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Variation in millipede (Diplopoda) assemblages in oak woodlands of the Eastern European Plain

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Abstract

Variation in millipede (Diplopoda) assemblages in oak woodlands of the Eastern European Plain was studied based on 46 soil samples collected from the vast territory: from west (Moldova and the extra-Carpathian part of western Ukraine) to east (Ural Mountains), and from south (central Ukraine and Russia) to north (subtaiga region) covering 4 vegetation belts: steppe, forest-steppe, deciduous forests and mixed forests. Altogether, 30 species were found in the samples. The millipede assemblages from the forest-steppe belt appear to be particularly rich in species and the most diversified. The species turnover estimated using ordination techniques (DCA) was very high. Among 21 factors considered in CCA to explain variation in the species data set, 12 showed to be significant, 2 of them: humus depth and mean annual deficit of humidity were the most important. Nevertheless, the climatic-geographical variables also cause at least as much variability of millipede assemblages of the Eastern European Plain as do habitat factors. The variability in each vegetation belt is determined by different main factors: in the steppe by humidity, in the forest-steppe by longitude, and in mixed forests by latitude.

Keywords: Diplopoda assemblages, diversity, Eastern European Plain, oak forests, multivariate analysis, environmental factors, vegetation belts

1. Introduction

There are only a few studies relating the distribution and ecology of Diplopoda to certain environmental factors, all hitherto effectuated locally in Europe. Thus, Haacker (1968), in his autoecological investigations of millipedes along the Rhine and Main rivers, Germany noticed that the diversity of millipedes was affected by abiotic factors such as humidity and temperature. Kime & Wauthy (1984) demonstrated the influence of climatic factors and soil properties on the patterns of occurrence of diplopods in broad-leaved forests in Belgium, both soil calcium content and acidity also playing important roles (Kime et al. 1992). Branquart et al. (1995) showed that the most important effects on the diversity of millipede communities in Belgium were related to humidity and the presence of humus, each particular diplopod morphotype being associated with certain humus types. Landscape-related variation in millipede communities was confirmed both on lime-oak-hornbeam sites (a grass and forest catena in Thuringia) (Dunger & Steinmetzger 1981) and maquis regions of southern France (open, semi-open and forest habitats) (David et al. 1999).

More commonly, some problems of millipede distribution in Europe have been considered in a historical perspective, in the framework of historical zoogeography (e.g. Kime 1990, Golovatch 1992, 1997, Spelda 1996). Such attempts have been large-scale rather than local, up to covering entire biogeographical regions or continents (e.g. Enghoff 1993, Golovatch 1997). In contrast, no large-scale patterns of variation in millipede assemblages have hitherto been performed, even such which would concern the same or a very similar type of habitat.

In the temperate belt of Europe, millipedes are mostly associated with deciduous, or nemoral, forests (Golovatch 1992, Kime 1992, Kime & Golovatch 2000). Oak, beech or hornbeam forests form the largest biome in Europe. Regrettably, at least in the region concerned, oak forests are often the most degraded, currently represented only by local residual subclimax or climax communities. Forests dominated by *Quercus robur* form the climax stage of biocoenoses ranging from the northern part of the Iberian Peninsula and British Isles to the Ural Mountains (Razumovsky 1981). The oak forest habitat thus lends itself as the best model for tracing variation in millipede assemblages and for identifying the patterns of response of these assemblages on different geographical scales.

In 1988–1991, one of the research programmes funded by and coordinated at the Institute of Evolutionary Morphology and Ecology of the Soviet Academy of Sciences (presently the Institute for Problems of Ecology and Evolution, Russian Academy of Sciences) was ‘Spatial variation in soil macrofauna communities of the Eastern European oak forests in relation to environmental factors’. The material obtained during these investigations has since been used in eco-faunistic reports concerning only some of the groups of soil macrofauna sampled across the Eastern European, or Russian, Plain, i.e., Elateridae (Penev 1992), spiders (Esjunin et al. 1993, 1994, Penev et al. 1994c) and earthworms (Penev et al. 1994a, b). Certain qualitative information on millipedes has also been used in analyses of the geographical distribution and origin of the millipede fauna (Golovatch 1992, 1997). Yet no quantitative data as regards Diplopoda derived from that project have ever been presented.

This paper is the first attempt to consider the impact of some environmental factors on Diplopoda assemblages on a very large geographical scale as based on purely quantitative sampling information.

2. Study area

A total of 46 samples covering an area of 1100 km from north to south and 2300 km from west to east were sampled across the Eastern European Plain, ranging from Moldova to the Urals (Fig. 1). The following three large subregions were covered: west of the Dnepr (samples 1–14), central Russia, mainly between the Dnepr and Don rivers (samples 15–38), and the Eastern European Plain’s eastern part, i.e., the middle part of the Volga Region, as well as Cisuralia (= immediately west of the Urals) (samples 39–46).

The oakwood sites lay within the mixed forest (samples: 1, 15–25, 39, 42–46), deciduous forest (2 and 3), forest-steppe (4–6, 8–10, 26–32, 40–41) and steppe belts, or zones (7, 11–14, 33–38). Research was carried out in mature climax or subclimax forest stands, where the species richness was expected to have reached saturation as a result of interspecific relations leading to an established pattern of dominance and a limited number of supported species. With such a vast study area involved, selection of sites for sampling had to take into account the phytosociological variation in oak forests as the most characteristic, albeit too often relictual, plant association in a given subregion.

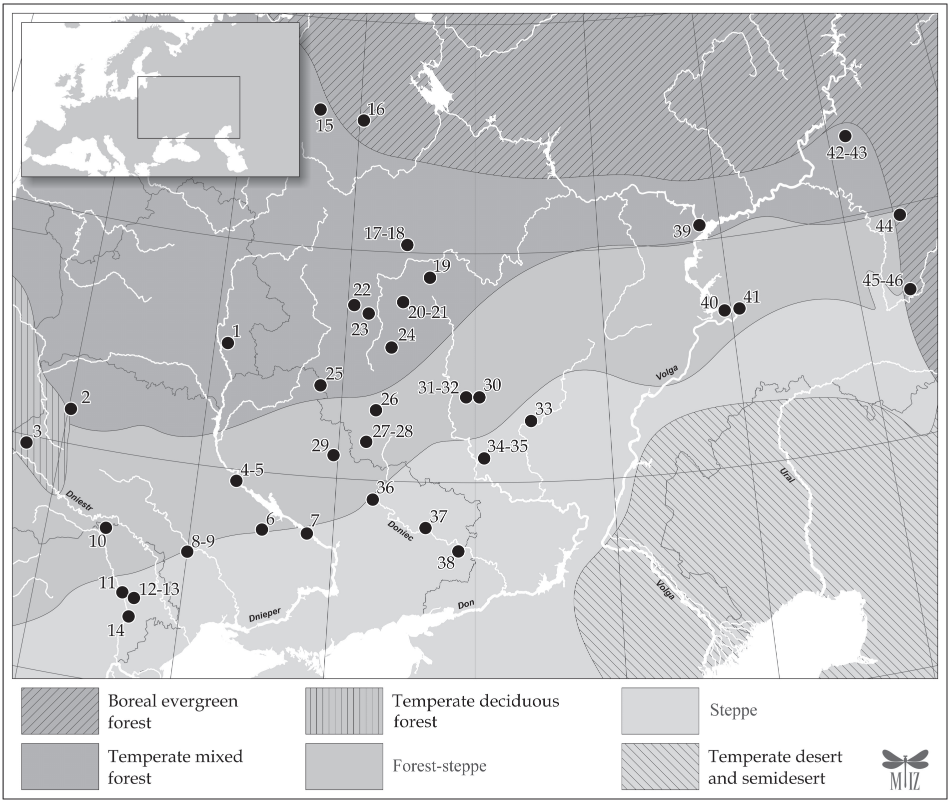

Fig. 1 Location of the samples:

