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Effect of hydrologic disturbance regimes on Protura variability in a river floodplain

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Protura, an almost neglected taxon in ecological studies of soil microarthropods, were examined at highly vulnerable sites of fluvial forest stands of the Transcarpathian Lowland. To compare the effects of different hydrologic disturbance regimes on Protura assemblages, we examined part of a river floodplain subjected to periodical inundation, and a non-inundated part with limited fluvial activity, behind the river embankment. Ten sites were selected for sampling, with four sites dominated by oak and one dominated by poplar in each part. The type of hydrologic disturbance regime in the river floodplain shaped Protura assemblages and influenced their variability. Highest abundance and species richness were correlated with the non-inundated part of the floodplain under oak stands, although Protura also tolerated soil conditions of exposure to regular inundation. We present and discuss several hypotheses concerning the causes of distribution patterns of Protura in the river floodplain with different hydrologic disturbance regimes, including sensitivity to mycorrhizal associations and the role of Protura assemblages as a potential ecological bioindicator of pedogenic transformations in riverine wetlands.

Introduction

Disturbances are defined as temporary events that disrupt ecosystem structure, communities or populations and change resource availability or the physical environment (White & Pickett 1985, Jentsch *et al*. 2002). Studies of disturbances have a long tradition in ecology, including the development of the concept of succession or community response (White & Jentsch 2001). Natural disturbances of various kinds, such as fires, storms, droughts or floods, are an important and integral element of many ecosystems and landscapes. They influence all levels of the organization of the ecosystem, including the maintenance of biodiversity. The relationship between disturbance and diversity is often described as unimodal, with the highest diversity at intermediate levels of disturbance (Grime 1973, Connell 1978). A broader range of predictions than those possible with the intermediate disturbance hypothesis can be made with

Huston's dynamic equilibrium model (Huston 2002). Huston's model predicts that diversity fluctuates in a range of values maintained by the interaction of the rates of population growth and competitive displacement due to disturbances. Most disturbance ecology studies focus on the ecological effect of individual disturbance events rather than on assessment of the impact of different disturbance regimes, defined as a sum of all disturbances over space and time (Jentsch *et al*. 2002). Effects of disturbances on soil animal communities have been extensively discussed by Wolters (2001), Bengtsson (2002) or Lindberg and Bengtsson (2005).

In fluvial systems of rivers, flood "pulses" are natural hydrologic disturbances that directly modify many resources and processes in floodplain ecosystems (Tockner *et al*. 2000, Ward & Tockner 2001). Variation in hydrology strongly influences the distribution of organic and inorganic material (Nilsson & Svedmark 2002), habitat heterogeneity (Turner *et al*. 2001, Huston 2002) and the diversity of fauna (Robinson *et al*. 2002). Human-induced alteration in hydrologic regimes of river, due to the pervasiveness of dams, levee systems, and other methods of flood and flow control, modifies water resources, soil deposits, vegetation and soil biota in riverine floodplains (Tockner & Stanford 2002, Kamocki & Banaszuk 2008, Sterzyńska 2009).

Many terrestrial invertebrates are highly adapted to regular inundation, but they can demonstrate different survival strategies (Rothenbücher & Schaefer 2006). Soil microarthropods can apply different life-history tactics that are probably key factors regulating survival and colonization of habitats after a disturbance (Norton 1994, Petersen 1995, Siepel 1995, Shaw 1997, St. John *et al*. 2002). It has also been suggested that the ability to survive in sheltered microsites is important for most soil microarthropods (Wall & Moore 1999). Research on soil fauna assemblages in river floodplains has been mainly restricted to soil macrofauna of open grassland ecosystems because they have an important effect on physical soil properties and organic matter decomposition (*see* Plum 2005), with few studies on soil microarthropods, such as oribatid mites or collembolans (Russel *et al*. 2004, Sterzyńska 2009).

