, *Pocadicnemis pumila* Blackwall, *Antistea elegans* Blackwall, *Ozyptila simplex* O. P. Cambridge and *Tmarus piger* Walckenaer.

Specific spiders represent elements of an older population or a newly established population. Many of these spiders characterised habitats (hygro- and

Table 3. Significant decrease in DFflood values when comparing the status of ceanothus spiders in the absence of flooding in the forests of the Danube Delta and comparing with values in study sites on the Morava River where there was no flooding.

Study site	Floods					
	yes			no		
	DF_{hygro}	DF_{eury}	DF_{flood}	DF_{hygro}	DF_{eury}	DF_{flood}
KL	91.21	2.42	37.69	81.55	15.37	5.31
BO	69.92	21.41	3.26	64.05	24.53	2.61
DO	80.47	14.63	5.50	62.50	31.75	1.97
HVA	—	—	—	53.27	41.67	1.28
HVB	—	—	—	52.69	39.67	1.32
Šrek	—	—	—	49.74	34.45	1.44

Note: Abbreviations Danubian sites: KL = Kráľovská lúka, DO = Dobrohošť, BO = Bodícka Brána, Abbreviations Moravian sites: HVA = Horniacky včelín A, HVB = Horniacky včelín B and Šrek.

hemi-hygrophilous species) or signalled newly emerging habitat changes. The position and proportion of predominantly euryhygrophilous species in communities was a very important indicator of habitat sustainability.

D. Tourist species (alien; non-native) of the floodplain forests of Germany, Austria, Moravia, Slovakia, Hungary and Romania are – *Crustulina guttata* Wider, *Clubiona saxatilis* L. Koch, *Zora silvestris* Kulczyński, *Mioxena blanda* Simon, *Trichopterna cito* O. P. Cambridge, *Agalenatea redii* Scopoli, *Gibbaranea gibbosa* Walckenaer, *Hypsosinga sanguinea* C. L. Koch, *Alopecosa aculeate* Clerk, *A. pulverulenta* Clerk, *Agroeca lusatica* L. Koch, *Haplodrassus signifier* C. L. Koch, *Zelotes aeneus* Simon, *Z. electus* C. L. Koch, *Clubiona brevipes* Blackwall or *Centromerus capucinus* Simon. These species often came from adjacent habitats. Most of the non-native species had different requirements for the moisture and light conditions of the habitats. Non-native spiders formed a random assemblage and were represented by only a few individuals. However, they influenced the species structure by their increasing dominance. The invasion of tourist spiders was strongly observed in the hydrologically altered floodplain forests on the Danube.

Each habitat type has a stable diversity and abundance of spiders, so the coexistence of 16 species (preferably and typically floodplain species – Table 2) forms the core of floodplain forest spider communities. Their relative abundance and frequency of occurrence has emerged as a fundamental criterion for a balanced and stable spider community in floodplain forests in Central Europe.

A simple calculation using the DF-index with application to a bio-indicative group (spiders in our case) can classify the state of the studied environment. The assessment of wetland habitats, supported by the exact results of the bio-indicative group of epigeic invertebrates, reflects the stability of the ecosystem or its disturbance.

4. Discussion

4.1. Limiting factors

The highly diversified structure of floodplain forests provides a wide range of ecological niches for spiders that inhabit strictly defined microhabitats. Limiting factors include physical realities such as temperature, light, humidity, and wind, as well as biotic factors such as vegetation structure, food availability, and competitive or predation pressure. According to the results obtained in our study, epigeic spiders (Araneae) in floodplains of the inland Danube Delta show a close relationship between spider community composition and environmental factors. The community composition of epigeic spiders in Danube floodplain forests is also strongly influenced by periodic flooding and high groundwater levels (Thaler et al. 1984; Krumpálová 2005, 2024). Spider communities are related to habitat type and their composition depends on shading as well as habitat moisture (Entling et al. 2007). Our results, in agreement with other experts, show that periodic flooding determines vegetation – herb and tree composition, habitat structure and also have a significant impact on spiders, which in turn affects their species composition (Krumpálová 2005; Petillon et al. 2008; Gallé et al. 2011). As early as Duffey (1966) stated that conditions in riparian forests serve as key factors for many arthropod species. For example, beetle communities in the floodplain forests of the Danube, Morava, and Dyje rivers reflect the presence of floods, their dynamics, and their intensity (Šustek 1994).