1: Struki 12 km NE Buda-Koshelevo, Gomel; **2**: Derno 30 km E Lutsk, Volyn; **3**: Rostochye Nature Reserve, 40 km WNW Lvov, Lvov; **4**: Peruny nr. Mikhailovka, 10 km N Kanev, Cherkassy; **5**: Peruny nr. Mikhajlovka, 10 km N Kanev, Cherkassy; **6**: Chernyi Les nr. Znamenka, Kirovograd; **7**: Komissarovski Les 12 km W Volnogorsk, Dnepropetrovsk; **8**: Savranski Les nr. Polyanetsko, Odessa; **9**: Savranski Les nr. Polyanetsko, Odessa; **10**: Rossoshanski Les, 3 km N Briceani, Moldova; **11**: Kodry Nature Reserve nr. Lozova, Moldova; **12**: Kotovskii Les nr. Kotovsk, Moldova; **13**: Kotovskii Les nr. Kotovsk, Moldova; **14**: Tigechskii Les 5 km S Tigecei, Moldova; **15**: Sokolovo 15 km E Dubniki, Novgorod; **16**: Dubniki 16 km NNE Udomlya, Tver; **17**: Sharapovo 50 km SW Moscow, Moscow; **18**: Sharapovo 50 km SW Moscow, Moscow; **19**: Vasilevskii 10 km N Venev, Tula; **20**: Tulskiye Zaseki nr. Krapivna, Tula; **21**: Tulskiye Zaseki nr. Krapivna, Tula; **22**: Chernysheno ca 30 km WSW Kozelsk, Kaluga; **23**: Trud ca 20 km SE Ulyanovo, Kaluga; **24**: Setukha 50 km E Orel, Orel; **25**: Khinel 25 km SW Sevsk, Bryansk; **26**: Kazatskii Les 25 km SW Kursk, Kursk; **27**: Les-na-Vorskle Nature Reserve, Borisovka, Belgorod; **28**: Les-na-Vorskle Nature Reserve, Borisovka, Belgorod; **29**: 10 km SW Trostyanets, Sumy; **30**: Venevitinovo 33 km NE Voronezh, Voronezh; **31**: Voronezh Nature Reserve, Verkhnyaya Khava Distr., Voronezh; **32**: Voronezh Nature Reserve, Verkhnyaya Khava Distr., Voronezh; **33**: Tellerman Forestry nr. Borisoglebsk, Voronezh; **34**: Shipov Les nr. Vorontsovka, Voronezh; **35**: Shipov Les nr. Vorontsovka, Voronezh; **36**: Gaidary S Gotvald, Kharkov; **37**: Serebryanskoye Forestry nr. Kremennaya, Lugansk; **38**: Stanichno-Luganski Nature Reserve, Lugansk; **39**: Volga-Kama Nature Reserve, 50 km S Kazan, Tatarstan; **40**: Zhiguli Nature Reserve, Bakhilova Polyana, Samara; **41**: Novosemeikino ca 15 km NW Samara, Samara; **42**: Sarashi 20 km S Barda, Perm; **43**: Sarashi 20 km S Barda, Perm; **44**: Vilyai 20 km S Asha, Chelyabinsk; **45**: Shulgan-Tash Nature Reserve, Bashkiria; **46**: Shulgan-Tash Nature Reserve, Bashkiria.

Tab. 1 Species of Diplopoda found in the quantitative samples taken in the East European Plain.

No	Species	Abbreviation
1	*Polyxenus lagurus* (Linnaeus, 1758)	*Plxlaguru*
2	*Altajosoma golovatchi* (Shear, 1990)	*Altajgolov*
3	*Mastigona bosniensis* (Verhoeff, 1897)*	*Masbosn*
4	*Brachydesmus superus* Latzel, 1884	*Brcsuperu*
5	*Polydesmus complanatus* (Linnaeus, 1761)	*Pldcompla*
6	*Polydesmus denticulatus* C. L. Koch, 1847	*Plddentic*
7	*Polydesmus inconstans* Latzel, 1884	*Pldincons*
8	*Polydesmus montanus* Daday, 1889	*Pldmontan*
9	*Polydesmus schaessburgensis* Verhoeff, 1898	*Pldschaes*
10	*Schizoturanius dmitriewi* (Timotheew, 1899)	*Sztdmitri*
11	*Strongylosoma stigmatosum* (Eichwald, 1830)	*Strstigma*
12	*Glomeris tetrasticha* Brandt, 1833	*Glotetrast*
13	*Glomeris hexasticha* Brandt, 1833	*Glohexast*
14	*Trachysphaera costata* (Waga, 1857)	*Tracostat*
15	*Archiboreoiulus pallidus* (Brade-Birks, 1920)	*Arcpallid*
16	*Nopoiulus kochii* (Gervais, 1847)	*Nopkochii*
17	*Brachyiulus jawlowskii* Lohmander, 1928	*Brajawlow*
18	*Cylindroiulus boleti* (C. L. Koch, 1847)	*Cylboleti*
19	*Cylindroiulus burzenlandicus* Verhoeff, 1907	*Cylburzen*
20	*Enantiulus nanus* (Latzel, 1884)	*Enananus*
21	*Leptoiulus proximus* (Němec, 1896)	*Lptproxim*
22	*Megaphyllum projectum* Verhoeff, 1894	*Megprojec*
23	*Megaphyllum rossicum* (Timotheew, 1897)	*Megrossic*
24	*Megaphyllum sjaelandicum* (Meinert, 1868)	*Megsjaela*
25	*Megaphyllum transsylvanicum* (Verhoeff, 1897)	*Megtrnssy*
26	*Ommatoiulus sabulosus* (Linnaeus, 1758)	*Ommsabulo*
27	*Rossiulus kessleri* (Lohmander, 1927)	*Roskessle*
28	*Unciger transsilvanicus* (Verhoeff, 1899)	*Unctranss*
29	*Xestoiulus laeticollis* (Porat, 1889)	*Xeslaetic*
30	*Polyzonium germanicum* Brandt, 1837	*Plzgerman*

**Mastigona bosniensis* (Verhoeff, 1897) = *Mastigona vihorlatica* (Attems, 1899) (Hauser 2004)

3. Sampling methods

Twenty soil subsamples of 25 x 25 cm each were taken per sampling date. 46 samples (altogether 960 subsamples) from 36 oak woods were analysed. On 10 sites, samples were taken twice a year: in spring (May and early June) and in autumn (late August and September). Altogether, 27 spring and 19 autumn samples were received. Soil macrofauna were collected from the litter layer and then from 10-cm thick soil layer. Litter was sieved. Animals were picked up by hand-sorting from both parts of each sample in the field. Samples were taken along short transects (200–500 m) in three-sample series: at an oak-tree trunk, between trees and in a small forest gap (until all 20 samples were obtained).

4. Study material and methods of analysis

Altogether, the analysed material included 2265 individuals belonging to 30 millipede species (Tab. 1). The total number of specimens of each species in 20 subsamples taken on any sampling date was used as response variables. All study oak woods were characterised by 21 explanatory (environmental) variables (Tab. 2). The variables describe the geographical localities (geographical: No 1–2), as well as climatic factors (climatic: No 3–11), soil properties (soil: No 12–19) and other factors (other: 20–21). The data were analysed using ordination methods contained in the program Canoco 4.5 (ter Braak & Šmilauer 2002).

Tab. 2 Environmental variables used in multivariate analyses.

No	Abbreviation	Variable	Measurement scale	Value of rank
1	LONG	longitude	ordinal	
2	LATI	latitude	ordinal	
3	TANN	mean annual temperature, in °C	ordinal	
4	TMIN	mean temperature of the coldest month	ordinal	
5	TAMP	annual temperature amplitude (the difference between the mean temperatures of the warmest and coldest months)	ordinal	
6	FRL	number of frostless days	ordinal	
7	PR	mean annual precipitation in mm	categorical <1–3>	400–500
				500–600
				600–700
8	WA	precipitation for the warm period, in mm	categorical <1–6>	250–300
				300–350
				350–400
				400–450
				450–500
				500–550
9	CO	precipitation for the cold period, in mm	categorical <1–5>	100–125
				125–150
				150–175
				175–200
				200–225

Tab. 2 cont.