The Protura, in some cases, are third most common after mites and Collembola, mycophagous class of microarthropods found in almost every place where decaying organic matter is deposited (Nosek 1975, Szeptycki 2004). Protura occur mostly in the rhizosphere of trees and appear to be at least partially dependent on the presence of ectotrophic mycorrhiza and the physical condition of trees (Curry & Ganley 1977, Nosek 1975, Stumpp 1990). The consequences of different types of disturbances, natural and human-induced, on the proturan abundance, dispersion and diversity pattern have rarely been examined (Hågvar 1984, Christian & Szeptycki 2004). European Protura populations were studied in grasslands ecosystems (Raw 1956, Rusek 1984), woodlands (Gunnarson 1980, Alberti *et al*. 1989), coniferous forests (Szeptycki & Sterzyńska 1995, Stumpp 1990) and in the forest edges as typical ecotone habitats (Rusek 1989, Rusek *et al*. 2007), but little research on Protura was conducted in riparian forests (Rusek 1965, Rusek *et al*. 2007). In particular, we know little about the diversity and distribution patterns of Protura assemblages in floodplain ecosystems with natural periodic inundations and altered hydrologic regimes.

The aim of our study was to examine the diversity and distribution patterns of Protura assemblages in a river floodplain subjected to different hydrologic disturbance regimes.

We sought answers to the following questions: (1) what is the variability of Protura assemblages in inundated and non-inundated parts of floodplain ecosystems, and does proturan variability allow for predicting environmental changes in fluvial forests; (2) do hydrologic disturbance regimes represent a crucial factor for shaping the specific structure of Protura assemblages in a river floodplain, (3) what is the persistence of Protura populations in inundated and non-inundated parts of a river floodplain.

Material and methods

Study sites

The study was carried out on the floodplain of the Latorica river tributary in two different sections.

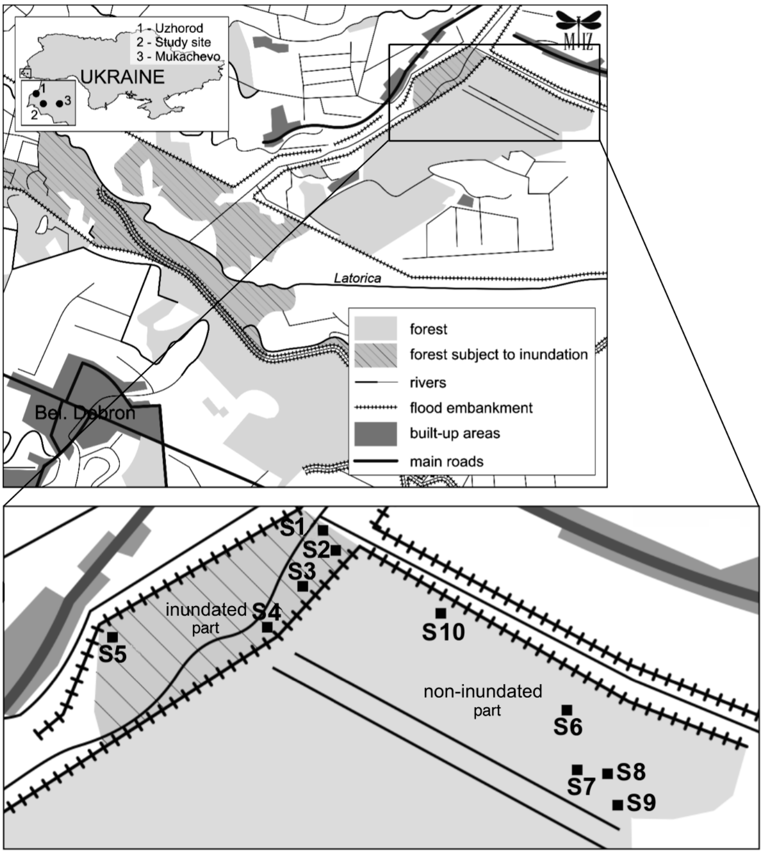

Fig. 1. Location of the area studied in Ukraine (top); and (bottom) location of the study area on the floodplain. Sites S1–S5 are on the inundated part and S6–S10 on the non-inundated part.

One section had a natural hydrologic regime and was subjected to regular, periodical inundation "pulses"; the other section had limited fluvial activity with significant departure from usual hydrological regime due to a flood protection embankment (Fig. 1). The Latorica river is the main tributary of the Tisza river and is located at the southeastern edge of the Central Danubian Lowland in the Mukachevska depression, in the Ukrainian part of the Transcarpathian Lowland. The average air temperature in this area in 2007 was 11.5 °C, the average annual maximum air temperature was 33.4 °C, the average annual minimum air temperature was –8.6 °C, and the average annual precipitation was 791 mm. The study sites were set up in Medio-European fluvial forest stands, *Querco-Ulmetum minoris* habitat code 91F0 according to the European Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 [http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:NOT). The oak–elm–ash forest habitat, spread throughout the central part of the floodplain, moderately inundated and formed on alluvial deposits, is subjected to periodical flooding with regular shallow inundation or unconfined groundwater rising. The tree overstory is formed by *Quercus robur* and *Fraxinus angustifolia* with inclusions of *Ulmus laevis* and *U. minor* in oak stands, and by *Populus alba* in poplar stands. The alluvial soil deposits under studied forest stands were classified according to the system of the World Reference Base for Soil Resources (1998).