The spider communities in floodplains differ significantly from all other forest communities. We confirmed that wetland spiders were mainly influenced by the presence of flooding as well as vegetation cover (Uherčíková in Lisický et al. 1997) (Fig. 4). Thus, epigeic spiders in the inundation were affected by changes in the hydrological regime and responded rapidly to the altered conditions, developing a new, modified coenoses structure. Thaler et al. (1984) and Bonn et al (2002) pointed out that long-term floodplain forests are typically low in species richness, dominated primarily by mobile generalists, but also provide habitat for wetland-loving species. The same is true in our study. Floodplain forests are generally characterized by low species richness, low numbers and low proportions of forest specialists. In contrast, the proportion of forest generalists is highest (Milasowszky et al. 2015). The high proportion of generalists is also due to their mobility abilities, as they are good dispersers and can quickly colonize pioneer sites after a disturbance event. However, with increasing duration of flooding, Bonn et al. (2002) and Krumpálová (2005) found a generalist decline in the number of species.

In such habitats, only a few specialists with adaptations to inundation survive, and many generalists that otherwise dominate periodically inundated sites are unable to survive. The first problem is the response of spider communities – to disturbance during flooding, and the second problem is the recovery of spider communities to their typical or original state, however very dynamic. The three-year absence of flooding on the Danube or Morava caused a rapid penetration of xerophilic, semi-xerophilic and euryhygrophilic spiders into the communities (Table 3). Similarly, the drop in groundwater levels caused striking and permanent changes in spider coenoses. Similar results were reached by Hornung et al. (2008), who found that species composition differs between degraded and natural habitats, and the degree of degradation plays a critical role in shaping terrestrial communities.

4.2. Ecological groups

Our classifications of species into ecological groups, which distinguish the spiders of riparian forests of different landscapes, specify their microclimatic conditions. We noted that alien spiders represented a random community type and were represented by only a few individuals. However, their increasing dominance influences the species structure of the communities. The occurrence Species diversity, dominance, frequency of occurrence and stability of spider representation in habitats are important ecological criteria in floodplain assessment. Based on our results, the coexistence of 16 spider species (preferential and typical species) (Table 2) appears to be a suitable and simple method to assess the real status of the habitat. Milasowszky et al. (2015) identified the same species as we did and defined them as the mainstay of the community in riparian forests. They further reported that the proportion of common species is not very high, as it ranges from 45 to 52%, indicating high beta diversity among riparian forests.

We summarize that the typical spiders seem to be the same for all floodplain forests in Central Europe. The coexistence of these species forms a fundamental element of the ground-dwelling spider communities in the floodplain forests of the inland Danube Delta. On the other hand, specific spiders showed more or less moderate variation in habitat characteristics, often had low dominance and low frequency; they had an optimum at the extremes of the gradients. This suggests that the percentage of specialists in a habitat can be used to rank habitats according to their conservation priority.

5. Conclusions

Our data on spider coexistence in floodplains in Central Europe can be used to assess habitat quality. In agreement with Godoy (2019), an important aspect is that we consider species interactions as one species influencing another, and the network of species interactions is built through chains of pairwise interactions. That is, indirect effects arise from changes in species density (Chesson & Kuang 2008).

The DF-index can be used to assess environmental quality and habitat sustainability. According to our results, co-dominant spider species with DF-index values ≥ 1 seem to be suitable for optimally solving the problem of assessing the current state of the environment and its conditions. We can use the DF-index to assess habitat conditions, and values below 2.5 indicate some environmental disturbance. Finally, our data and methodology can be used to identify particularly threatened or disturbed habitats. Such research should be carried out with a time lag (e.g., more than 10 years). Repeated monitoring can indeed answer the question of whether human-induced disturbance has caused a reduction in ecological stability using spiders as bioindicators. Such an approach would move the use of spiders into the position of assessing the sustainability of the landscape.

The basic element is the specification of community species into categories according to their ecological requirements (trophic guilds, moisture requirements, light intensity or environmental temperature). We hypothesize that this simple index values would make it possible to assess the biota in different habitat types, at the same time as assessing the stability of the environment under study and planning rational forest management.

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