No	Abbreviation	Variable	Measurement scale	Value of rank
10	HUMI	mean annual relative humidity of the air, in %	ordinal	
11	DEFI	mean annual deficit of humidity	ordinal	
12	SAND	sandy soil	categorical <0/1>	non sandy/sandy
13	MECH	soil texture (in borderline cases 0.5 is added to the lower value)	categorical <1–3>	light sandy, sandy loam or loess-moderate loam heavy loam to clayish
14	GREY	grey forest soil	nominal <1/0>	
15	PODZ	podzolised soil	nominal <1/0>	
16	CHER	chernozem (black soil)	nominal <1/0>	
17	BROW	brown forest soil	nominal <1/0>	
18	LIT	thickness of the litter layer, in cm	categorical <1–4>	0–2
				2–4
				4–6
				6–8
19	HUM	humus depth, in cm (averages for each site estimated from 20 samples)	categorical <1–9>	0–5
				5–10
				10–15
				15–20
				20–25
				25–30
				30–35
				35–40
				>40
20	MAGE	Maximum age of wood	ordinal	
21	SEASON		categorical <0/1>	Spring/Autumn

Canonical Correspondence Analysis (CCA) finds a linear combination of the measured environmental variables that maximally separates the realised niches of the species as indicated by peaks in their relative abundances. This defines axis 1 and successive axes find other linear combinations that maximally separate the species but are uncorrelated with the previous axes. CCA was used here as the main method to assess how species composition relates to measured variables. The method, being considered as the best multivariate constrained ordination technique developed to date, extracts the major gradient in the species abundance data that can be accounted for by the measured environmental variables (Palmer 1993, McGarigal et al. 2000). Detrended Correspondence Analysis (DCA) was used as an auxiliary method. As DCA extracts the largest gradient in the species data without regard to environmental variables (unconstrained gradient), the analysis brings additional information which allows to learn how closely the gradient constrained by measured environmental variables match this overall gradient (McGarigal et al. 2000, Lepš & Šmilauer 2003). Besides this, DCA with detrending by segments and with Hill’s scaling helps to recognise the species abundance pattern as linear/unimodal (ter Braak & Prentice 1988, Lepš & Šmilauer 2003).

CCA, a unimodal method which operates with standardised data alone, required removal of ‘empty’ samples from analysis. This is why samples 30, 45 and 46 which did not contain millipedes could not be included into multivariate analyses.

Variance partitioning procedure (Borcard et al. 1992, Lepš & Šmilauer 2003) was used to assess the importance of two different groups of explanatory variables.

5. Results

5.1. Variation in alpha-diversity

The Diplopoda assemblages of the oak woodlands show high variability across the Eastern European Plain. The density of millipedes ranged in particular samples from 0 to 228 ind. m^{-2}, eight species found as the maximum per sample (Fig. 2a). The highest values of richness and diversity indices were noted mainly in samples from the sites situated west of the Dnepr (in particular, samples 2–6 and 8–13), as well as from some lying between the Dnepr and Don rivers (samples 24–29) (Fig. 2b). Most of these sites belong to the zones of forest-steppe and steppe (Fig. 1). On average, four species and 42 ind. m^{-2} per sample (mean) have been recorded. Species diversity measured by the Shannon index ranges from 0.21 to 1.66, whereas the Pielou evenness index in 2/3 of all cases exceeds 0.6 (samples 2–6, 8–13 and 24–29) (Fig. 2b), both concerning the same group of samples. All of them come from the area lying between the middle Dnestr and middle Don flows, representing mainly the forest-steppe or steppe belts (only samples 2 & 3 come from sites laying in the deciduous forest belt) (Fig. 1).

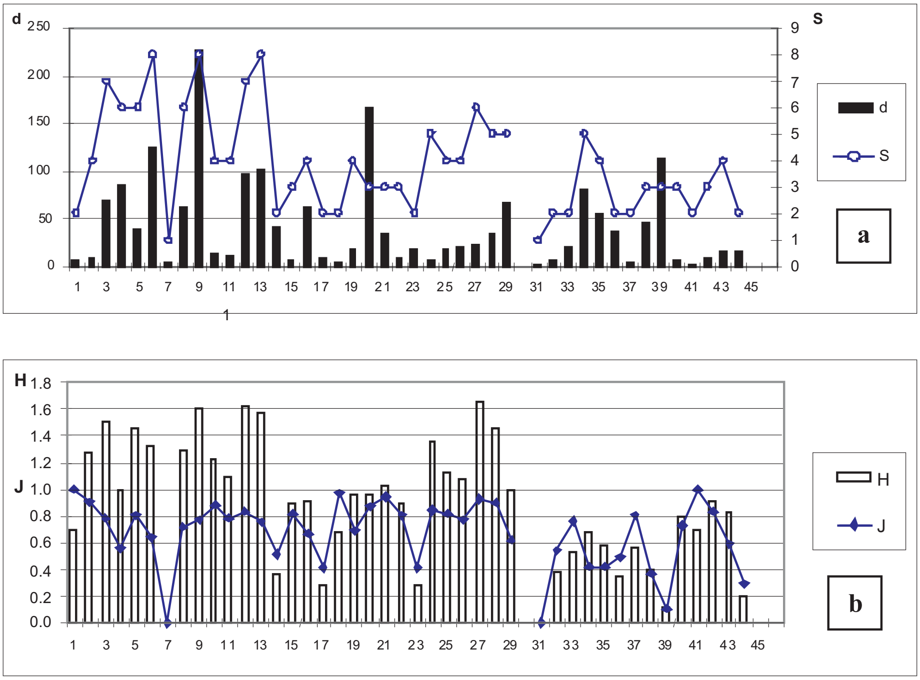

Fig. 2a–b Alpha-diversity parameters for the study Diplopoda assemblages; d: density; S: number of species; H: Shannon species diversity index; J: Pielou evenness index.

The differences between the millipede assemblage parameters measured for the vegetation belts were compared (Fig. 3) and studied using the non parametric Kruskal-Wallis ANOVA test. The density of millipedes fails to vary greatly between the vegetation belts; the values not being statistically significant ($p = 0.4020$). The richness appears to be the highest in the Diplopoda assemblages from the forest-steppe belt. In contrast, the assemblages from mixed forests are mostly poor in species. Statistically, the richness in the vegetation belts does not differ much according to the Kruskal-Wallis test ($p = 0.0958$), Yet, significant differences are found between the mixed forest and forest-steppe belts and between the mixed forest and steppe belts with the help of *t*-test (p = 0.02 and 0.05). The value of Shannon index is evidently the highest in the forest-steppe, with the differences revealed to be significant ($p = 0.0283$). In contrast, no significant differences were noted in the Pielou index ($p = 0.2081$).

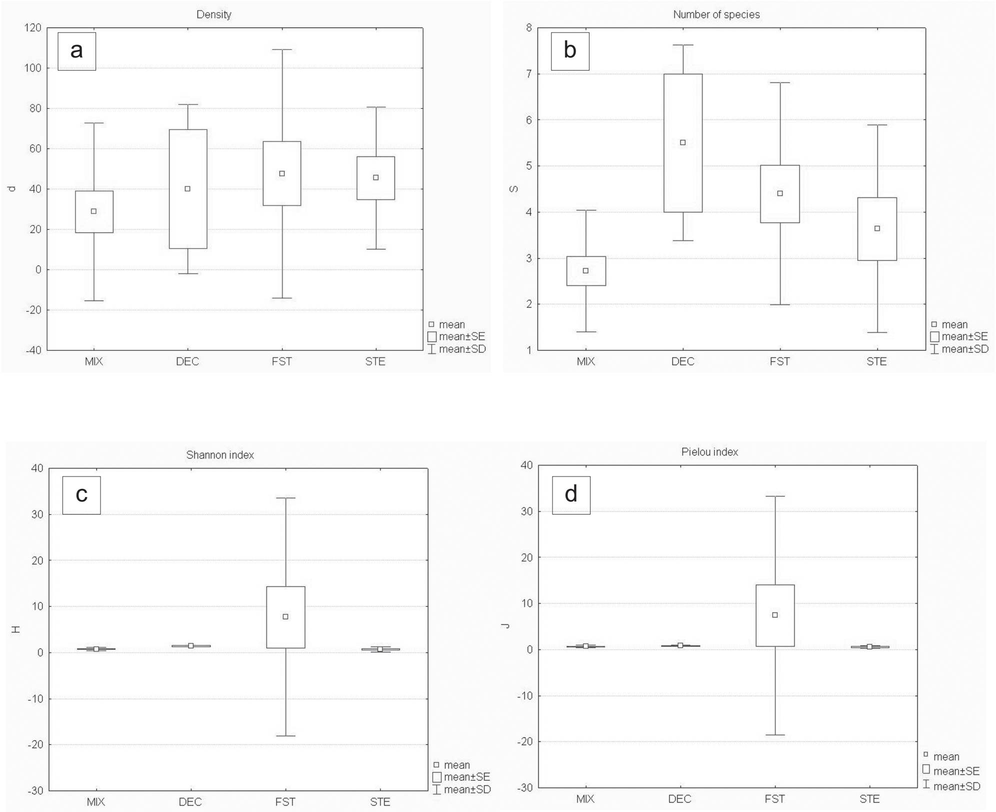

Fig. 3a–d Comparison of millipede assemblage parameters (a: density; b: number of species; c: Shannon index; d: Pielou index) in different vegetation belts in oak forests of the Eastern European Plain; MIX: mixed forests; DEC: deciduous forests; FST: forest-steppe; STE: steppe; statistical differences found in the number of species (b) and in the values of Shannon index (c).