Altogether ten sites were selected: five in the inundated part and five in non-inundated part of the river floodplain, with four sites dominated by oak and one by poplar in each part. Only one poplar site in each part of the floodplain was designated because poplar was uncommon in the studied fluvial forest stands. Locations of the sites on the Latorica river floodplain together with their classification according to tree species composition and spatial coordinates are shown in Fig. 1 and Table 1.

Methods

Sampling was performed on three occasions (31 March, 14 July and 18 October 2007). The sites dominated by oak in the inundated and non-inundated parts of the floodplain were sampled three times, while the poplar sites were sampled only once, in autumn. The poplar sites were usually flooded and inaccessible during our sampling effort. At each site, the soil samples for Protura were taken randomly from the top 10 cm of the soil, using a steel corer with a diameter of 5.5 cm. Twenty separate soil cores were taken from each site on each sampling occasion. Arthropods were extracted from each sample in a modified Macfadyen high gradient extractor for 10 days. All proturan specimens were mounted on slides and identified to the species level using several keys (Rusek 1975, Szeptycki 1985, 1986, 1991, 2007). All specimens are deposited in the State National History Museum, NASU (Lviv, Ukraine).

Soil properties

Mechanical and chemical analyses were carried out on soils from oak and poplar stands from the inundated and non-inundated parts of the floodplain (Van Reeuwijk 2006). For each type of soil three, replicated measures of the soil properties (pH, CEC, organic matter content and silt, sand and clay fractions) were done. Soil pH was measured potentiometrically in the supernatant suspension of a 1:2.5 soil:liquid mixture. The liquid was either distilled water (pH_{H2O}) or a 1 M KCl solution (pH_{KCl}). Cation exchange capacity (CEC) was determined at pH 7 with ammonium acetate. The Walkley–Black procedure was followed to determine the organic carbon in the tested soil material (organic matter content [%]). The organic matter of the soil was oxidized with an acid dichromate reagent by heat of dilution and the excess of chromate left after C oxidation was titrated with ferrous ammonium sulfate. The mechanical analysis technique was used to determine the soil texture, with pre-treatment of the sample, removing organic matter by H_2O_2 and carbonates by HCl. After pre-treatment, the sample shaken with a dispersing agent and sand was separated from clay and silt with a 63 μm sieve. The sand was fractionated by dry sieving and the clay and silt fractions were determined by the hydrometer method.

Data analysis

We used the Kruskal-Wallis one-way ANOVA to compare the soil properties of the upper soil layers under oak and poplar sampling sites. We determined the significance of differences with a multiple comparison test of mean ranks, which was used after the Kruskal-Wallis ANOVA. To assess the significance of differences in the basic characteristics of community structure of the proturan assemblages, we used the two-tailed Mann-Whitney *U*-test for species abundance (*A*), species richness (*S*), Shannon's diversity index (*H*´), and Pielou's evenness index (*J*´) for comparisons between the inundated and non-inundated parts of the floodplain.

Differences in species composition in different hydrologic disturbance regimes and the

Table 1. Type of forest stand and geographic coordinates of the sites studied on the inundated and non-inudated parts of the river floodplain.

Inundated part		Non-inundated part	
Site/forest stand	Coordinates	Site/forest stand	Coordinates
S1/Oak	48°28´24´´N, 22°28´41´´E	S6/Oak	48°27´52´´N, 22°29´50´´E
S2/Oak	48°28´18´´N, 22°28´39´´E	S7/Oak	48°27´49´´N, 22°30´06´´E
S3/Oak	48°28´22´´N, 22°28´44´´E	S8/Oak	48°27´45´´N, 22°29´55´´E
S4/Oak	48°28´25´´N, 22°28´46´´E	S9/Oak	48°27´48´´N, 22°29´53´´E
S5/Poplar	48°30´20´´N, 22°28´35´´E	S10/Poplar	48°28´19´´N, 22°29´15´´E

