THE ROLE OF EDAPHIC AND VEGETATION FACTORS IN STRUCTURING BETA DIVERSITY OF THE SOIL MACROFAUNA COMMUNITY OF THE DNIPRO RIVER ARENA TERRACE

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Abstract

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The article presents the results of evaluation of the role of edaphic and vegetation factors on beta diversity of soil macrofauna by means of the MDM-approach. The multinomial diversity model (MDM) is a method for relating the Shannon diversity to ecological factors. The research was conducted in the 'Dnipro-Orils'kiy' Nature Reserve (Ukraine). The research polygon was laid in the forest within the Orlova ravine (48°31'13 "N, 34°48"15 "E). The study site comprises 1.0 ha of deciduous woodland bordered by an area of herbaceous cover within the ravine. In the soil of the studied polygon, 38 species of soil invertebrates were identified, which characterizes the gamma diversity. Alpha diversity, or the number of species on average at each sample point is 4.3. Beta diversity is 8.8. The principal component analysis of the edaphic parameters revealed four statistically significant principal components. For vegetation characteristics, six statistically significant principal components were identified. The sequential analysis of the effects shows that edaphic factors accounted for 20.9% (0.81 bit) of the available entropy (1.71–0.91). The largest decrease in the community entropy takes place under the action of the principal components 2 and 3 (0.06 bit and 0.05, respectively). A permutation test showed that these effects are statistically significant. In turn, 28.4% of the community β-diversity is attributable to vegetation factors. The greatest decrease in community entropy is related to the principal vegetation components 1, 3 and 4 (0.07, 0.05 and 0.04 bits, respectively). A permutation test indicated that this effect is statistically reliable. Geostatistical models substantially describe the varying effects on the beta-diversity of edaphic principal components 1 and 2, and the vegetation principal components 1 and 3. It was found that edaphic and plant factors play an important role in structuring the communities of soil macrofauna on the level of beta diversity. Community sensitivity to environmental factors varies in space and is spatially structured. For different environmental factors, specific spatial patterns of community sensitivity are allocated. Beta diversity may be due to the fact that the species of soil macrofauna communities also vary in the degree of sensitivity to various environmental factors. The species of soil microfauna are also divided according to their extent of sensitivity to different ecological factors.

Key words: diversity, ecological factors, spatial patterns, variogram, Mattern model.

Introduction

Soils provide one of the most important ecosystem services such as supporting the most agro-sylvo-pastoral production systems (Lavelle et al., 2006). Soil biota is highly diverse, representing 23% of the described organism diversity (Decaëns et al., 2006). Forest soil biodiversity responds to environmental changes and has been shown to be one of the key drivers of ecosystem function and service delivery (Lukac et al., 2017). An important component of soil biota is represented by soil macrofauna (Lavelle, 1997). Soil macrofauna significantly contributes to the dynamics of the soil properties (Ayuke et al., 2009).

Soil biodiversity demonstrates considerable spatial and temporal heterogeneity at multiple scales (Carpenter et al., 2012; Eggleton et al., 2005; Burton, Eggleton, 2016). Scale-dependent drivers affect the species distributions and community composition at various spatial levels (Berg, 2012). The scale-specific response to habitat heterogeneity may be an essential property of a given taxon or species (Vanbergen et al., 2007). The large-scale determinants of soil macrofauna diversity are climate, soil type, land-use management practices and landscape structure (Dauber et al., 2003). Very little is known about the effect of landscape variables on soil biota (Wolters, 2001; Dauber et al., 2005). Soil animals significantly vary in size, adaptations to movement and, consequently, vary considerably in mobility (Gilarov, 1949; Zhukov, 2015). Differences in local community structure may be affected by ecological processes occurring at larger spatial scales. Species differing in size and mobility can be regulated by different processes on one and the same spatial scale (Olff, Ritchie, 2002). It is highly probable that functional or ecological features of species are the important determinant of which habitat heterogeneity component is relevant and at which spatial scale (Dauber et al., 2005). Differences were found in the spatial scales where the landscape affects species abundances and species richness for Collembola (Chust et al., 2003), Homoptera and Diptera (Chust et al., 2004).

Heterogeneity in soil properties induced by vegetational spatial patterns define the patchy distribution of soil organisms (Berg, Bengtsson, 2007; Berg, 2012). It has been discovered that on a smaller spatial scale, the diversity of tree species influences the earthworm density (Cesarz et al., 2007). Diverse tree cover is important in the conservation of the soil macrofauna communities and in making a significant contribution to their activity in the soil ecological functions (Kamau et al., 2017). The litter quality of a given tree species can significantly contribute to the changes observed in the soil fauna communities (Korboulewsky et al., 2016). The importance of small scale heterogeneity has been shown for plant and soil macrofauna biodiversity (Burton, Eggleton, 2016). The presence of dead wood is positively correlated with soil arthropod abundance and diversity (Jabin et al., 2004). It has been shown that spatial patterns of herbaceous vegetation influence soil macrofauna biodiversity; therefore, full understanding of the soil macrofauna distribution in a grassland ecosystem requires an accurate study of the vegetation cover around the places where the samples of animals were collected (Mathieu et al., 2009). Soil animals, which are classified as ecosystem engineers, can significantly increase the spatial heterogeneity of the soil, and hence, the spatial patchiness of soil fauna (Nuutinen et al., 2017). Ecosystem engineers are able to modify important drivers of the spatial distribution of soil organisms such as soil structure, pore space, porosity and bulk density, water content, and mix organic matter and inorganic matrix (Lavelle, 2002; Berg, 2012).

Diversity is the most important aspect of the community structure. Diversity can be seen in terms of three components: alpha, beta and gamma. Alpha diversity is the species diversity at individual sites. Gamma diversity is that of the whole region of interest of the study. Beta diversity is the variation in species composition among sites within the geographic area of interest (Legendre et al., 2005). Variation of biological communities across space or time (i.e., beta diversity) has attracted increasing attention (Alahuhta et al., 2017; Viana et al., 2016). Beta-diversity partition may provide additional insights into the causes of spatial variability in biotic communities compared to the total beta diversity itself (Soininen et al., 2017). Beta diversity can reflect two different phenomena: nestedness and spatial turnover (Baselga, 2010). The principal current hypotheses about the origin of beta diversity are as follows: 1) species composition is uniform in large areas; 2) species composition fluctuates in a random, autocorrelated way; 3) species distributions are related to environmental conditions (Legendre et al., 2005). Obviously, all these mechanisms may occur in relation to soil macrofauna communities. It is important to directly relate community beta-diversity to multiple environmental factors. This problem may be resolved by means of the multinomial diversity model (MDM). This approach can divide community entropy and diversity within and between sites, species, and models, and changes in entropy or diversity can be attributed to model predictors (De'ath, 2012).

The aim of our work is to define the role of edaphic and vegetation factors in the partitioning of beta diversity of the soil macrofauna community.

Material and methods

Site description

Studies were conducted in the 'Dnipro-Orils'kiy' Nature Reserve (Ukraine). The research polygon was laid in the forest within the Orlova ravine (48°31'13 "N, 34°48" 15 "E). The territory has a temperate-continental climate with an annual mean maximum decade temperature of 25.7 °C, and a minimum of –10.0 °C, and with a mean annual precipitation of approximately 565 mm (20-year average according to the data of the Dnipro meteorological station).

The study site comprises 1.0 ha of deciduous woodland bordered by grassland valley territory (Fig. 1). Forests in the steppe zone of Ukraine have a very restricted distribution and usually have an island status. To the east, the natural forest of the site borders an artificial pine plantation. The soils are fertile sandy loam with the underlying geology comprising quaternary aeolian sandy sediments. The site consists of 7 transects. Each transect is made up of 15 test points. The distance between rows in the site is 3 m.

Sampling methods

Soil macrofauna was defined as invertebrates visible to the naked eye (macroscopic organisms) (Warren, Zou, 2002). Geobionts (large soil invertebrates that permanently inhabit the soil) and geophiles (organisms that live in the soil only for some phase of their life) (Krivolutsky, 1994; Gholami et al., 2016) were assessed. Sampling was carried out during May 2016. Samples consisted of a single block of soil, 25×25×30 cm^3 deep, dug out quickly. A quadrat was fixed on the soil surface prior to taking the soil samples. The litter macrofauna was collected from the soil samples hand. The soil macrofauna were sorted and the animals were stored in 4% formaldehyde (Mathieu et al., 2004).