5.2. Range of variability: beta-diversity

The lengths of axes in DCA with detrending by segments and Hill's scaling are expressed in standard deviation units of species turnover (SD) (Hill & Gauch 1980). Thus, the longest axis is considered as a value of beta-diversity along the theoretical overall gradient (ter Braak & Verdonschot 1995, Jongman et al. 1995, Lepš & Šmilauer 2003). The longest gradient (= 7.0 SD) for the Diplopoda assemblages in the oak woodlands of the Eastern European Plain was found along the 2nd ordination axis (Tab. 3). This value (> 4 SD, i.e. over the interval where the response curve with tolerance once rises and falls) explicitly shows that the response curves of many species are contained within the length of the axis and they are strongly unimodal. The gradient represented by the 2nd axis explains nearly 10 % of the total species variability, being only a little lower than the first axis (more than 10 %). The lengths of both the 1st and even the 3rd axes also represented quite high extents of the species turnover (6.0 and 5.7, respectively). Simultaneously, all four axes are well correlated with environmental data, being relatively long. This indicates that variation in Diplopoda assemblages in the oak woodlands are multigradient.

Taking into account the long overall gradient, only such a unimodal method of constrained gradient analyses as CCA is appropriate for the dataset considered (Lepš & Šmilauer 2003).

Tab. 3 Results of DCA with detrending by segments and Hill's scaling; environmental variables were projected afterwards only (to the ordination diagram); none of the four eigenvalues reported here is canonical; the corresponding axes are not constrained by the environmental variables.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.924	0.865	0.633	0.384	8.924
Lengths of gradient	5.961	**7.008**	5.699	3.234	
Species-environment correlations	0.95	0.809	0.894	0.888	
Cumulative percentage variance:					
of species data	10.4	20	27.1	31.4	
of species-environment relation	13	20.7	0	0	
Sum of all eigenvalues					8.924
Sum of all canonical eigenvalues					6.031

5.3. Effect of explanatory variables

Importance

The results of CCA (Tab. 4) show that 2/3 of the total variance (total inertia) are explained by four constrained ordination axes. A comparison of the results of both ordination analyses used (Tabs 3, 4) reveals that the percentage variances explained by each of the four canonical axes in CCA are very close to those explained by the proper axes in unconstrained DCA (9.9 compared to 10.4, 18.8 to 20.0, etc.). Besides this, the species-environment correlations are only slightly higher in constrained ordination CCA than in unconstrained DCA (for two calculated axes). All this suggests that both gradients considered, unconstrained (in DCA) and constrained (explainable by measured variables in CCA), are close. In fact, the CCA axes are strongly correlated with DCA ones. The Pearson product moment correlation between ordination scores for the samples (n = 43) is 0.88 for the 1st axes and 0.67 for the 2nd axes, significant value (0.65, $p = 0.05$) still to be found for the 4th DCA and the 3rd CCA axes. Thus, the measured environmental variables can be responsible to a considerable degree for the variation in Diplopoda species composition in the study oak woodlands.

Tab. 4 Results of CCA (Hill's scaling).

Axes	1	2	3	4	Total inertia
Eigenvalues	0.881	0.801	0.73	0.542	8.924
Species-environment correlations	**0.982**	**0.968**	**0.978**	**0.932**	
Cumulative percentage variance:					
of species data	**9.9**	18.8	27	33.1	
of species-environment relation	14.6	27.9	40	49	
Sum of all eigenvalues					**8.924**
Sum of all canonical eigenvalues					**6.031**
Share of explained variance					**67.6 %**

Since the relative importance of the canonical axes decreases from the first to the last one, all accounted axes were statistically tested. This was accomplished using the Monte Carlo permutation test which relates to null hypothesis stating the independence of the species data (or proper scores in the case of the 2nd or following axes) on the values of the environmental variables (or proper scores). The first three axes appear to be significant ($p = 0.002$, 0.008 and 0.002 for the consecutive axes, 499 permutations under a reduced model) and thus worth interpreting; only the 4th axis may be neglected.

Hierarchy of importance

The impact of the environmental variables on Diplopoda species abundance is highly complicated: 17 of 21 variables show high correlations (> 0.5) with more than one variable.

To clarify the importance of the studied environmental variables for variation in Diplopoda assemblages, the procedure of forward selection in CCA was used. In this procedure the variables are first tested singly in order of the variance they explain (λ_1), i.e. an independent effect of each environmental variable is checked (marginal effect) (Tab. 5). Next, the environmental variables were evaluated according to their inclusion into the model, together with the additional variance each variable explains at the time it was included (λ_A) (conditional effect). As a result of the procedure, 12 significant variables (Monte Carlo test, $p < 0.05$) emerged and they were ordered according to decline in the values of λ_1 and next λ_A: TANN, DEFI, TAMP, LONG, FRL, LATI, HUM, WA, MAGE, CO, BROW and PODZ (Tab. 5, right part). Six climatic and geographical variables are in the top significant twelve. The highest positions of variables related to soil properties belong to humus depth (HUM) and stand age (MAGE) while the characters associated with soil type (BROW, PODZ) show to be least important among statistically significant variables.

Tab. 5 Results of the forward selection procedure in CCA; the variables selected as significant using the Monte Carlo permutation test ($p < 0.05$) are marked in bold and sorted according to λ_1, variance explained when only one variable is used in the model; and next according to λ_A, variance explained at the time when any new variable is included in the model.

Marginal Effects		Conditional Effects				Selected and sorted variables		
Variable	λ_1	Variable	λ_A	p	F	Variable	λ_1	λ_A
TANN	0.58	**TANN**	**0.58**	**0.0020**	**2.85**	TANN	0.58	0.58
TMIN	0.58	**DEFI**	**0.66**	**0.0020**	**3.41**	DEFI	0.57	0.66
DEFI	0.57	**MAGE**	**0.40**	**0.0100**	**2.19**	TAMP	0.57	0.41
LONG	0.57	**HUM**	**0.42**	**0.0020**	**2.29**	LONG	0.57	0.31
TAMP	0.57	**LATI**	**0.40**	**0.0460**	**2.28**	FRL	0.55	0.26
FRL	0.55	**WA**	**0.36**	**0.0260**	**2.13**	LATI	0.53	0.40
LATI	0.53	**CO**	**0.40**	**0.0040**	**2.50**	HUM	0.51	0.42
LIT	0.53	**PODZ**	**0.36**	**0.0040**	**2.25**	WA	0.50	0.36
HUM	0.51	**LONG**	**0.31**	**0.0060**	**2.03**	MAGE	0.44	0.40
WA	0.50	**TAMP**	**0.41**	**0.0040**	**2.83**	CO	0.40	0.40
PR	0.45	**BROW**	**0.29**	**0.0340**	**2.11**	BROW	0.39	0.29
MAGE	0.44	**FRL**	**0.26**	**0.0360**	**1.86**	PODZ	0.33	0.36
CO	0.40	HUMI	0.15	0.2520	1.17			
HUMI	0.39	LIT	0.16	0.2220	1.20			
BROW	0.39	SEASON	0.19	0.1340	1.38			
MECH	0.38	MECH	0.13	0.4360	0.97			
SAND	0.34	SAND	0.16	0.2420	1.21			
PODZ	0.33	PR	0.13	0.3380	1.06			
SEASON	0.29	GREY	0.14	0.3500	1.06			
GREY	0.23	TMIN	0.12	0.5040	0.90			
CHER	0.17							

Contribution to canonical axes

Inspection of the values among the canonical axes and explanatory variables in the correlation matrix shows which of the environmental variables correlate strongly (positively or negatively) with particular species axes (Tab. 6), i.e., how important are certain variables in the creation of consecutive canonical axes. Two variables have the greatest importance to form the 1st canonical axis: HUM and DEFI, which can be termed ‘habitat’ ones. The 2nd axis ‘collected’ small pieces of variance from all of the considered variables; nevertheless, it can be regarded as ‘longitudinal’ because LONG has there the greatest share, and some other longitude-related variables such as FRL, TANN and TMIN are also to be considered here (Tab. 6). The greatest contribution to the 3rd axis was likewise clearly due to geographical variables, i.e., TANN, TMIN, FRL and LATI, as well as two purely habitat variables, LIT and MAGE. The variables PR and WA distinctly provided the highest contributions to the 4th axis, but this axis was not significant.