response of Protura species to environmental gradients were evaluated with ordination methods. We performed the analysis using a data matrix with row data in which the value in each cell was the sum of specimens retrieved from 20 soil cores collected from each site on each sampling occasion. We treated the different times of sampling (spring, summer and autumn) at the sites as replicates. We applied the square-root transformation of species data in multivariate analysis to preserve appropriate distance bases and scaling of the scores (Legendre & Gallagher 2001). In order to determine turnover in Protura species composition, we carried out a detrended correspondence analysis (DCA) with Hill's scaling. In our case, the gradient length calculated for the first axis of DCA was 2.69 in multiples of the standard deviation (SD) units. Therefore, we used the linear method (RDA) to test the effect of environmental factors on composition and distribution patterns of Protura in the river floodplain (Lepš & Šmilauer 2003). We calculated the RDA constrained by nominal environmental variables (with classes between brackets): hydrologic disturbance regimes (inundated part, non-inundated part), season (spring, summer, autumn) and type of forest stands (oak, poplar). These factors were coded as a series of dummy variables. In the analysis, we did not use type of soil deposits and measured soil properties as separate factors, because they were redundant with the factors hydrologic disturbance regimes and forest stands. To remove the intrinsic source of variation, due to repeated sampling of sites on three occasions (spring, summer, autumn), we used season as a co-variable (blocking factor) in the partial RDA analysis. The automatic procedure for statistical model selection of environmental variables was used to assess the potential value of each variable separately (marginal effect) and the partial (conditional) effect for predicting the model explaining the highest amount of variability in Protura species composition. Because the forward selection procedure treats each dummy variable as an independent predictor, we used a separate RDA analysis to calculate the variation of Protura assemblages due to analyzed predictive factors. The significance of models was estimated by the Monte Carlo permutation test. Calculations were made with the Statistica 7.0 and Canoco 4.5 software packages (terminology after Lepš & Šmilauer 2003).

Results

Characteristic traits of the upper soil layers of alluvial deposits

Significant differences in soil properties of the oak and poplar forest stands were found in the inundated and non-inundated parts of the study area (Table 2). Soils from the two parts differed significantly in their pH, CEC, organic carbon (%) and the proportion of the clay fraction in soil texture (Kruskal-Wallis one-way ANOVA: for pH: $H = 10.42$, df = 3, $n = 12$, $p = 0.02$; CEC: $H = 8.74$, df = 3, $n = 12$, $p = 0.03$; organic carbon: $H = 9.67$, df = 3, $n = 12$, $p = 0.02$; clay fraction $H = 8.44$, df = 3, $n = 12$, $p = 0.04$). The multiple comparison test of mean rank used after the Kruskal-Wallis ANOVA showed that Haplic Fluvisols, the natural soil deposit under poplar stands, had significantly lower content of organic carbon and higher pH as compared with Stagnic Luvisols, the soil deposit under oak stands in the non-inundated part of the floodplain (pH: $p = 0.01$, df = 3; organic carbon: $p = 0.02$, df = 3).

Species composition, diversity and abundance pattern

Eight species of Protura belonging to 3 genera and 3 families were recorded across the ten study sites in the inundated and non-inundated parts of the floodplain (Table 3). Among them *Eosentomon carpaticum* was dominant, and was the only species found under poplar in the inundated part of the floodplain (Table 4).

The values of species richness (S), diversity (H') and evenness indexes (J'), and abundance (A), were significantly lower in the inundated part of the floodplain when their medians were compared using a two-tailed Mann-Whitney U-test (Fig. 2; for species richness: $U = 3.5$, $p = 0.00003$; abundance: $U = 9.0$, $p = 0.0001$; diversity index: $U = 45.5$, $p = 0.0460$; evenness index: $U = 9.5$, $p = 0.0001$; $n_1 = n_2 = 13$ in all cases).

Variation of Protura assemblages

The RDA analysis showed that the selected environmental (nominal) variables explained 45.3% of the total variance in Protura species composition. The eigenvalues of the RDA axes were $\lambda_1 = 0.305$, $\lambda_2 = 0.408$, $\lambda_3 = 0.056$ and $\lambda_4 = 0.047$. The species–environment correlation was highest for

Table 2. Soil properties at the oak and poplar stands on the inundated and non-inudated parts of the river floodplain.