Vegetation survey

This was carried out in 9 m^2 quadrats, in the centre of which the macrofauna samples were collected. The projective cover of plant species was recorded at ground level, the understory (up to 2 m height) and canopy (above 2 m height). We were able to make species level identification for all the quadrats. Within the studied polygon, 48 species of plants were found. The forest stand was dominated by *Quercus robur* L. and *Pyrus communis* L. *Sambucus nigra* L.,

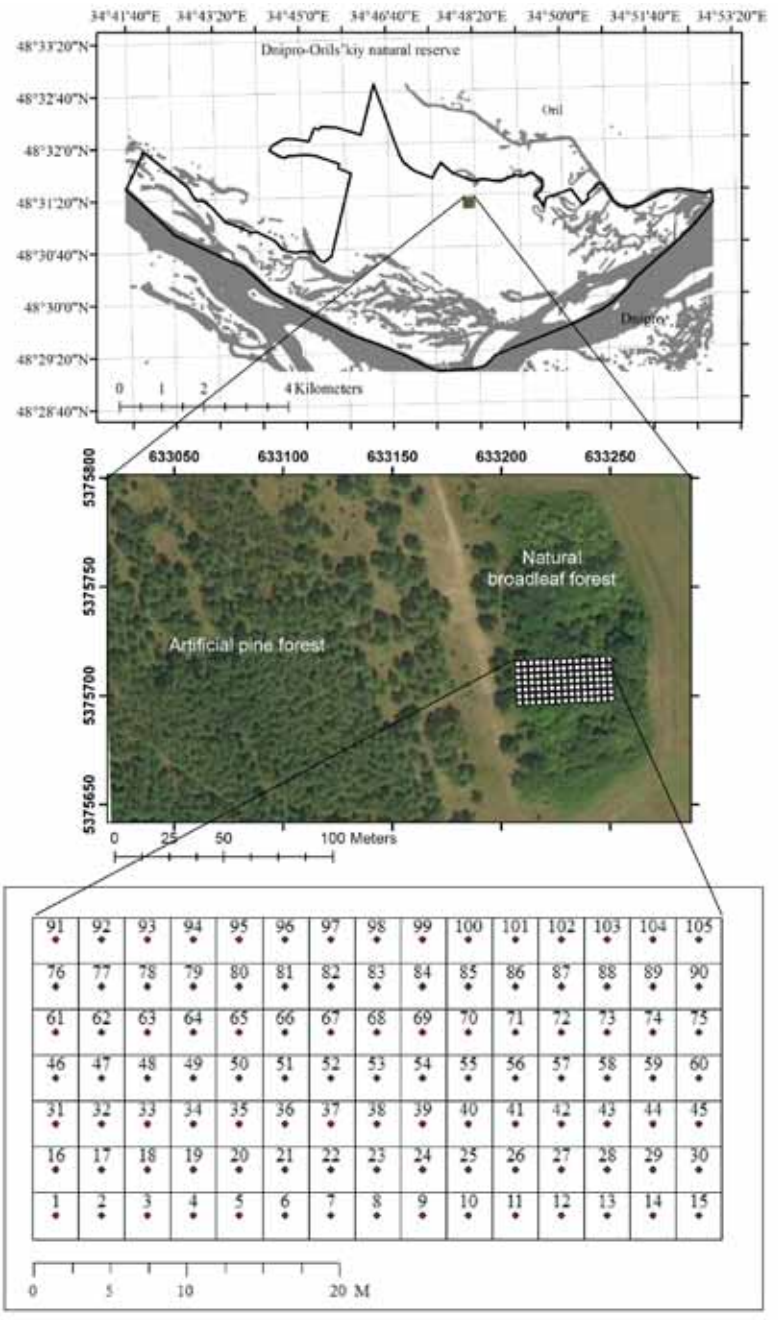

Fig. 1. Placing of experimental polygon and the sampling points.

Acer tataricum L. and *Crataegus fallacina* Klokov predominated among the bushes. The herbaceous layer was dominated by *Urtica dioica* L., *Anthriscus sylvestris* (L.) Hoffm., *Chelidonium majus* L., *Glechoma hederacea* L. and *Vincetoxicum hirundinaria* Medikus. In syntaxonomic aspect, the vegetation can be identified as follows (Sokolova, 2011):
Class *Querco-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937,
Ordo *Quercetalia pubescenti-petraeae* Klika 1933,
Union *Aceri tatarici-Quercion* Zolyomi 1957,
Ass. *Vincetoxico hirundinariae-Quercetum roboris* Sokolova, 2011.

Environmental variables

Based on the geobotanical descriptions, phytoindicative assessment of environmental factors, according to Belgard (1950, 1971), Didukh (2011, 2012) and Ellenberg (1974), was made.

A system of plant ecomorphs was used according to Belgard (1950) and Tarasov (2012). Hygromorphs are represented by xerophytes (humidity level 1), mesoxerophytes (humidity level 2), xeromesophytes (humidity level 3), mesophytes (humidity level 4), hygromesophytes (humidity level 5). The humidity level by hygromorphic structure *(Hygr)* is calculated as:

$$Hygr = \frac{\sum_{i=1}^{i=N}(i \times P_i)}{100},$$

where i is the moisture level; P_i is the projective cover of plants of the corresponding hygromorph (Zhukov, Zadorozhnaya, 2016).

Trophomorphs are represented by oligotrophs (trophy level 1), mesotrophs (level of trophy 2) and megatrophs (trophy level 3). Nutrient status level by trophomorphic structure (*Troph*) is calculated as:

$$Troph = \frac{\sum_{j=1}^{j=N}(j \times P_j)}{100},$$

where j is the level of trophicity; P_j is the projective cover of plants of the corresponding trophomorph.

Heliomorphs are represented by heliosciophytes (level of light 2), scioheliophytes (level of light 3), helophytes (level of light 4). The level of illumination by the heoliomorphic structure (*Hel*) is estimated as:

$$Hel = \frac{\sum_{z=1}^{z=N}(z \times P_z)}{100},$$

where z is level of light; P_z is the projective cover of plants of the corresponding heliomorph.

Didukh phytoindication scales (2011, 2012) include edaphic and climatic scales. The edaphic phytoindication scales include the soil water regime (Hd), the variability of damping (fH), the soil aeration (Ae), the soil acidity (Rc), the total salt regime (Sl), the carbonate content in the soil (Ca) and nitrogen content in the soil (Nt). The climatic scales include the parameters of the thermal climate (thermoregime, Tm), humidity (Om), cryo-climate (Cr) and the continentality of climate (Kn). In addition to these, the lighting scale (Lc) is highlighted, which is characterized as a microclimate scale. Thermal properties of soils are indicated by a scale of the thermal regime, and hydrothermal is the scale of ombro mode. Phytoindicational evaluation of the environmental factors is performed by the ideal indicator method of Buzuk (2017).

Ellenberg indicator values (1974) include: *L*-scale of illumination/shading (9 classes, *Light Regime*), *T*-scale of thermo climate (9 classes, *Temperatures*), *K*-scale of climate continentality (9 classes, *Continentality of Climate*), *F*-scale of soil moisture (9 classes, *Humidity*), *R*-scale of soil acidity (9 classes, *Acidity*), and *N*-scale of soil nitrogen (9 classes, *Nutrients Availability*). Calculation of values of environmental factors was carried out using the method of average weighted values of indicator scales taking into account the projective cover of plants.

Measurement of soil mechanical impedance was carried out in the field using a hand penetrometer Eijkelkamp, to a depth of 100 cm with an interval of 5 cm. The average error of the measurement results of the device is ± 8%. The measurements were made by a cone with a cross-sectional dimension of 2 cm^2. Within each measurement point, the mechanical impedance of the soil was made in a single repeatability.

To measure the electrical conductivity of the soil *in situ*, a sensor HI 76305 was used (Hanna Instruments, Woonsocket, R. I.). This sensor works in conjunction with the portable device HI 993310. The tester estimates the total electrical conductivity of the soil, that is, combined conductivity of soil air, water and particles. The results of measurements of the device are presented in the units of saturation of the soil solution with salts is g/l. Comparison

of measurement results of HI 76305 with laboratory data allowed us to estimate the conversion factor of units as 1 dS/m = 155 mg/l (Pennisi, van Iersel, 2002).

The aggregate structure was evaluated by the dry sieving method, according to Savinov (Vadunina, Korchagina, 1986). The percentage content of such fractions is established: < 0.25, 0.25–0.5, 0.5–1, 1–2, 2–3, 3–5, 5–7, 7–10, > 10 mm, and plant roots. The soil bulk density was estimated by Kachinskiy and the soil moisture by weight method (Vadunina, Korchagina, 1986).

Soil macrofauna identification

Adult and larvae specimens were counted and identified to species level. Earthworms were identified using Perel (1978), Vsevolodova-Perel (1997), and Kunah et al. (2010), Lithobiomorpha with Zalesskaya (1978), Geophilomorpha using Bonato et al. (2014), Diplopoda using Cherny and Golovach (1993), imago ground beetles using Kryzhanovsky (1964), larvae of ground beetles using Gilyarov (1964), Dolin (1978), Andreeva (1990), Kabakov (2006), and Krivosheina (2012), woodlice using Schmolzer (1965), molluscs using Gural-Sverlova and Gural (2012).

Statistical analysis

Statistical calculations were performed using the Statistica 7.0 program and the Project R 'R software shell: A Language and Environment for Statistical Computing' (http://www.R-project.org/). Estimation of confidence intervals and the standard deviation of the number of soil animals was made using a bootstrap approach and implemented by means of the bootES package (Kirby, Gerlanc, 2013).

The assessment of the soil macrofauna community biodiversity and 95% of their confidence intervals and its partitioning on alpha, beta and gamma diversity was done by using the entropart package (Marcon, Herault, 2015). Environmental variables were studied through the analysis of principal component using the package vegan (Oksanen et al., 2017). The number of significant principal components was calculated on the basis of the Horn procedure (Horn, 1965). The operation was completed using the paran package (Dinno, 2012). The partitioning of beta-diversity in relation to external predictors was conducted using multinomial diversity models with the help of MDM (De'ath, 2012, 2013). Spatial variation of differential entropy was displayed using the 'Surfer® 12 from Golden Software, LLC (www.goldensoftware.com)'.

Geostatistical analysis

Kriging is an important tool in geostatistics. Kriging is a linear predictor by the method of the least squares (Minasny, McBratney, 2005). The variogram is a key concept in geostatistics. Knowledge of the exact mathematical form of the variogram allows one to quantify spatial variation (McBratney, Pringle, 1999) as well as the prediction of soil properties on a local or regional level (Minasny, McBratney, 2005). A variogram is usually calculated using spatial data using the method of moments, and subsequent fitting to the theoretical model of empirical variogram using a nonlinear least-squares method (Webster, Oliver, 2001). It is customary to refer to the intercept of the variogram model curve as the nugget (τ^2), the difference between the asymptote and the nugget as the sill (σ^2), and the distance at which the theoretical variogram curve reaches its maximum as the range. For models with an infinite range, the value at which the variogram reaches 95% of the asymptote is called the practical range. These names correspond to the parameters τ^2, σ^2 and φ respectively, where the latter is usually multiplied by a constant depending on the model. For instance, the practical range is 3φ for the exponential, $\sqrt{3}\varphi$ for the Gaussian, 4φ and 5φ for the Mattern model with $\kappa = 1$ and 2, respectively, and equals φ for the spherical model (Ribeiro et al., 2003).