Tab. 6 Part of the correlation matrix in CCA with four canonical axes; the correlations with an absolute value of > 0.5 are marked in bold.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4
LONG	0.348	0.4829	0.443	–0.1046
LATI	–0.0411	0.3402	**0.5935**	0.2544
TANN	–0.0729	–0.4317	**–0.6509**	–0.176
TMIN	–0.2118	–0.4299	**–0.6157**	–0.0205
TAMP	0.4097	0.3288	0.4958	–0.1912
FRL	–0.026	–0.4817	**–0.5988**	–0.114
PR	0.0654	0.1968	0.3591	**0.6093**
WA	–0.322	0.2293	0.1347	**0.6275**
CO	–0.051	0.0807	0.303	0.4409
HUMI	–0.4184	0.0411	0.2339	0.4822
DEFI	**0.5028**	–0.2364	–0.3737	–0.4927
SAND	–0.2182	–0.0351	–0.1641	0.4325
MECH	0.2227	0.1303	0.4629	–0.2133
GREY	0.0505	0.0312	0.1577	–0.2641
PODZ	–0.2324	0.0065	–0.1217	0.4658
CHER	0.4059	0.015	0.0338	0.0016
BROW	–0.0675	–0.1146	–0.1634	–0.4157
LIT	0.3613	–0.1908	**–0.6315**	–0.1102
HUM	**0.6509**	–0.0638	0.048	0.1026
MAGE	–0.2041	–0.1082	**0.605**	0.0273
SEASON	–0.3112	–0.1006	–0.1938	0.2514

Explanatory effect of groups

As a result of variance partitioning (Lepš & Šmilauer 2003), 12 variables selected in the procedure of forward selection were found to explain 54 % of the total inertia (= total variance in species scores in unimodal methods) in the model (Tab. 7), the remaining variables accounting for another 33 %. These values relate to the amounts of variance explained by one group of variables when the variables from the second group are to be ignored (covariables in CCA).

When the whole group of 21 explanatory variables was considered as two parts: geographical plus climatic variables (=11) and the remaining variables (=10; soil and other), the explanatory effect amounted properly: 47 % and 32 % (Tab. 7). The importance of geographical factors alone is emphasized by the fact that only two variables, LONG and LATI, provide 12 % of the total inertia in the model. Both variables most important for the 1st axis, HUM and DEFI combined, also explain nearly 12 % of the total inertia.

Tab. 7 Partitioning of the variance; I: total variance (= inertia); VE: variance explained by all 21 explanatory variables; A: partial effect of the variables from group one; B: partial effect from the variables from group two (remaining variables); C: joint effect of the variables from both groups.

Fraction of variance	Value	% of I
I	8.924	100.00
VE	6.031	67.58
I–VE	2.893	32.42

	Groups of variables <A>							
	<12 significant>		<11 climatic>		<LONG&LATI>		<HUM&DEFI>	
	Value	% of I	Value	% of I	Value	% of I	Value	% of I
A	3.064	**34.33**	3.133	**35.11**	0.612	**6.86**	0.421	**4.72**
B	1.186	13.29	1.847	20.70	4.949	55.46	4.985	55.86
A+B	4.25	47.62	4.98	55.80	5.561	62.32	5.406	60.58
C=VE–(A+B)	1.781	19.96	1.051	11.78	0.47	5.27	0.625	7.00
A+C	4.845	**54.29**	4.184	**46.88**	1.082	**12.12**	1.046	**11.72**
B+C	2.967	**33.25**	2.898	**32.47**	5.419	**60.72**	5.61	**62.86**

5.4. Diplopoda assemblages from different biomes across the variability gradient

Most of the samples from three biomes, i.e. the mixed forest, forest-steppe and steppe belts, form a quite large and relatively continuous swarm, except for a few samples, in the ordination space seen in the projection determined by the 1st and 2nd axes (Fig. 4a, b). The samples crowd along the 1st axis which strongly correlates with such significant variables as HUM and DEFI, less strongly so with TAMP or LONG (Tab. 6, Fig. 4a). Three groups of samples can be distinguished along the 1st axis. The first group is associated with high values on the axis ($x > 4$) and contains the samples from the steppe belt only. The second group is associated with medium values on the axis ($0 < x < 4$) and comprises samples mainly from the forest-steppe belt. Both of these groups are located near the centroids of nominal variables CHER or GREY. The remaining samples are associated with negative values on the axis ($x < 0$), but they come from different vegetation belts. Most of the samples are also associated with negative values on both axes, lying near the centroids of other nominal variables like PODZ or BROW. In addition, this compact agglomeration (consisting of samples with similar millipede compositions) is restricted to the area, where most of the considered environmental variables show moderate values. Only a few samples from the far Northeast (42–44) outlie the main swarm, demonstrating the lowest similarity to all other samples according to the 2nd ordination axis. However, in the projection to the plane determined by the 1st and 3rd axes these samples are seen as typical members of sample communities from the mixed forests (Fig. 5a). Generally, the sample swarm is less compact in this projection. Different directions of swarm dispersion for the samples from different vegetation belts are noteworthy (Fig. 5b).

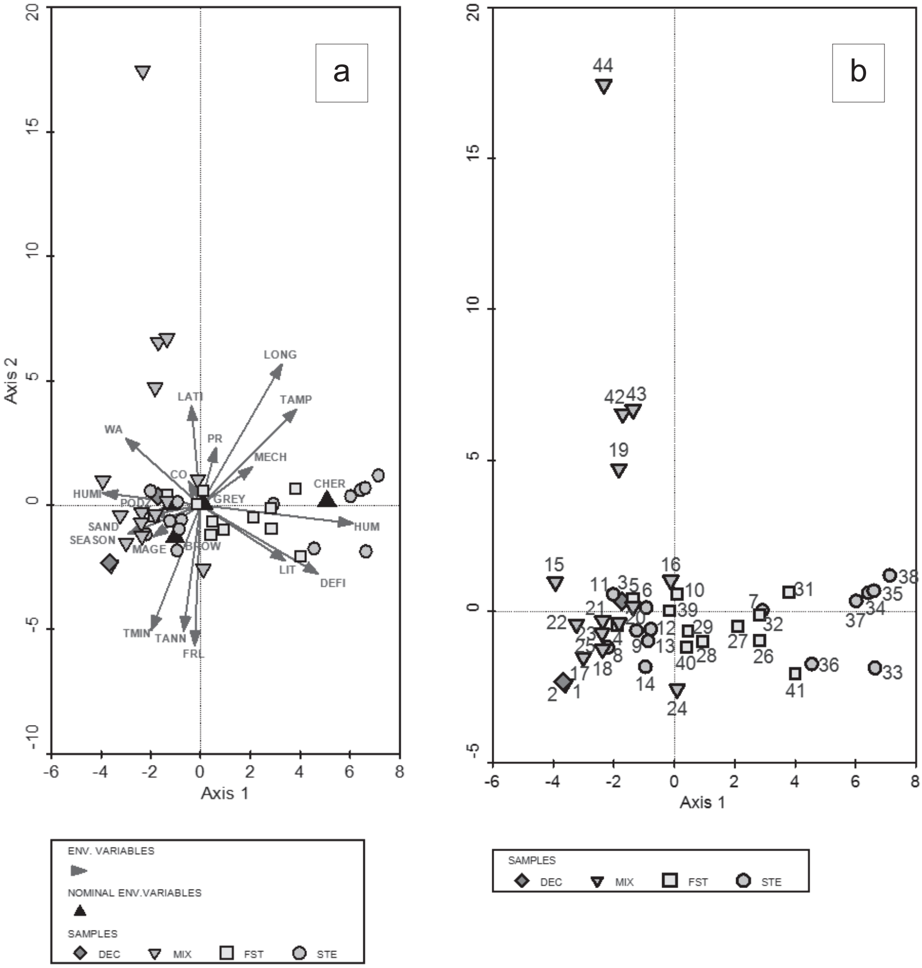

Fig. 4a–b Ordination plots of CCA in projection to the plane determined by the 1st and 2nd axes; a: sample scores and the environmental variables; b: sample scores with identifying numbers. The arrangement of samples is the best two-dimensional approximation of the turnover distance between them. The arrows point in the direction of an increase in a particular environmental variable; their length shows the marginal effect of the respective variables; the symbols of nominal variables represent centroids of the scores of samples that have a value of 1 for a particular variable. Sample symbols projected perpendicularly onto the line overlying the arrow show approximately the variable value in an individual sample.