	Inundated part				Non-inundated part			
Type of forest stand → Type of soil deposits →	Oak Stagnic Mollic Fluvisols		Poplar Haplic Fluvisols		Oak Stagnic Luvisols		Poplar Haplic Arenosols	
Soil properties	Mean	SD	Mean	SD	Mean	SD	Mean	SD
pH	5.26	0.22	7.57	0.17	3.59	0.12	6.53	0.15
CEC meg/100 g	26.93	3.58	10.93	4.41	23.33	4.23	12.97	3.49
Organic carbon (%)	4.01	0.73	1.76	0.73	5.95	0.45	2.49	0.09
Fractions (%)								
Sand 1–0.05	19.57	6.37	51.93	6.17	21.93	7.16	45.97	19.55
Silt 0.05–0.01	43.73	3.66	32.87	4.74	47.93	3.87	37.10	16.27
Clay < 0.01	36.70	2.97	15.20	4.86	40.13	9.96	16.93	3.35

Table 3. Checklist of the Protura and with species name abbreviation.

Order	Familiy	Species	Abbreviation
Acerentomata	Protentomidae	*Proturentomon noseki*	Protnos
	Acerentomidae	*Acerentulus xerophilus*	Acexero
Eosentomata	Eosentomidae	*Eosentomon carpaticum*	Eocarpat
		Eosentomon pinetorum	Eopinet
		Eosentomon semiarmatum	Eosemi
		Eosentomon stachi	Eostach
		Eosentomon transitorium	Eotran
		Eosentomon cf. *pinetorum*	Eocfp

Table 4. Distribution pattern and abundance of the Protura (1000 indiv. m^{-2}) in river floodplain. SD = standard deviation.

	Type of hydrologic disturbance regime							
	Inundated part				Non-inundated part			
Type of forest stand →	Oak		Poplar		Oak		Poplar	
Species abbreviation	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Protnos	0	–	0	–	0.003	0.012	0	–
Acexero	0	–	0	–	0.006	0.023	0	–
Eocarpat	0	–	0.560	–	0.940	1.506	0.520	–
Eopinet	0	–	0	–	0.050	0.114	0	–
Eosemi	0	–	0	–	0.067	0.140	0	–
Eostach	0	–	0	–	0.067	0.023	0	–
Eotran	0	–	0	–	0.030	0.103	0	–
Eocfp	0	–	0	–	0.017	0.058	0	–

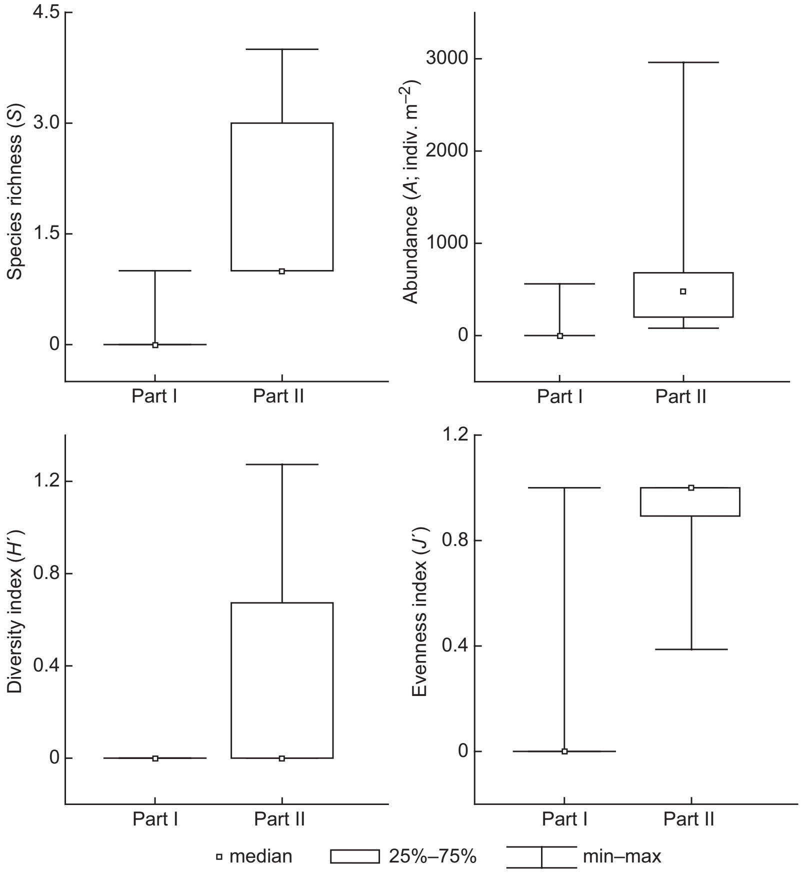

Fig. 2. The basic characteristics of Protura assemblages in the inundated (Part I) and non-inundated (Part II) parts of the river floodplain.