However, the method of moments can give erroneous results, as commonly used variogram models (spherical, exponential and gauss) are characterized by lack of flexibility (Stein, 1999). As an alternative, one can consider the Mattern variogram class of models (Matern, 1986). Mattern models have considerable flexibility for modelling the spatial covariance and are able to describe a wide variety of local spatial processes. Based on this, the Mattern model is proposed to be used as a general approach for the simulation of soil properties (Minasny, McBratney, 2005). Mattern isotropic covariance function has the form (Handcock, Stein, 1993; Stein, 1999):

$$F(h) = \frac{1}{2^{\kappa-1}\,\Gamma(\kappa)}\left(\frac{h}{\varphi}\right)^{\kappa} K_{\nu}\left(\frac{h}{\varphi}\right),$$

where h is the separation distance; K_{ν} is the modified Bessel function of the second kind of order κ (Abramowitz, Stegun, 1972), Γ is the gamma function, φ is the range or distance parameter ($\varphi > 0$), which measures how fast cor-

relation decays with distance; κ is the smoothness parameter. The Mattern model is characterized by high flexibility compared with conventional geostatistical models in view of the smoothing parameter κ. When the κ parameter is small (κ → 0) the model assumes a rough spatial process, if the κ parameter is large (κ → ∞) it assumes a smoothed spatial process (Minasny, McBratney, 2005). When the parameter κ = 0.5 , the Mattern model fully corresponds to an exponential model. When κ → ∞ , the Mattern model corresponds to a Gaussian model. If κ = 1, it corresponds to a Whittle's function (Whittle, 1954; Webster, Oliver, 2001; Minasny, McBratney, 2005). If the range parameter *r* is large ($r \to \infty$), then the spatial process is approximated by the power function when κ > 0, and a log function or de Wijs function if κ → 0 (de Wijs, 1951, 1953). Calculations are made using geoR library (Paulo et al., 2016).

The nugget to sill ratio is an indicator of the strength of the spatial autocorrelation. A variable is considered to have a strong spatial dependence if the ratio is less than 25%, and has a moderate spatial dependence if the ratio is between 25 and 75%; otherwise, the variable has a weak spatial dependence (Sun et al., 2003).

Map accuracy, cross-validation, ME, NRMSE, and MSDR

To measure the accuracy of differential entropy maps, we use the cross-validation procedure and consequently, we compute the normalized root mean squared error (NRMSE), mean error (ME) and mean squared deviation ratio (MSDR) (Vašát et al., 2013). Mean squared error (RMSE) was calculated as follows:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(x_{1,i} - x_{2,i})^2}{n}} .$$

Normalized root mean squared error (NRMSE) was calculated as follows:

$$NRMSE = \frac{RMSE}{x_{1,max} - x_{1,min}} .$$

Mean error (ME) was calculated as follows:

$$ME = \frac{\sum_{i=1}^{n}(x_{1,i} - x_{2,i})}{n} .$$

Mean squared deviation ratio (MSDR) was calculated as follows:

$$MSDR = \frac{\sum_{i=1}^{n}\left[\frac{(x_{1,i} - x_{2,i})^2}{var_i}\right]}{n}.$$

Where x_1 is a prediction of the variable X; x_2 is a measure of that variable; *n* is the number of records; *var* is a kriging variance. The smaller the NRMSE and ME values, the more accurate the map. The MSDR indicates whether the variance of measurement data is well reproduced with the kriging interpolation, and ideally, it equals to 1 (Vašát et al., 2013). The *R*-squared of the regression between the observed and predicted after cross validation values was used as they are very intuitive. Cross-validation procedure was performed using the function *xvalid* from the package geoR library (Paulo et al., 2016).

Results

In the soil of the studied polygon, 38 species of soil invertebrates were found, which characterises the gamma diversity : (2.5% quantile is 34.2, 97.5% quantile is 41.2) (Fig. 2). Alpha diversity, or the number of species on average in each sampling point is 4.3 (2.5% quantile is 4.2, 97.5% quantile is 4.5). Beta diversity is 8.8 (2.5% quantile is 8.0, 97.5% quantile is 9.6).

The abundance of soil macrofauna was 197.8 ± 27.9 ind./m^2 (Table 1). The endogeic earthworm *Aporrectodea rosea* was the dominant species in the macrofauna community. Endogeic *A. trapezoides*, epigeic *Dendrobaena octaedra* and anecic *Octodrilus transpadanus* were represented in the community. Millipedes were represented by four species, with domination of endogeic Geophilidae compared to epigeic Lithobiidae. There was a variety of soil insects,

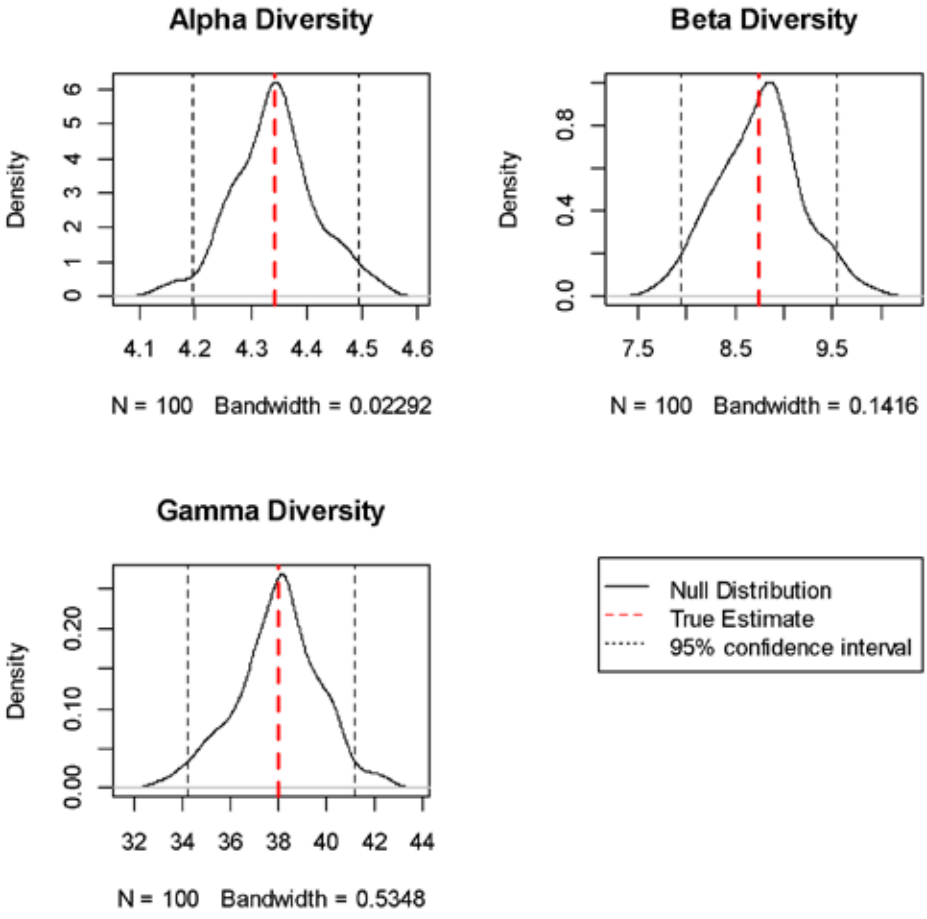

Fig. 2. Alpha, beta and gamma diversity of soil macrofauna.

among which were both imagoes and larvae. Molluscs were represented by five species, but their abundance was not great.

Beta diversity of the community may be affected by edaphic and (or) vegetation factors. Principal component analysis of the edaphic indicators revealed 9 principal components, having eigenvalues greater than 1. Using the Horn procedures, we found that the first four principal components are statistically significant. These components describe 64.2% of the total variation of the edaphic indicators. Principal component 1 is correlated with the soil mechanical impedance at a depth of 35–100 cm, litter depth, density and electric conductivity of the soil and the content of the roots and aggregate fractions of size < 0.25–1 mm and 5–10 mm (Table 2). Principal component 2 is correlated with the soil mechanical impedance

T a b l e 1. Taxonomic composition and abundance of soil macrofauna.