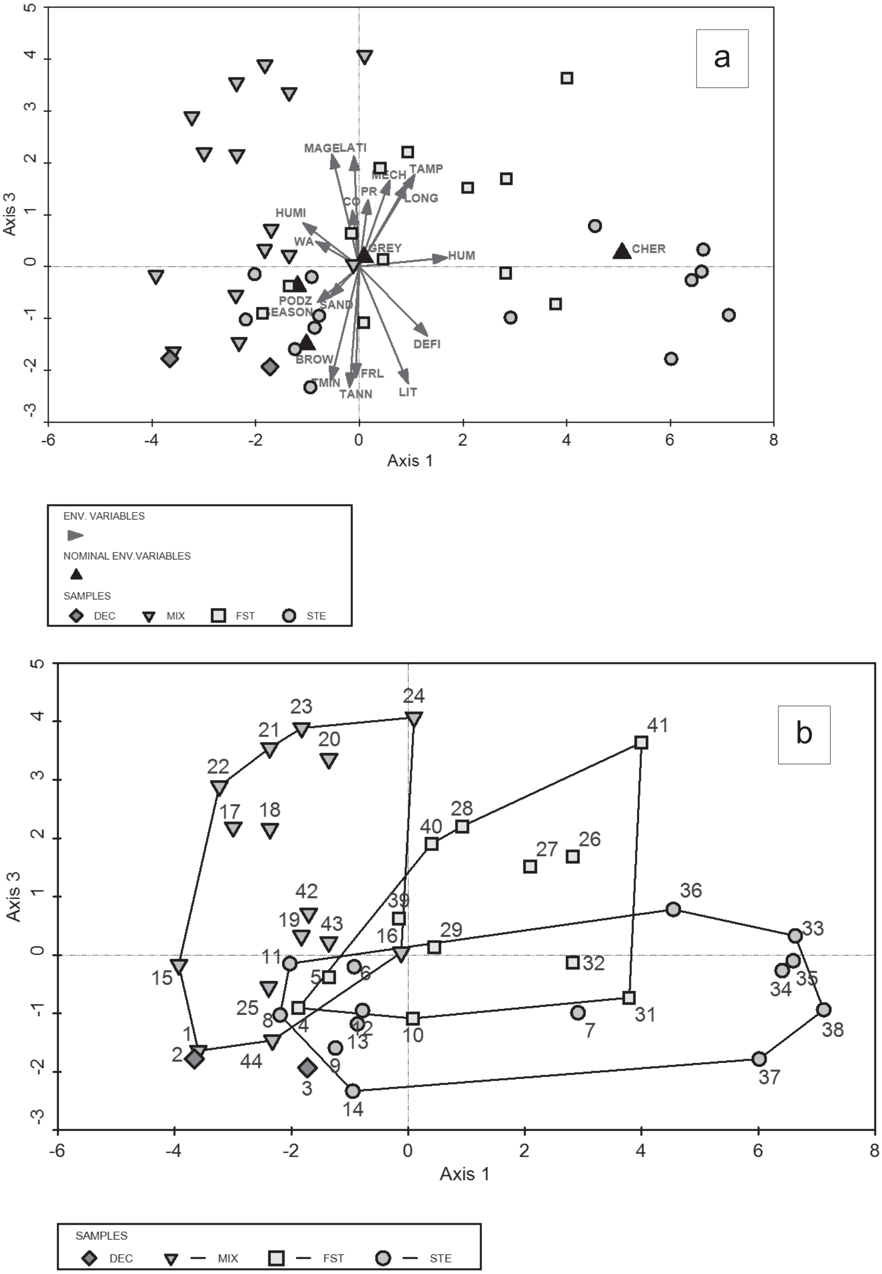

Fig. 5a–b Ordination plots of CCA in projection to the plane determined by the 1st and 3rd axes; a: samples and significant environmental variables; b: envelopes mark the samples (identified by numbers) from one biome.

Dispersion of the samples from the steppe belt runs in the ordination space in the direction of an increase in HUM values while the samples from the forest-steppe are dispersed mainly with increasing TAMP and LONG values. On the other hand, LATI, MAGE, CO and WA determine the variability of the samples from mixed forests. However, also in this projection (1st axis versus 3rd axis) there are some samples that create relatively compact agglomerations. These samples come from mixed forests in Cisuralia near the taiga border, as well from deciduous forests in the Ukraine or from the forest-steppe and steppe belts in Moldova (Figs 1, 5a, b). Yet the most compact group in both considered projections (planes) is only formed by several samples from the basins of Dnestr and Dnepr rivers (No 4–6, 8–13).

5.5. Variation in diversity across the variability gradient

The samples with the highest species richness are found under the low absolute values of the 1st axis and under rather low negative values of the 2nd axis in the ordination space (Fig. 6a). Most of them represent forest-steppe or steppe assemblages of Diplopoda from the basins of Dnestr and Dnepr rivers (cp. Figs 6a, 4b). Similar observations concern samples with the highest diversity measured by the Shannon index (Fig. 6b); yet some more samples join this group, e.g. some from central Russia located in the forest-steppe or nearby within the mixed forest belt (24–29). The response curves of species richness ($p = 0.0249$), as well as Shannon index ($p = 0.0167$), fitted using a generalised additive model show that the maximum values of the indices are near the same value on the 1st ordination axis (about –1), where an agglomeration of samples is also seen.

5.6. Changes in Diplopoda species along the variability gradient

The peaks of relative abundance of at least 18 species among all 30 found in the study oak forests form a compact agglomeration inside the part of the ordination space that corresponds to moderately low values of most of the considered environmental variables (Fig. 7a, b). These species are: *Polyxenus lagurus*, *Mastigona bosniensis, Polydesmus complanatus, P. denticulatus*, *P. montanus*, *P. schaessburgensis*, *Strongylosoma stigmatosum*, *Glomeris tetrasticha*, *G. hexasticha*, *Trachysphaera costata*, *Cylindroiulus boleti*, *C. burzenlandicus*, *Enantiulus nanus*, *Leptoiulus proximus*, *Megaphyllum projectum*, *M. transsylvanicum*, *Unciger transsilvanicus*, *Polyzonium germanicum.* According ordination plot they are predicted to occur with the highest relative frequency in grey, brown or podzolised soils. They all are members of the richest and most diversified assemblages of the Eastern European Plain's south-western part.

Such species as *Brachyiulus jawlowskii*, *Schizoturanius dmitriewi, Rossiulus kessleri, Megaphyllum rossicum* are predicted to occur most abundantly in the samples from the steppe belt east of the Dnepr, in the lower Don basin (samples 33–38). This means that the optima of these species coincide with the highest values of HUM and DEFI according to the CCA diagram.

Some clearly synanthropic species such as *Nopoiulus kochii, Polydesmus inconstans* and *Archiboreoiulus pallidus* are placed between the above two groups in the ordination space. They are predicted to occur most abundantly under moderately high values of HUM and DEFI. They are present mainly in samples from the forest-steppe belt in central Russia, in the higher Don basin.