the first axis of RDA (0.67). All these factors explained the significant amount of variation in Protura species composition (Monte Carlo permutation test for the first canonical axis: $\lambda_1 = 0.428$, F-ratio = 15.722, $p = 0.012$; all canonical axes: $\lambda_{\text{trace}} = 0.453$, F-ratio = 4.350, $p = 0.01$). The automatic forward selection procedure, in the context of linear regression model (RDA), demonstrated that the hydrologic disturbance regime (inundation and non-inundation) had the highest explanatory power when the marginal modeling approach was used. However, the conditional approach only identified inundation as a significant predictor of variation in Protura assemblages (Table 5).

The hydrologic disturbance regime explained 30.5% of the variation in Protura assemblages using co-variables from classes season (spring, summer, autumn) and forest stand (oak, poplar) as blocking factors. The eigenvalues of the first four axes of the RDA ordination were $\lambda_1 = 0.305$, $\lambda_2 = 0.408$, $\lambda_3 = 0.056$, $\lambda_4 = 0.047$. The effect of hydrologic disturbance regime on the distribution pattern of Protura assemblages was significant (Monte Carlo permutation test for the canonical axes: $\lambda_{\text{trace}} = 0.305$, F-ratio = 11.715, $p = 0.002$). Forest stand explained only 1.4% of variability in Protura assemblages, when we performed a partial RDA analysis with co-variables from the classes 'hydrologic disturbance regime' and 'season' as blocking factors, and the effect of this factor was not significant (Monte Carlo permutation test for the canonical axes: $\lambda_{\text{trace}} = 0.014$, F-ratio = 0.555, $p = 0.662$). Both these factors (hydrologic disturbance regime and forest stand) explained a significant portion of Protura variability (Monte Carlo permutation test for the first canonical axis: $\lambda_1 = 0.314$, F-ratio = 11.952, $p = 0.012$; all canonical axes: $\lambda_{\text{trace}} = 0.319$, F-ratio = 6.120, $p = 0.014$) and affected the distribution pattern of Protura assemblages in the river floodplain. The higher

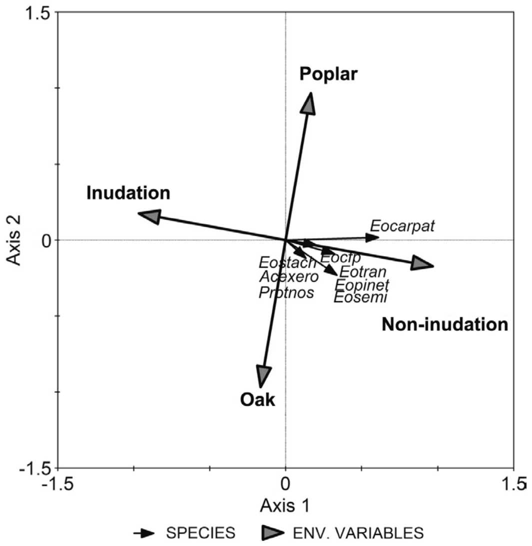

Fig. 3. RDA correlation biplot with environmental variables displaying distribution pattern of Protura in river floodplain (inter species correlation scaling, species scores divided by SD and centering by species) with season as the blocking factor. For species name abbreviations *see* Table 3.

Table 5. Environmental (nominal) variables ranked according to their importance (forward selection in RDA) by their marginal and conditional effects on Protura assemblages variability in the river floodplain. λ_1 = fit = eigenvalue with only one variable; λ_{cum} = cumulative increase in eigenvalue, p = significance level of the effect tested by Monte Carlo permutation test under model with 499 permutations, F-ratio = overall goodness of fit of the variables in regression model. The total sum of all canonical eigenvalues λ_{total} = 0.453.