Taxons		**Density, ind./m² ± st. error**
Phylum Annelidae Class Oligohaeta Order Haplotaxida		
Family Lumbricidae	*Aporrectodea caliginosa trapezoides* (Duges, 1828)	9.90 ± 1.39
	Aporrectodea rosea rosea (Savigny, 1826)	117.49 ± 8.15
	Dendrobaena octaedra (Savigny, 1826)	15.54 ± 2.27
	Octodrilus transpadanus (Rosa, 1884)	5.64 ± 1.17
Order Tubificida		
Family Enchytraeidae	*Enchytraeus albidus* Henle 1837	7.92 ± 1.56
Phylum Arthropoda Class Arachnida Order Araneae		
Family Lycosidae	*Pardosa lugubris* (Walckenaer 1802)	0.91 ± 0.42
Class Chilopoda Order Geophilomorpha		
Family Geophilidae	*Geophilus proximus* C.L.Koch 1847	3.96 ± 1.00
	Pachymerium ferrugineum (C.L.Koch 1835)	1.83 ± 0.56
Order Lithobiomorpha		
Family Lithobiidae	*Lithobius (Monotarsobius) aeruginosus* L. Koch 1862	0.91 ± 0.42
	Lithobius (Monotarsobius) curtipes C.L. Koch 1847	1.83 ± 0.59
Class Insecta Order Coleoptera		
Family Carabidae	*Amara (Amara) aenea* (De Geer 1774)	0.15 ± 0.15
	Amara similata (Gyllenhal, 1810)	2.29 ± 0.85
	Calathus (Calathus) fuscipes (Goeze, 1777)	0.15 ± 0.15
	Carabus (Cancellocarabus) cancellatus Illiger, 1798	0.30 ± 0.30
Family Cetoniidae	*Cetonia aurata* (Linnaeus 1761) (larvae)	0.46 ± 0.33
Family Chrysomelidae	*Chrysolina (Fastuolina) fastuosa* (Scopoli 1763) (larvae)	0.76 ± 0.32
Family Curculionidae	*Otiorhynchus (Cryphiphorus) ligustici* (Linnaeus 1758) (larvae)	0.30 ± 0.21
Family Elateridae	*Athous (Athous) haemorrhoidalis* (Fabricius 1801) (larvae)	6.70 ± 1.18
	Agriotes (Agriotes) lineatus (Linnaeus 1767) (larvae)	0.15 ± 0.15
	Cardiophorus rufipes (Goeze, 1777) (larvae)	0.46 ± 0.26
Family Staphylinidae	*Othius angustus angustus* Stephens 1833 (larvae)	0.15 ± 0.15
	Othius punctulatus (Goeze 1777) (larvae)	0.15 ± 0.15
Family Tenebrionidae	*Helops coeruleus* (Linnaeus 1758) (larvae)	0.30 ± 0.22
Family Melolonthidae	*Anoxia pilosa* (Fabricius 1792) (larvae)	0.30 ± 0.21
	Melolontha melolontha (Linnaeus 1758) (larvae)	2.29 ± 0.58
	Serica brunnea (Linnaeus 1758) (larvae)	0.46 ± 0.26
Order Dermaptera		
Family Forficulidae	*Forficula auricularia* Linnaeus 1758	0.61 ± 0.31
Order Diptera		
Family Rhagionidae	*Rhagio scolopaceus* (Linnaeus 1758) (larvae)	4.88 ± 1.21
Family Stratiomyidae	*Stratiomys longicornis* (Scopoli 1763) (larvae)	0.15 ± 0.15
Family Tabanidae	*Tabanus bromius* Linnaeus 1758 (larvae)	0.30 ± 0.21
Family Tipulidae	*Tipula (Lunatipula) lunata* Linnaeus 1758 (larvae)	3.66 ± 0.73
Order Lepidoptera		
Family Noctuidae	*Agrotis clavis* (Hufnagel 1766) (larvae)	5.03 ± 1.07
Class Malacostraca Order Isopoda		
Family Trachelipodidae	*Trachelipus rathkii* (Brandt 1833)	0.15 ± 0.15
Phylum Mollusca Class Gastropoda Order Pulmonata		
Family Cochlicopidae	*Cochlicopa lubrica* (O.F. Muller 1774)	0.15 ± 0.15
Family Helicidae	*Cepaea (Austrotachea) vindobonensis* (C. Pfeiffer 1828)	0.15 ± 0.15
Family Succineidae	*Succinella oblonga* (Draparnaud 1801)	0.61 ± 0.30
Family Valloniidae	*Vallonia pulchella* (O.F. Muller 1774)	0.15 ± 0.15
Family Vitrinidae	*Vitrina pellucida* (O.F. Muller 1774)	0.61 ± 0.30

T a b l e 2. Descriptive statistics and principal component analysis of the edaphic parameters (presenting statistically significant correlation coefficients with $p < 0.05$).

Parameters, mean ± st. error		**Principal components**			
		1	**2**	**3**	**4**
Soil mechanical impedance at depth, MPa					
0–5 cm	0.65 ± 0.01	–	–0.55	–	–
5–10 cm	0.76 ± 0.02	–	–0.76	–	–
10–15 cm	0.89 ± 0.04	–	–0.90	–	–
15–20 cm	0.96 ± 0.04	–	–0.91	–	–
20–25 cm	0.98 ± 0.04	–	–0.89	–	–
25–30 cm	0.95 ± 0.04	0.20	–0.84	–	–
30–35 cm	0.94 ± 0.03	–	–0.78	–	–
35–40 cm	1.04 ± 0.03	–0.41	–0.59	–0.26	–
40–45 cm	1.31 ± 0.03	–0.50	–0.42	–0.47	–
45–50 cm	1.56 ± 0.03	–0.66	–0.32	–0.32	–
50–55 cm	1.81 ± 0.04	–0.72	–0.33	–0.23	–
55–60 cm	2.02 ± 0.04	–0.82	–0.24	–	–
60–65 cm	2.28 ± 0.05	–0.79	–0.21	–	–
65–70 cm	2.41 ± 0.05	–0.87	–	–	–
70–75 cm	2.53 ± 0.05	–0.90	–	–	–
75–80 cm	2.59 ± 0.05	–0.89	–	–	–
80–85 cm	2.69 ± 0.06	–0.87	–	–	–
85–90 cm	2.72 ± 0.06	–0.90	–	–	–
90–95 cm	2.74 ± 0.07	–0.91	–	–	–
95–100 cm	2.84 ± 0.08	–0.84	–	–	–
Other edaphic parameters					
Litter depth, cm	3.40 ± 0.10	–0.35	0.55	–	–
Moisture, %	30.96 ± 0.69	–	–0.59	–	–
Bulk density, g/cm^3	0.98 ± 0.01	–0.71	0.58	–	–
Electrical conductivity, dSm/м	0.21 ± 0.01	–0.35	0.55	–	–
Aggregate fractions (mm) and plant roots content, %					
> 10	12.91 ±0.71	–	–	0.86	–
7–10	7.28 ± 0.28	–0.24	–	0.64	–
5–7	9.81 ± 0.35	–0.26	–	–	0.52
3–5	23.13 ± 0.85	–	–	–0.54	0.58
2–3	27.68 ± 0.82	–	–	–0.79	–
1–2	13.96 ± 0.86	–	–	–0.66	–0.41
0.5–1	1.37 ± 0.12	0.27	–	–0.44	–0.60
0.25–0.5	2.29 ± 0.29	0.22	–	–0.35	–0.61
< 0.25	0.61 ± 0.09	0.37	–	–0.27	–0.66
Roots	0.95 ± 0.08	0.25	–	–	0.36
Eigen values		9.42	6.72	3.23	2.47
% total variation		27.71	19.77	9.50	7.27

Notes: Litter – thickness, cm; Moisture – moisture of soil, %; Density – soil density, g/cm3; E – electronic conductivity of the soil, d Sm/M.

T a b l e 3. Descriptive statistics and principal component analysis of the vegetation parameters (presenting statistically significant correlation coefficients with $p < 0.05$).

Parameters, mean ± st. error		Principal components					
		1	2	3	4	5	6
Diduh scales							
Hd	9.20 ± 0.13	–0.21	–	–0.69	–	–	–
fH	5.16 ± 0.10	–0.53	0.50	–0.24	0.37	–	–
Rc	6.11 ± 0.14	–0.39	–	–0.26	0.26	–0.50	–0.47
Sl	7.10 ± 0.10	–	–0.49	–	0.41	–0.65	–
Ca	4.97 ± 0.23	–0.84	–	0.21	–	–	–
Nt	12.21 ± 0.12	0.60	–	0.19	–0.53	–0.33	–0.20
Ae	5.50 ± 0.16	–	0.37	–0.51	–0.36	–	–
Tm	11.18 ± 0.06	0.38	–	0.48	–	–	–
Om	12.56 ± 0.13	0.71	0.21	–0.49	–	–	–
Kn	7.05 ± 0.20	–0.86	–	0.30	–	–0.22	–
Cr	9.93 ± 0.10	0.27	0.56	–	0.43	–	0.30
Lc	5.30 ± 0.15	–0.72	–	–0.21	–	–	–0.26
Indexes based on Belgard's ecomorphs							
Troph	2.28 ± 0.02	–0.26	0.57	–	–0.46	–0.39	0.32
Hygr	3.23 ± 0.03	0.25	–	0.84	–	–	–
Hel	3.00 ± 0.01	–0.78	–0.31	–	–	0.40	–
Ellenberg scales							
Light Regime	6.79 ± 0.03	–0.52	–0.66	–	–	0.34	–
Temperatures	5.80 ± 0.02	–0.70	–	–	–0.33	–0.45	–
Continentality of Climate	5.31 ± 0.04	–0.81	–0.37	–	–	–	0.24
Humidity	5.15 ± 0.02	0.71	–0.33	–	0.23	–	0.29
Acidity	6.02 ± 0.02	–	–0.51	0.69	0.29	–	–0.23
Nutrients Availability	6.74 ± 0.08	0.89	–	0.23	–	0.20	–
Raunkiaer's life forms							
Ph	0.34 ± 0.011	0.20	–0.30	–0.78	–	–0.22	0.40
nPh	0.27 ± 0.011	–	–0.84	–	–	–	–0.40
HKr	0.28 ± 0.012	–	0.59	0.50	0.42	–	0.22
T	0.10 ± 0.007	–	0.62	0.31	–0.44	0.14	–0.28
G	0.01 ± 0.002	–0.32	0.44	–0.39	–	0.29	–0.28
Eigen values		7.19	4.21	3.96	2.01	1.77	1.48
% total variation		27.64	16.19	15.22	7.74	6.79	5.6

Notes: Hd – soil water regime; fH – variability of damping; Rc – soil acidity; Sl – total salt regime; Ca – carbonate content in soil; Nt – nitrogen content in soil; Ae – soil aeration; Tm – thermoregime; Om – humidity; Kn – continentality of climate; Cr – cryo-climate; Lc – lighting scale; Hygr – humidity level by hygromorphic structure; Troph – nutrient status level by trophomorphic structure; Hel – level of illumination by the geoliomorphic; Ph – phanerophytes; nPh – nanophanerophytes; HKr – hemicryptophytes; T – therophytes; G – geophytes.

at a depth of 0–65 cm and some other edaphic parameters. Principal component 3 correlated with soil mechanical impedance at a depth of 35–55 cm and a content of aggregate fractions of size < 0.25–5, 7–10 and > 10 mm. Principal component 4 is correlated with the content of roots and aggregate fractions < 0.25–2 and 3.7 mm.