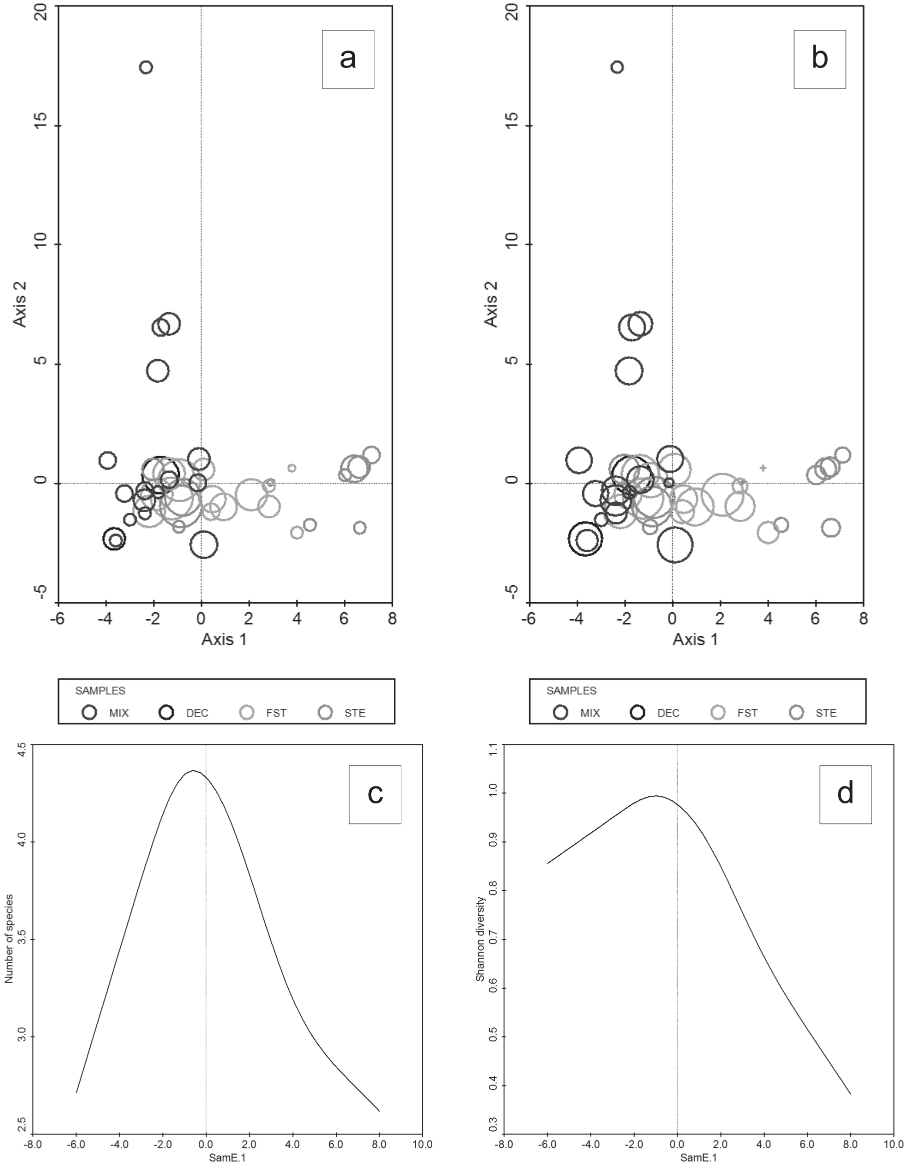

Fig. 6a–d The sample-environmental variable biplots with symbol size corresponding to the number of species (a) and the Shannon diversity index (b) in the sample and the respective response curves fitted using a generalised additive model (c, d).

A few species like *Xestoiulus laeticollis*, *Megaphyllum sjaelandicum*, *Brachydesmus superus*, *Ommatoiulus sabulosus* and, finally, *Altajosoma golovatchi* lie mostly outside the main group of species in the CCA diagram. The optima of these species are predicted to be under low values of HUM and DEFI, but under higher values of WA and HUMI. They are found most often in the mixed forests than any other.

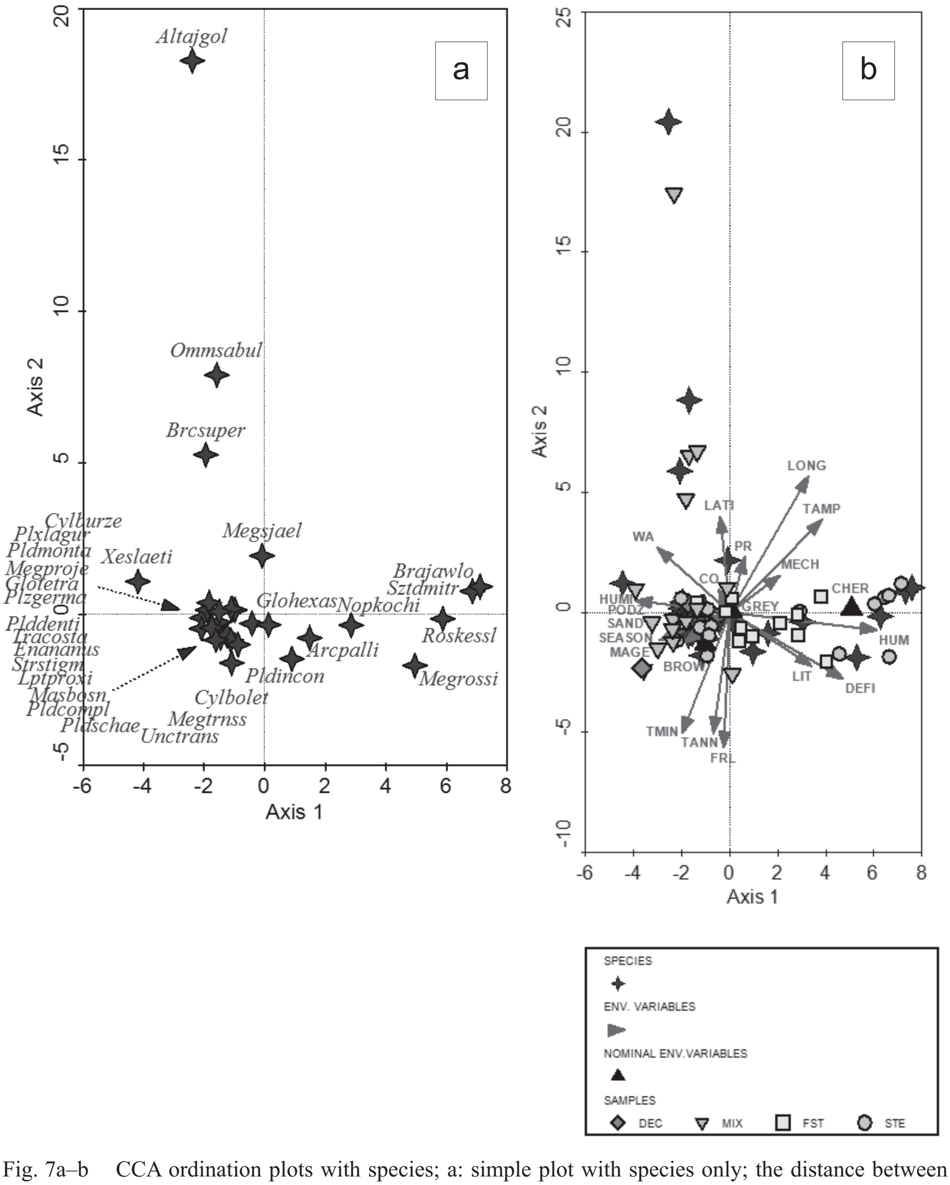

Fig. 7a–b CCA ordination plots with species; a: simple plot with species only; the distance between symbols approximate the dissimilarity of distribution in the relative abundance of these species across the samples; b: triplot; the species symbol projected perpendicularly onto the line overlying the arrow of a particular environmental variable shows the optimum of the species in respect to the value of that environmental variable.

6. Discussion

Our review of all simple parameters of Diplopoda assemblages of the oak woodlands in the Eastern European Plain showed this type of habitat to be the best for millipedes in the forest-steppe belt, in particular west of the Dnepr and between the Dnepr and Don rivers, where the highest species richness and diversity was found. The millipede assemblages from the forest-steppe belt appear to be especially rich in species and most diversified according to the Shannon index (statistically significant differences). However, neither the density of millipedes nor species evenness in the assemblages of the forest-steppe was found to differ significantly from the assemblages of the oak woodlands in the other vegetation belts.