	Marginal effect (forward: step 1)	
Variable	λ_1	Percentage
Inundated part	0.35	77.78
Non-inundated part	0.35	77.78
Spring	0.12	26.67
Summer	0.05	11.11
Autumn	0.03	6.67
Oak	0.02	4.44
Poplar	0.02	4.44

	Conditional effect (forward: continued)		
Variable	λ_{cum}	F-ratio	p
Inundated part	0.35	13.20	0.002
Spring	0.07	2.58	0.072
Summer	0.02	0.74	0.478
Oak	0.01	0.56	0.498

level of hydrologic disturbances had the strongest negative effect on the diversity of Protura assemblages. Protura species in the river floodplain avoided alluvial deposits exposed to regular flood “pulses” and preferred the embankment part of the floodplain, where the influence of river dynamics was diminished (non-inundated part). Species strongly and positively associated with oak stands in the non-inundated part of the river floodplain were *E. transitorium*, *E. pintorium* and *E. semiarmatum*; *E. carpaticum* was slightly correlated with poplar stands (Fig. 3).

The partial constrained RDA results showed that 7.4% of the Protura assemblage’s variability was explained by season when environmental variables from the classes ‘hydrologic disturbance regime’ and ‘forest stand’ were taken as co-variables and constrained permutation within a block. The eigenvalues of the first four axes of the ordination were, respectively, $\lambda_1 = 0.066$, $\lambda_2 = 0.008$, $\lambda_3 = 0.408$, $\lambda_4 = 0.056$. The species–environment correlations were low for the first and second axes of RDA (0.406, 0.262, respectively). The effect of season on the distribution pattern in the ordination space was not significant for the first axis and for the canonical axes of RDA ($\lambda_1 = 0.066$, F-ratio = 2.511, $p = 0.2440$; $\lambda_{\text{trace}} = 0.074$, F-ratio = 1.422, $p = 0.2460$). The highest diversity and abundance of *E. semiarmatum*, *E. carpaticum*, *E. stachi*, *Proturentomon noseki* and *Acerentulus xerophilus* were associated with spring, whereas, *E. pinetorum*, *E* cf. *pinetorum* and *E. transitorum* were associated with summer (Fig. 4).

Discussion

The study has taken a step in the direction of defining the relationships among the distribution pattern, diversity and abundance of Protura assemblages in a river floodplain in terms of habitat requirements, persistence of Protura species in inundated areas and the environmental factors that most influence their community composition and structural attributes. This is the first study to show that Protura can tolerate soil subjected to regular inundation, although most of the species recorded from the forested wetlands avoided alluvial deposits exposed to regu-

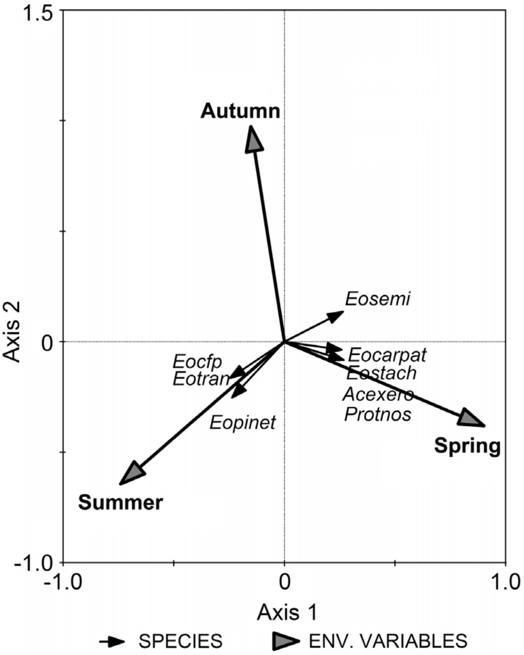

Fig. 4. RDA correlation biplot with environmental variables displaying seasonally distribution pattern of Protura (inter species correlation scaling, species scores divided by SD and centering by species) with 'hydrologic disturbance regime' and 'forest stand' as blocking factors. The full names of the abbreviated species are given in the checklist of species (Table 3).

lar flood "pulses". We found that Protura from the embankment part of the floodplain, where the influence of river dynamic is diminished, were more diverse and abundant in contrast to the single-species assemblage found in the regularly, seasonally inundated part. The response of Protura to different hydrologic disturbance regimes was more pronounced than the response of other soil microarthropods (Russel *et al*. 2004, Sterzyńska 2009).