Principal component analysis of plant indicators identified 7 principal components, the eigenvalues of which are greater than 1. Using the Horn procedure, we found that the first six principal components were statistically significant. These components describe 73.6% of the total variation in the vegetation indicators (Table 3). The first principal component is characterized by the greatest correlation with the level of carbonates in the soil, as well as scales of continentality and illumination. This component is meaningful and can be interpreted as the ecotone effect. Principal component 2 is characterized by a positive correlation with phanerophites and nanophanerophites and negative correlation with other life forms according to Raunkiaer's classification. Thus, the principal component 2 represents the ratio between the herbaceous layer, on the one hand, and the shrub layer (to a lesser extent with forest stands), on the other hand. Correlation with other environmental factors reveals the contents of the processes associated with the specified value. The principal component 3 is correlated with phanerophytes; this allows us to interpret it as the forest stand density. The humidity, acidity, ecotope aeration, as well as some other ecological factors are connected with forest stand density. The principal component 4 is characterized by the greatest correlation with soil nitrogen content. The principal component 5 can be interpreted as the mineralization of the soil solution. The principal component 6 most likely represents the level of soil solution acidity.

The principal components are orthogonal, that is, mutually independent. However, vegetation and edaphic principal components can be correlated (Table 4). Only the principal component 6 is independent and reflects plant community properties only, since it is not correlated with the edaphic principal components. The edaphic principal components always correlate with vegetation principal components. These results indicate the complexity of the interaction between soil and vegetation.

On the basis of the MDM-approach, we evaluated the role of edaphic principal components in the partitioning of the macrofauna community β-diversity (Table 5). The results indicate that the γ-diversity is 1.71 bits, and a α-diversity is 0.91 bit. We found that 20.9% (0.81 bit) of β-diversity was caused by the edaphic factors. The largest decrease in community entropy took place under the action of principal components 2 and 3 (0.06 bit and 0.05 bit, respectively). The permutation test reveals that these effects are statistically significant. The influence of the principal component 1 and 4 is lower and is not statistically significant.

In turn, 28.4% of community β-diversity was caused by the plant factors (Table 6). The greatest decrease in community entropy is related to vegetation principal components 1, 3 and 4 (0.07, 0.05, 0.04 bits, respectively). The permutation test reveals that these effects are statistically significant. The effect of principal components 2, 5 and 6 are not statistically significant.

The effect of ecological factors leads to a change in the entropy of the community. This change can be positive, and then the factor information is transferred to the community. Or a change can be negative, and then the community is sent misinformation. Between the

T a b l e 4. Correlation matrix of the edaphic and vegetation principal components (presenting statistically significant correlation coefficients with $p < 0.05$).

		Vegetation principal components					
		Ph_1	**Ph_2**	**Ph_3**	**Ph_4**	**Ph_5**	**Ph_6**
Edaphic principal components	**Ed_1**	–	–0.20	–0.48	–	–	–
	Ed_2	0.37	–0.21	0.37	–	–0.34	–
	Ed_3	–	–	0.20	–	–	–
	Ed_4	–	–	–	0.22	–0.24	–

T a b l e 5. The analysis of deviance, entropy and diversity under edaphic impact on macrofauna on the basis of MDM-approach.

Model	**df**	**Δdf**	**Dev**	**ΔDev**	**Ent**	**ΔEnt**	**p–level**	**Div**	**ΔD**
γ-diversity	3432	–	359.5	–	1.71	–	–	5.54	–
Ed1	3399	33	353.8	5.74	1.69	0.03	0.37	5.39	1.03
Ed1+Ed2	3366	33	340.8	12.96	1.62	0.06	0.00	5.07	1.06
Ed1+Ed2+Ed3	3333	33	330.6	10.27	1.57	0.05	0.00	4.83	1.05
Ed1+Ed2+Ed3+Ed4	3300	33	324.3	6.25	1.54	0.03	0.29	4.69	1.03
α-diversity	0	3300	190.2	134.18	0.91	0.64	0.01	2.47	1.89

Notes: Ed1–4 – edaphic principal components; df – degrees of freedom; Δdf – changes in df; Dev – deviance; ΔDiff – changes in deviance; Ent – entropy; ΔEnt – changes in entropy; *p*–level – the significance level based on sequential permutation tests; Div – diversity; ΔD – proportional change in diversity.

T a b l e 6. The analysis of deviance, entropy and diversity under vegetation impact on macrofauna on the basis of MDM-approach.

Model	**df**	**Δdf**	**Dev**	**ΔDev**	**Ent**	**ΔEnt**	**p–level**	**Div**	**ΔD**
γ- diversity	3432	–	359.5	–	1.71	–	–	5.54	–
Ph1	3399	33	344.1	15.48	1.64	0.07	0.01	5.15	1.08
Ph1+Ph2	3366	33	337.9	6.20	1.61	0.03	0.28	5.00	1.03
Ph1+Ph2+Ph3	3333	33	328.3	9.56	1.56	0.05	0.02	4.78	1.05
Ph1+Ph2+Ph3+Ph4	3300	33	320.1	8.16	1.52	0.04	0.05	4.59	1.04
Ph1+Ph2+Ph3+Ph4+Ph5	3267	33	316.3	3.84	1.51	0.02	0.87	4.51	1.02
Ph1+Ph2+Ph3+Ph4+Ph5+Ph6	3234	33	311.4	4.90	1.48	0.02	0.57	4.41	1.02
α-diversity	0	3234	190.2	121.25	0.91	0.58	0.01	2.47	1.78

Notes: Ph1–Ph6 – edaphic principal components; df – degrees of freedom; Δdf – changes in df; Dev – deviance; ΔDiff – changes in deviance; Ent – entropy; ΔEnt – changes in entropy; *p*–level – the significance level based on sequential permutation tests; Div – diversity; ΔD – proportional change in diversity.

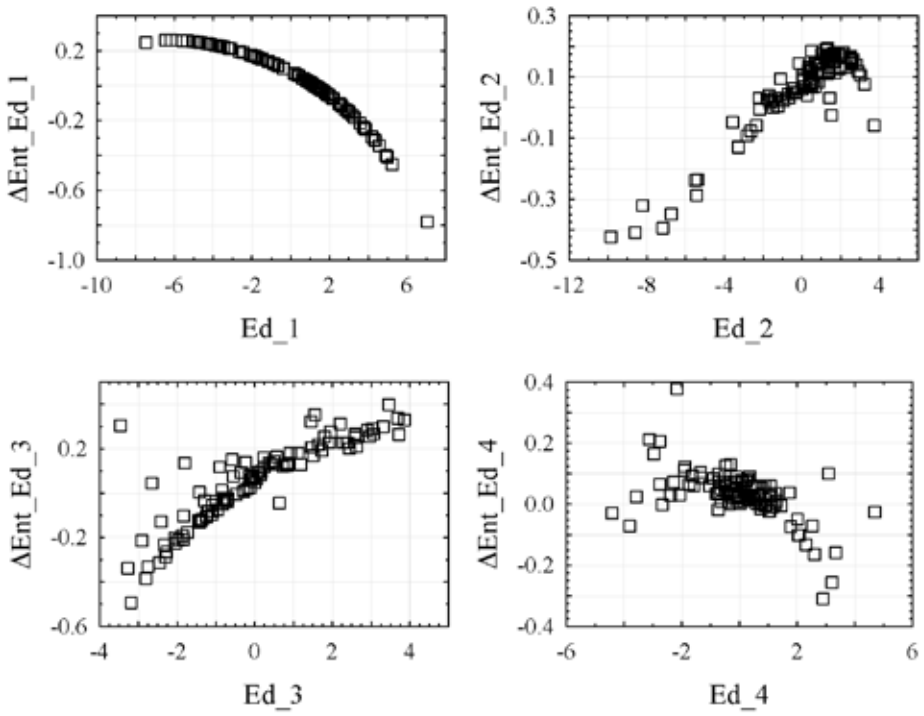

Fig. 3. Dependence of differential entropy on edaphic principal component scores.

values of the edaphic principal components, which reflect the cumulative variation of soil properties , and changes of entropy in each site, there is a dependency (Fig. 3). For example, the positive values of the principal components 1 lead to misinformation of the community. On the other hand, negative values are perceived by the community as an organization factor. Thus, the effects of ecological factors on the macrofauna community do not occur across the full range of values of the ecological factors. All dependencies are nonlinear, indicating that the there is a range of values of the principal components, when the highest amount of information is transmitted. In other words, when the community is most sensitive to the corresponding principal components.

Similar results were obtained for the dependence of entropy change of the vegetation principal component values (Fig. 4). All principal components have a range of values of the principal component, when the community receives misinformation. Also, for certain values of principal components, the transmitted information reaches the maximum values.