The present studies on the variability of the species dataset (DCA) show that the species turnover (beta diversity) is very high, something that could be expected across such a vast area, although species-recruiting resources in oak woodlands are limited to only 30 species found in the samples. This means that many millipede species occur in the Eastern European Plain to show a full range of their tolerance, with predicted unimodal responses of species. However, the distributions of the most of the species found there extend far more to the west in Europe and only a few, such as *Altajosoma golovatchi*, *Brachyiulus jawlowskii* or *Schizoturanius dmitriewi* (Golovatch 1992; http://www.faunaeur.org/distribution.php), are restricted to the study territory or its part. Hence, the variability of species abundance is so high that many of the recorded species can fully realise their niches.

The significant accordance of the constrained ordination axes (CCA) and unconstrained ones (DCA) suggests that the overall gradient matches well with the most important gradients explicable by the measured variables. The statistical significance of the considered environmental variables confirms that it is the variables that are responsible for the variability of the species dataset. This variability is multigradient, with at least three significant ordination axes in CCA that can be used in explaining variation in the species dataset and reflecting the high complexity of the gradient. Undoubtedly, it arose from many environmental factors that can be postulated as responsible for change in Diplopoda assemblages. Among them the available water, the thickness of the humus layer, soil texture, and temperature have already been mentioned as the most important (Kime & Wauthy 1984, Kime 1992, Kime et al. 1992, Branquart et al. 1995). Bearing in mind the importance of geographical aspects in the patterns of distribution and in the origins of millipede faunas (Golovatch 1992, 1997), the influence of different geographical factors on the assemblage variability cannot be neglected. The use of multivariate methods of analysis has allowed to estimate and compare the effect of different factors, both habitat and geographical, on millipede assemblages in oak woodlands of the Eastern European Plain.

Two-thirds of millipede assemblage variation revealed in the study dataset obtained from mature oak woodlands across the vast Eastern European Plain can successfully be accounted for by 21 environmental variables used in multivariate analyses. Thus, we can recognise some of these variables as relatively good predictors. Nevertheless, many of them mutually correlate, and some of them seem to multidirectionally influence millipede variability, correlating with more than one ordination axis. However, 12 of the considered variables are undoubtedly significant and can explain more than half of the whole variability (54 %). Yet it is noteworthy that nine of these 12 variables represent geographical locations of the sites, as well as climatic conditions. Admittedly, only the 2nd and 3rd axes appear to be dominated by the influence of geographical factors, but their strength measured over the distance from the steppe belt to the border of mixed forests with taiga was estimated as amounting to nearly half (47 %) of the whole variability in Diplopoda assemblages. This shows the importance of geographical-climatic aspects in variation in Diplopoda assemblages of oak woodlands in the Eastern European Plain. Only two basic geographical variables, LONG and LATI, determine over 12 % of the total variability found while only two most important factors, HUM and DEFI, provide nearly the same contribution. This is nothing strange because nature zonation so markedly expressed across the Eastern European Plain has long been recognised as being among the main factors to affect fauna (Chernov 1975), the more so that the topsoil of oak forests (only this habitat was considered in the present study) offers relatively stable conditions to millipedes in geographically close places. The importance of climatic factors has been emphasised in similar studies on wire-worm and spider assemblages of the east European oak forests (Penev 1992, Esjunin et al. 1994) while in the case of earthworm assemblages the nature zonation has been found to be subordinate (Penev et al. 1994a, b). A mixed (or intermediate) dependence on habitat and climatic-geographical factors is marked in the variability of millipede assemblages of the Plain.

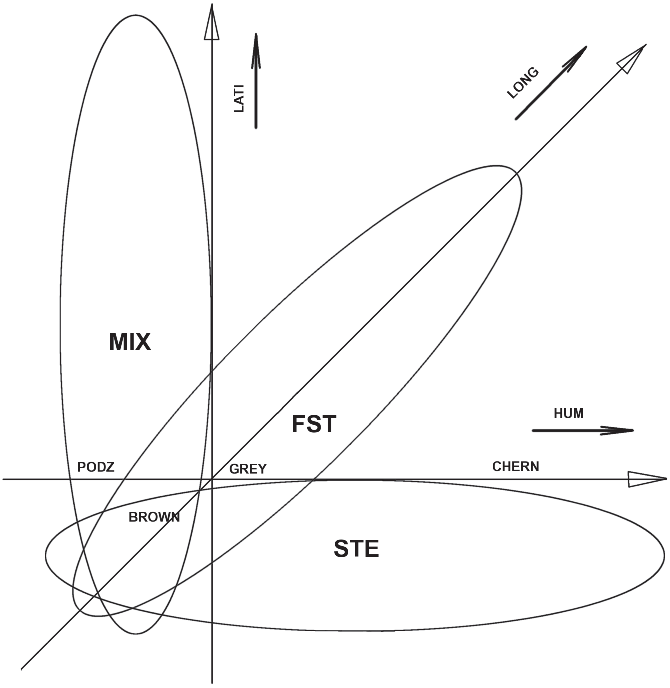

Fig. 8 Simplified diagram showing the differentiation of millipede assemblages against the background of some of the main environmental factors; abbreviations as in the previous figures.

The high range of species turnover and the ‘multidirectional’ variability are mainly the effect of different environmental conditions in oak woodlands in the main three biomes concerned. The assemblages must adapt to their environments, meaning that species will be replaced by others which better fit the local conditions. The samples from the steppe are ‘dispersed along the 1st axis’, which is quite in accord with an increase both in humus depth (HUM) and humidity deficit (DEFI) (Fig. 8, comp. Figs 4a, b and 5a, b). Lower values of these variables describe the forest-steppe samples distributed in the direction of an increase in such climatic-geographical variables as annual temperature amplitude (TAMP) and longitude (LONG). The samples from the mixed forest belt are characterised by the lowest or moderate values of humus depth (HUM) and humidity deficit (DEFI), but they are related to an increase either in precipitations for the warm period (WA) or latitude (LATI), or forest age (MAGE). In fact, these variables may be considered as the main factors responsible for differentiation in the millipede assemblages of oak woodlands of the eastern European Plain, splitting the assemblages in different ‘directions’. However, an increase in the mean annual temperature (TANN) and in the number of frostless days (FRL) fails to strongly differentiate the study assemblages, simply restricting their occurrences instead.

The present study shows that the diversity parameters of millipede assemblages of the oak woodlands are undoubtedly the highest where the variability of the assemblages is not under a strong influence of environmental factors. This concerns the samples related to brown soil irrespective of the biome they represent (Figs 6a–d, 4a). The abundance optima of most of the millipede species are also very close there (Fig. 7a–b). However, in comparison with the other biomes the forest-steppe belt seems to provide better conditions for richer and more diversified assemblages to thrive. This is seen along the 1st axis where the assemblages are most strongly correlated with humus depth (Figs 4a, 5a).

Most of the species agglomerated in the ordination space as the main compact group constitute the common source for the assemblages of different biomes in places where the conditions are relatively mild. They all are European faunal elements, often dominating this or that site lying west of or within central Russia. Some of them like *Mastigona bosniensis*, *Polydesmus schaesburgensis, Cylindroiulus boleti*, *Megaphyllum transsylvanicum* demonstrate a gradual decline towards the Dnepr River. A few more species, such as *Xestoiulus laeticollis* and *Glomeris hexasticha*, show distributions slightly more extended to the Northeast and better correlations with the samples from mixed forests. A few more European elements reach not only the Volga River, like *Strongylosoma stigmatosum* or *Leptoiulus proximus*, but also the Ural Mountains in the East, to totally decline there, like *Ommatoiulus sabulosus*, *Rossiulus kessleri* or *Megaphyllum sjaelandicum*. A minor group of synanthropic elements, naturally reacting similarly to disturbed environments, is also evident: *Nopoiulus kochii*, *Polydesmus inconstans*, *Archiboreoiulus pallidus.* Only two species show Siberian origins: *Altajosoma golovatchi*, distributed in Siberia and reaching the Volga and Kama areas in the West, and *Schizoturanius dmitriewi* which is endemic to the area lying roughly between the Dnepr and Don rivers. In part, these patterns can also be traced using the above, purely eco-geographical graphs.

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