Our study identified a strong negative effect of disturbance associated with natural hydrologic regime (= periodical inundation) on diversity of Protura assemblages. The relationship between disturbance and diversity is often described as unimodal, with the highest diversity at intermediate levels of disturbances (Grime 1973, Connell 1978). However, in our case, it is difficult to identify the hump-shaped pattern of diversity, because Protura assemblages from periodically inundated and non-inundated parts of the floodplain only were compared. A broader range of predictions is offered by Huston's (2002) dynamic-equilibrium model of species diversity. One of the main assumptions of this hypothesis is that the position of the diversity peak with respect to disturbance frequency depends on population growth rates. Although we did not assess the rate of Protura population growth, the observed decline in the Protura diversity at the more disturbed sites is predicted by the dynamic equilibrium model of species diversity for slow-growing populations (fig. 5.6a in Huston 2002). However, we observed persistence of the population of *E. carpaticum* in the periodically inundated part of the floodplain. This persistence may indicate that proturans can exhibit different rates of population growth. Haddad *et al*. (2008) showed that the autecological trait, intrinsic growth rate, was the best predictor of the species response to disturbance.

We noted that 30.5% of the observed variation in Protura assemblages was attributed to hydrologic disturbance regime and it was a crucial factor for shaping the specific structure of Protura assemblages in the river floodplain. The natural, alluvial deposits from the inundated part were characterized by high silt content, significantly lower organic carbon content and higher pH as compared with alluvial deposits from the non-inundated part. It is known that changes in water regime heavily modify soil properties, which leads to elimination of anaerobic conditions and higher mineralization rates (Kajak & Okruszko 1990, Lugo *et al*. 1990, Pinay *et al*. 2002, Pietsch *et al*. 2003, Sapek *et al*. 2003). In situations where natural pulse disturbances associated with seasonal inundation are limited and there is terrestrialization of wetland habitats in river floodplains, more diverse and abundant communities of soil invertebrates are present (Wasilewska 2006, Sterzyńska 2009).

The observed impact of season on the distribution pattern of Protura indicates that most of the Protura species appearing in the river floodplain probably showed the single peaked type of reproductive phenology with overwintering adults (Imadaté 1974). The observed temporal variations of Protura populations could also be related to the stability of microhabitats, effects of habitat drying or sampling efficiency (Walker

& Rust 1975, Leinaas 1978, Laiho *et al*. 2001).

Our results show that Protura may find favorable microhabitats in alluvial soils saturated by water, in contrast to earlier data presented by Walker and Rust (1975) and that they can persist in habitats with natural flood "pulses". We found *E. carpaticum* in Haplic Fluvisols under the poplar stand in the inundated part of the floodplain. The causes of the broader distribution pattern of this Carpathian endemic species in the alluvial deposits studied are unknown but several hypotheses could be identified. Its distribution pattern may be dependent on its dispersal ability, presence of sheltered microsites or presence of some pre-adaptation strategies to survive waterlogging. The trait that predicted persistence best was the measure of species ability to recover from disturbance, the intrinsic growth rate (Haddad *et al*. 2008).

The distribution pattern of Protura, like those of other soil microarthropods with restricted burrowing ability, depends on a macropore system in the soil (Kanal 2004). The high content of sandy particles in the deposits under the poplar stands indicates its higher macroporosity and lower water storage capacity. The faster rate of drying of deposits under poplar stands could offer some sheltered microsites to survive inundation in macropores or in the rhizosphere around the roots. Protura species demonstrate differences in vertical distribution (Stumpp 1990) and at least three different patterns of seasonal fluctuations (Imadaté 1974). Overwintering in the egg stage has been observed among the Eosentomidae. Their juveniles are found throughout the year and the development of two generations in spring and autumn has been observed (Imadaté 1974). This type of reproduction cycle with an overwintering in egg stage is regarded as flood-resistant (Tamm 1986).

The observed differences in the distribution pattern of Protura assemblages in the river floodplain may be attributed to their feeding ecology. Proturan abundance is highly correlated with fluctuations in mycorrhizal frequency and is closely related to ectotrophic mycorrhizae (Sturm 1959, Stumpp 1990, Malmström & Persson 2011). Two types of mycorrhizae may occur in the soils of a riparian system: arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (ECMF). Soil moisture and the frequency of inundation are the main possible mechanisms contributing to shifts between AMF and ECMF in floodplain soils. In early successional riparian soils along a freely-flowing river, regular flooding promotes arbuscular mycorrhizal fungi, whereas in the soils of the older successional stages, ectomycorrhizal fungi are more common (Piotrowski *et al*. 2008, Harner *et al*. 2010). Protura, which are closely associated with the distribution pattern of ectomycorrhizal fungi, could indicate changes in soil properties induced by water level fluctuations and show the effectiveness of on-going management and restoration work in threatened Medio-European fluvial forest stands of *Querco-Ulmetum minoris*.

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