The MDM-approach evaluates the components of entropy by sites. This provides a good opportunity to examine how changes in entropy vary in geographic space (Figs 5, 6). Within the study area, for each of the principal components, areas can be distinguished within which

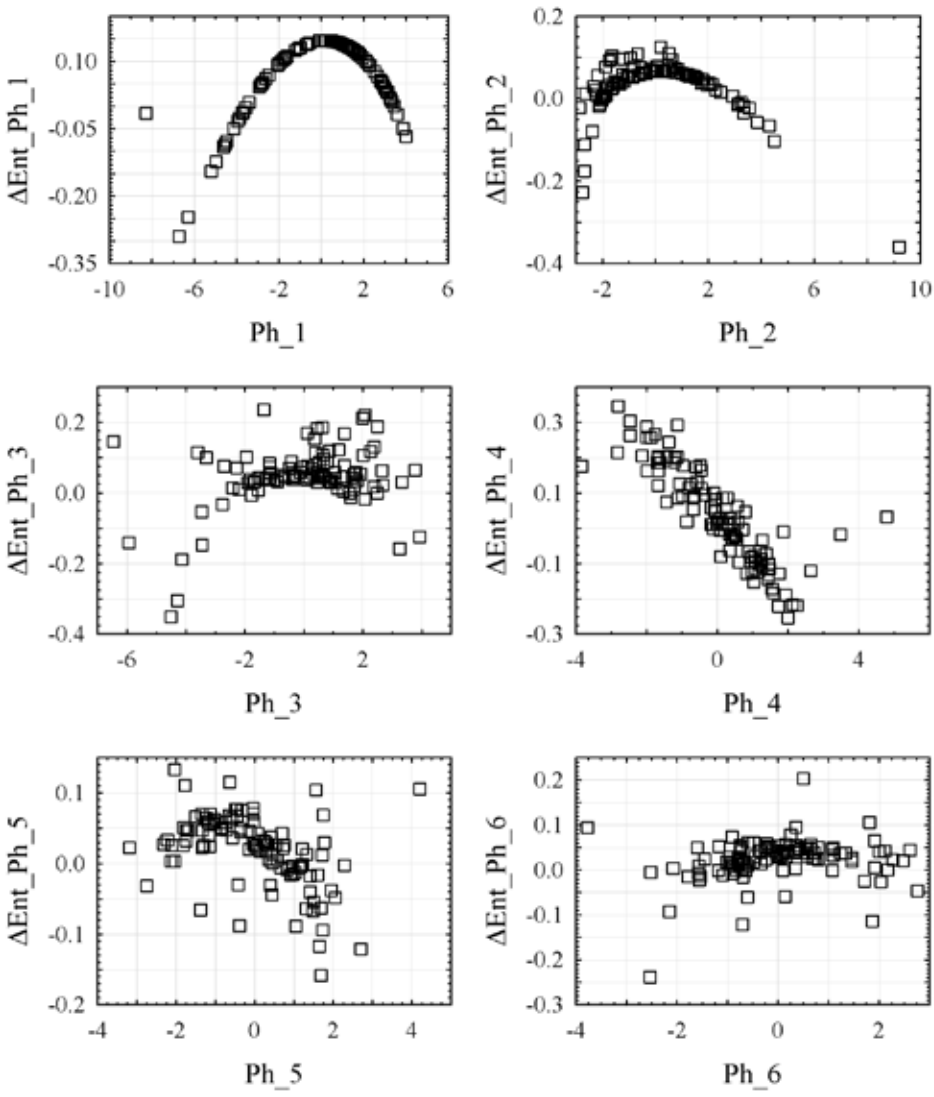

Fig. 4. Dependence of differential entropy on vegetation principal component scores.

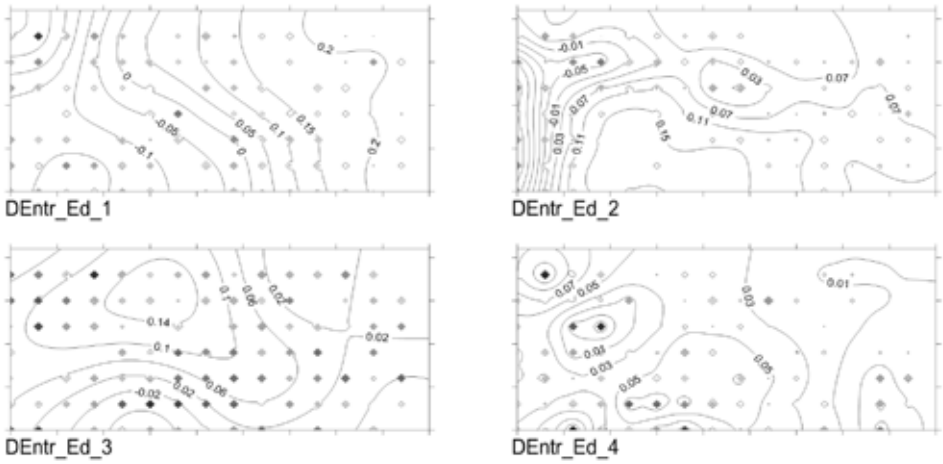

Fig. 5. Spatial variation of differential entropy under influence of the edaphic principal components.

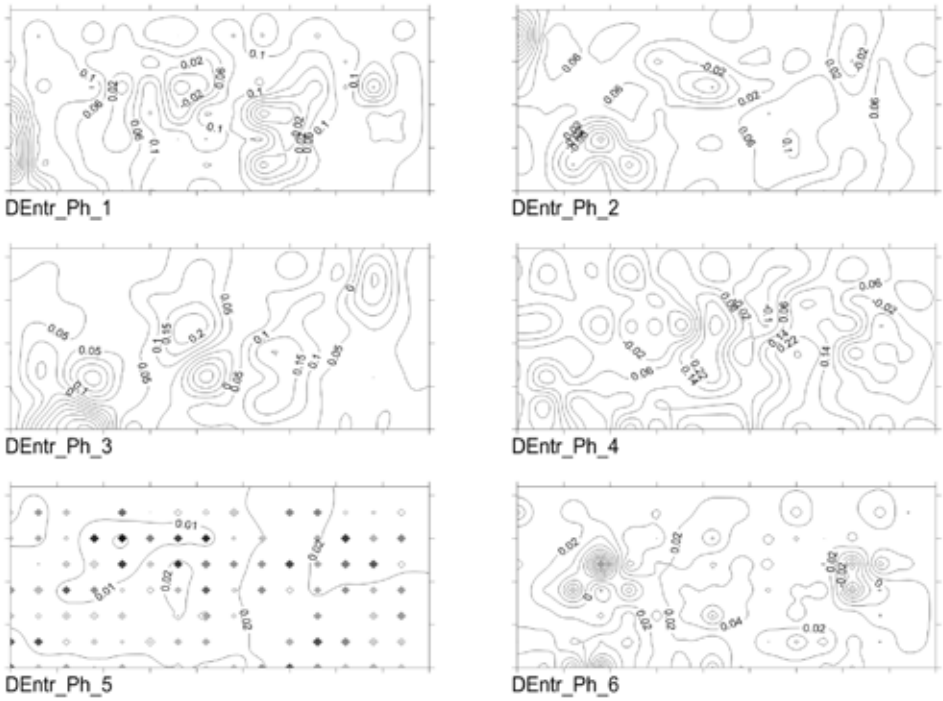

Fig. 6. Spatial variation of differential entropy under influence of the vegetation principal components.

T a b l e 7. Geostatistics of the spatial variation in the entropy change under the influence of edaphic and vegetation factors.

PC	Phi	Pr_Range	Sill	Nugget	SDL	Kappa	NRMSE	ME*10^{-5}	MSDR	R^2
Edaphic principal components										
Ed1	9.86	39.98	0.03	0.0097	23.92	1.03	0.11	5.50	0.38	0.61
Ed2	3.67	10.98	0.01	0.0064	41.41	0.50	0.16	-2.44	0.56	0.49
Ed3	1.55	15.59	0.01	0.0271	70.20	8.00	0.20	-2.53	0.95	0.05
Ed4	23.00	196.15	0.04	0.0056	11.15	5.60	0.12	-0.14	1.01	0.00
Alpha	0.20	0.12	0.13	0.0831	38.64	0.03	0.18	0.00	1.01	0.00
Vegetation principal components										
Ph1	22.69	113.55	2.53	0.0029	0.11	1.70	0.13	4.49	0.79	0.25
Ph2	5.66	30.14	8.07	0.0000	0.00	1.97	0.09	-15.99	1.44	0.09
Ph3	21.62	135.25	71.01	0.0002	0.00	2.83	0.06	4.38	0.55	0.47
Ph4	28.22	150.39	92.87	0.0004	0.00	1.97	0.21	23.24	2.03	0.01
Ph5	19.33	61.03	0.00	0.0025	81.58	0.57	0.17	1.18	0.96	0.03
Ph6	1.00	3.45	0.00	0.0001	3.83	0.70	0.11	0.20	1.01	0.00
Alpha	27.67	45.20	0.09	0.17	66.76	0.13	0.19	6.55	0.99	0.01

Notes: Phi is the range or distance parameter of the Mattern model; Pr_Range is a practical range; Kappa is a smoothing parameter; the nugget is the y-intercept of the graph, the sill is the semivariogram value (y value) where each graph becomes a plateau, the range is the distance (x value) where the plateau begins, and the spatial dependence level SDL ((Sill-Nugget)/Sill) is the ratio of structural to population variance, R^2 of cross-validation.

the relevant ecological factor has a structuring effect on the macrofauna community. Also, there are areas within which the ecological factor transmits misinformation to the community. The spatial patterns of the entropy changes are different under the influence of specific ecological factors.

Geostatistical models best describe the variation of entropy change induced by edaphic principal components 1 and 2 (Table 7). These models respectively describe 61 and 49% of their variation. The impact of principal component 1 on entropy change has a strong spatial dependence (SDL = 23.90%). The impact of principal component 2 has a moderate spatial dependence (SDL = 41.41%). The Mattern model can be regarded as a generalization of a number of theoretical variogram models (Minasny, McBratney, 2005). The geostatistical model of principal component 1 is closest to the Whittle function, as in the general Mattern model kappa = 1.03 (for the Whittle model kappa = 1) (Whittle, 1954). Spatial variation in differential entropy under the influence of the principal components 2 is best modelled by an exponential model for which kappa = 0.5 (Webster, Oliver, 2001; Minasny, McBratney, 2005). The effect on the community of edaphic components 3 and 4 has no significant spatial dependence or generally may be purely spatially modelled.

The spatial model best describes the effect of the vegetation principal components 1 and 3 on the soil macrofauna community (R^2 = 0.25 and 0.47 respectively). The impact of the vegetation principal components 1 and 3 on entropy change has a strong spatial dependence.

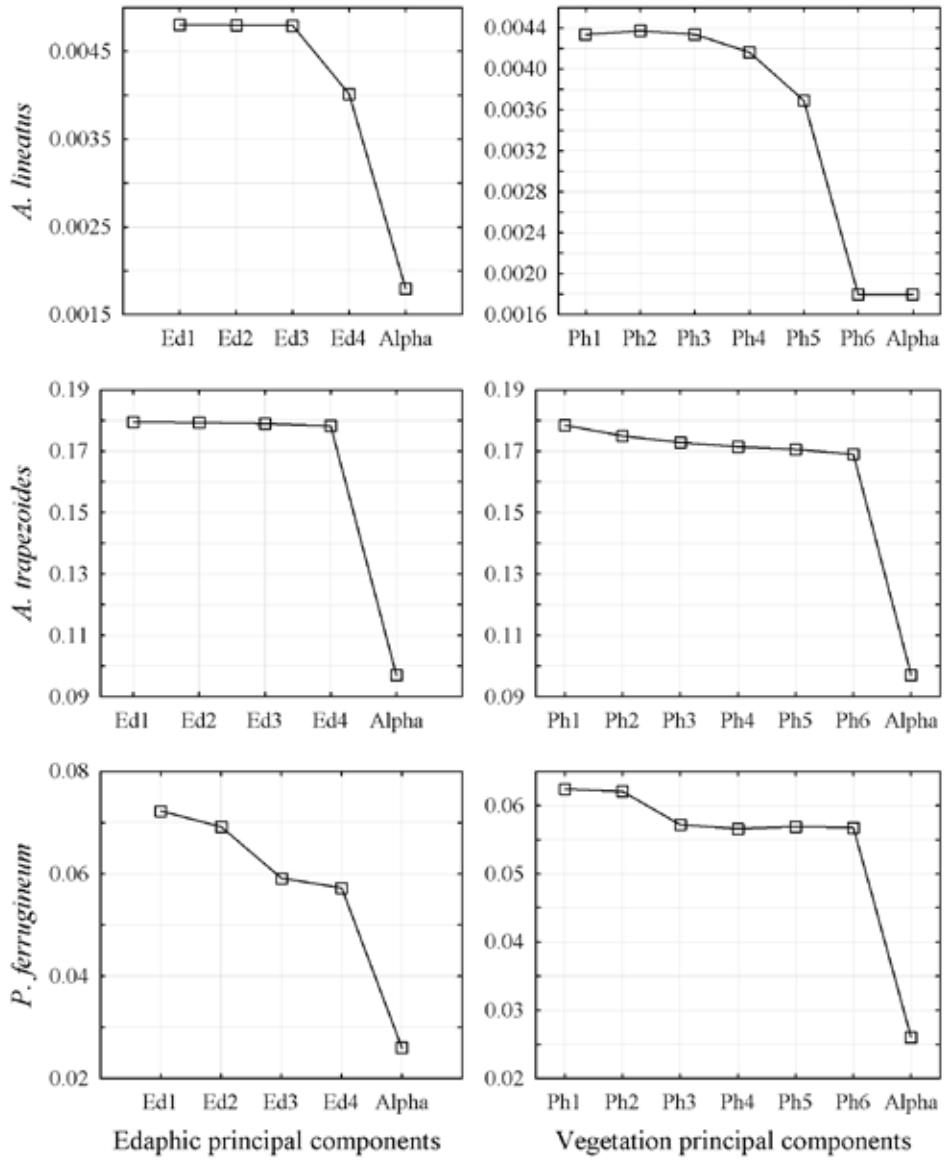

Fig. 7. Differential entropy for some species of soil invertebrates.

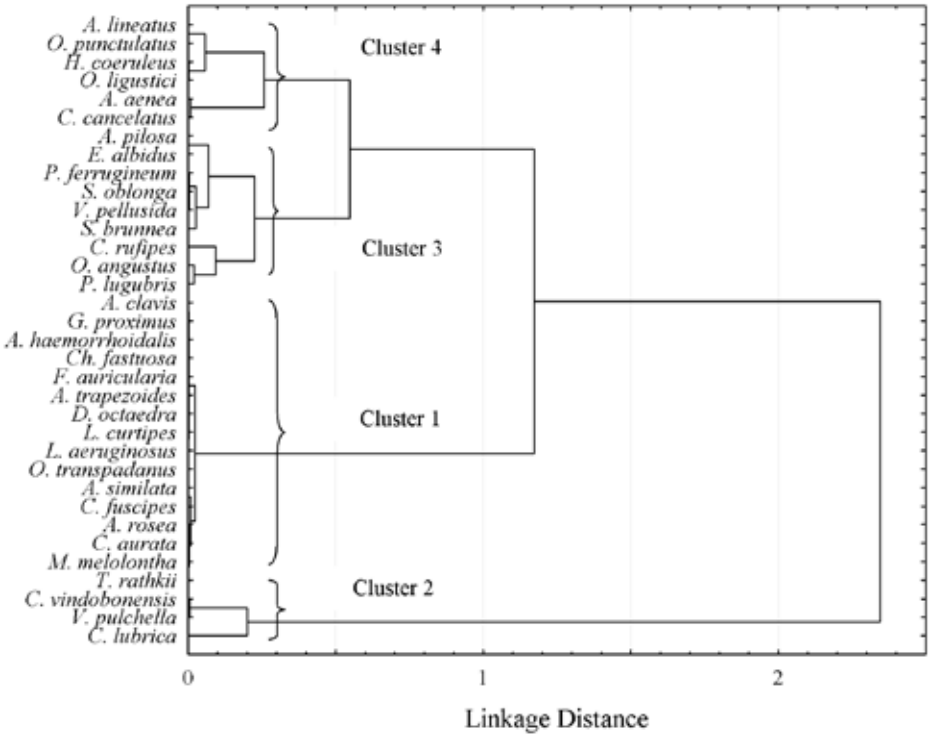

Fig. 8. Classification of macrofauna species on the basis of beta diversity transformation patterns under the influence of edaphic factors.

Parameter kappa indicates that the spatial patterns for the principal components 1 and 3 are smoother than the Whittle pattern.

The MDM-approach estimates the components of entropy by species (Fig. 7). The corresponding curves characterize the ecological features of the species that make up the community. According to the degree of similarity of these curves, one can perform a classification of the community by cluster analysis (Fig. 8). The cluster analysis of the species according to their response to the edaphic factors reveals four clusters. It is possible to build the integral curves of reaction to the environmental factors of the species included in each cluster. Cluster 1 combines the species for which edaphic factors have no effect on contribution to the total β-diversity of the community (Fig. 9). Cluster 2 combines the species sensitive to the action of the principal components 1 and 2. Cluster 3 combines the species in the community that are sensitive to all the principal components. Cluster 4 combines species sensitive to the action of principal components 3 and 4.

With respect to the influence of vegetation factors, the macrofauna species are classified into four clusters (Fig. 10). Cluster 1 combines species not susceptible to the action of

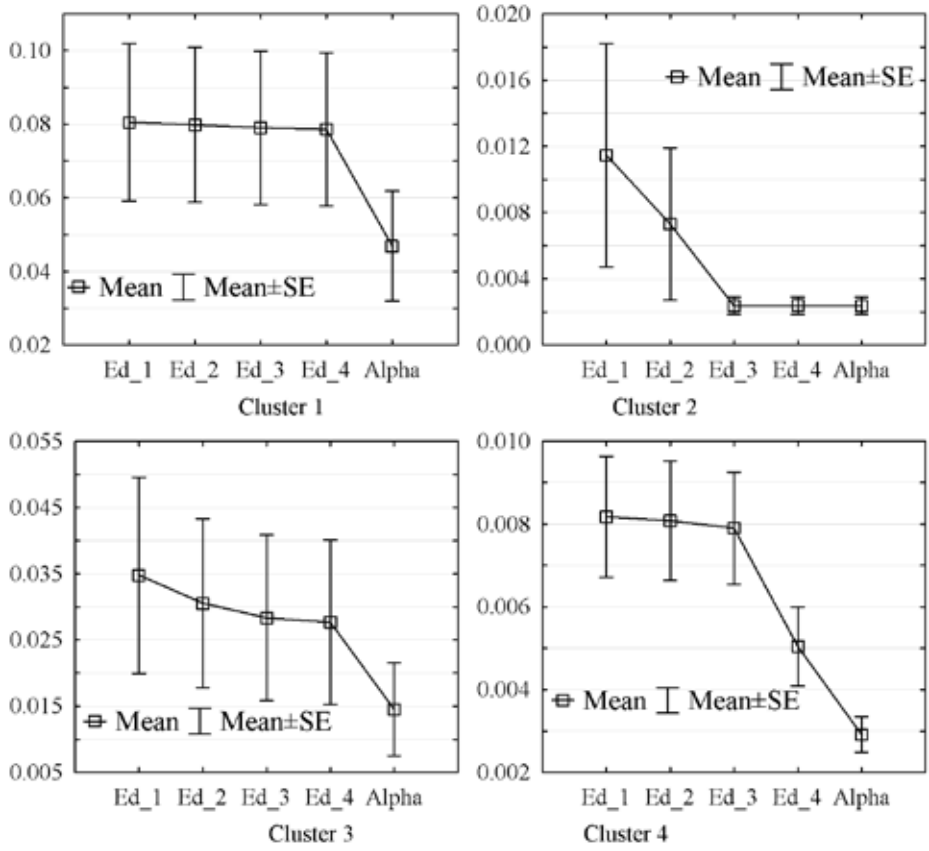

Fig. 9. Differential entropy under the influence of edaphic factors for clusters.

vegetation principal components within the studied site (Fig. 11). Species that are included in cluster 2 are sensitive to all vegetation principal components. Cluster 3 combines species sensitive to the action of vegetation principal components 1 and 2. Species included in cluster 4 are sensitive to principal components 1–5.

Discussion

The overall inertia of the tables of species occurrence has been demonstrated to be capable of corresponding with common diversity indices of species richness, such as the Simpson diversity, or the Shannon information index. This result allows one to examine from a general point of view the ordination techniques such as Correspondence Analysis, Non-Symmetric

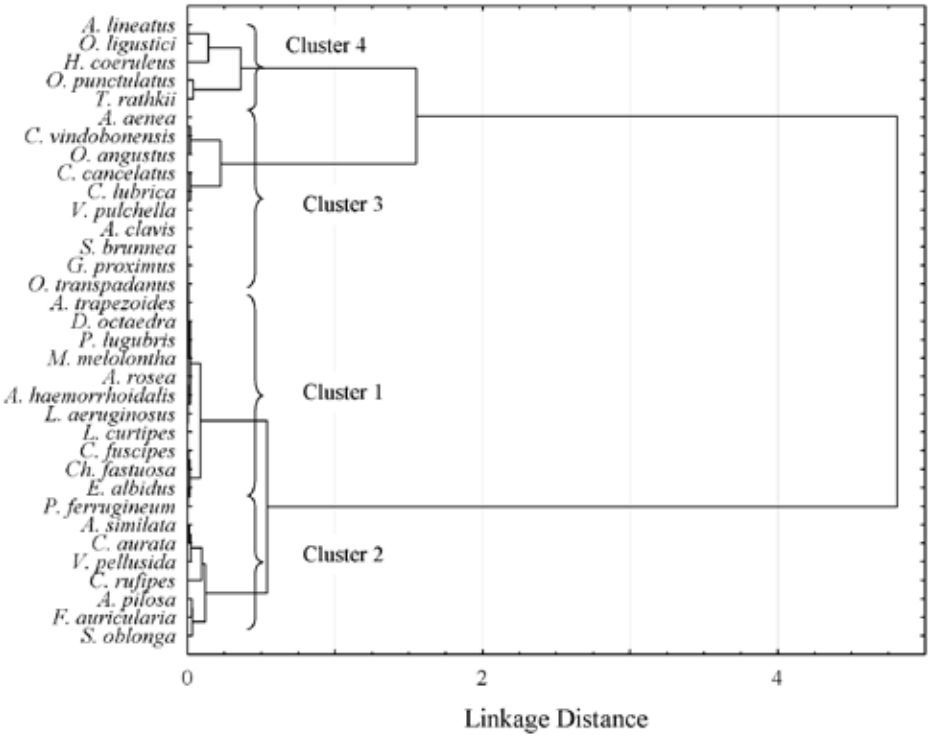

Fig. 10. Classification of macrofauna species on the basis of beta diversity transformation patterns under the influence of vegetation factors.

Correspondence Analysis, Canonical Correspondence Analysis, and Redundancy Analysis, and provides greater insight into interrelations between the ordination methods and diversity indexes (Pélissier et al., 2003). These interrelations explain why ordination techniques are widely used in studying beta diversity (Eggleton et al., 2005; Carpenter et al., 2012; Zbinden, Matthews, 2017). The multinomial diversity model (MDM) is a method for relating Shannon diversity to complex environmental, spatial and temporal predictors (De'ath, 2012).

In our work, we established the influence of plant and edaphic factors on beta diversity of a macrofauna community. Within the relatively restricted area of the studied polygon, beta diversity of the soil macrofauna community is 8.8 (2.5% quantile-8.0, 97.5%-9.6). We have shown that the effect of plant factors on beta diversity is greater than the effect of edaphic factors. It is notable that the edaphic principal component 1, which is dominant on level of variation, has no statistically significant effect on beta diversity of the macrofauna community. Probably, the reason for this is that the variation of relevant properties of edaphic properties is perceived by the community as a source of information and as a source of misinformation. Information increases the negative entropy and organizes community. In turn, the impact

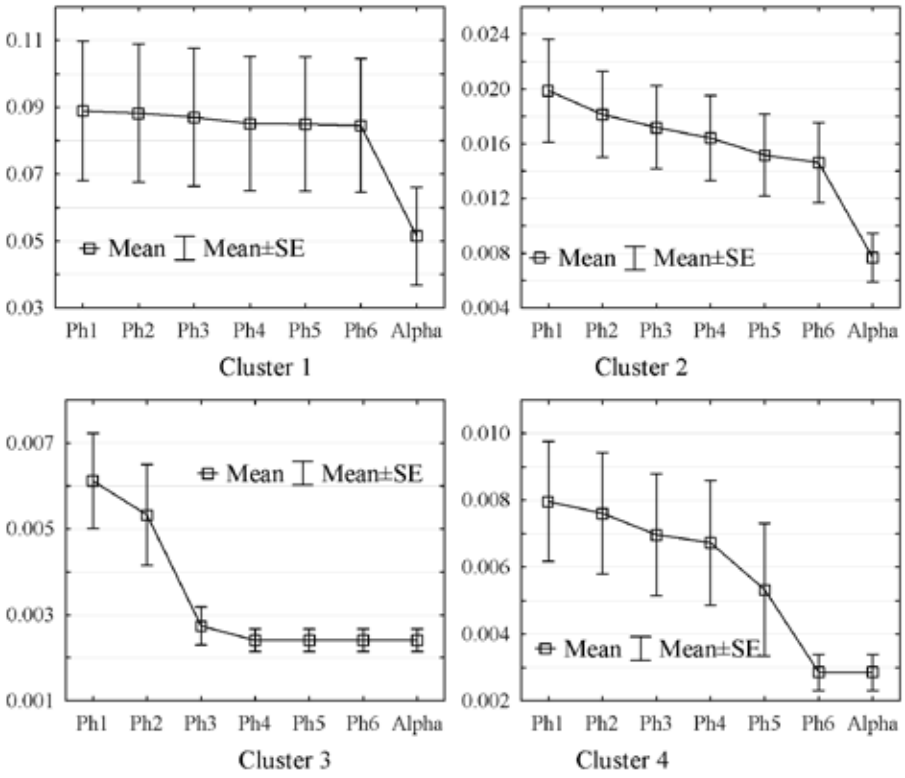

Fig. 11. Differential entropy under the influence of vegetation factors for clusters.

of misinformation increases entropy and disorder in the community. Only negative values of edaphic principal components 1 pass information to the community, whereas positive values are a source of misinformation. The edaphic principal component 1 is characterized by correlation with indicators of soil mechanical impedance at a depth of 35–100 cm. In the conditions of the floodplain at the specified depth, variation of the soil mechanical impedance can be a consequence of the mobility of the parent deposition. High soil mechanical impedance at relatively great depths may characterize the stable areas of the floodplain. Low soil mechanical impedance can be the result of the fact that the soil pores and cracks within moving parts of the floodplain are filled with loose material. Mechanical instability can lead to different scenarios of soil dynamics, to which soil animals react as to factors of disorganization of the community.

The edaphic principal components 2 and 3 are sensitive to the variations of the soil mechanical impedance at a depth of 0–65 and 35–55 cm. These dynamics of soil properties may be due to spatial variation of the vegetation structure. Plant and edaphic principal components are

correlated with each other. Statistics cannot confirm a causal relationship, but vegetation can be assumed to play a leading role in shaping soil ecological regimes at this scale level. This is also in line with the views on the factors of soil formation that ascribe the leading role to vegetation (Dokuchaev, 1883; Jenny, 1941; Bockheim et al., 2014).

The impact of vegetation principal components 1, 3 and 4 on the beta diversity of soil macrofauna community is statistically significant. Plants modify the microclimate in their vicinity by cooling down the soil and air in the shade of their leaves. They also modify humidity by intercepting wind and rain, and by absorbing water in the soil. As a consequence, vegetation creates specific physical conditions for the survival of macrofauna and influences the food availability regime (Jackson, Caldwell, 1993). The principal component 3 reflects the varying ecological regimes associated with an abundance of woody plants. There was a positive correlation between the diversity of the two groups but only at the local scale (single sample data), indicating that tree diversity can increase lumbricid diversity by the mechanism of creating small scale microhabitat diversity (Cesarz et al., 2007; Migge-Kleian et al., 2007).

The effect of vegetation principal component 2 on the soil macrofauna is not statistically significant. This component mainly reflects the ratio between nanophanerophytes and hemicryptophytes. Probably, the nature of the impact of these plant ecological groups on the soil environment is uniform and does not find its specific response in the community structure of soil macrofauna. The character of dependence of differential entropy on principal component 2 confirms this assumption (Fig. 4). The vegetation principal components 5 and 6 do not provide statistically significant effects on beta diversity of the soil macrofauna in view of the low level of the variability.

To determine the causes of community variation, it is necessary to link the scales at which variation is measured to the scales at which the processes potentially affecting diversity actually operate (Huston, 1999). In this regard, an important role is played by the spatial properties of the processes. Geostatistics provides an opportunity to assess the spatial distribution of the variability of environmental properties and soil organisms (Rossi et al., 1996; Rossi, 2003). Geostatistical models are sufficiently good at describing the varying effects on the beta-diversity of edaphic principal components 1 and 2 and the vegetation principal components 1 and 3. Effects of other principal components cannot be well described by geostatistical models in the framework of the chosen procedure. It is likely that to identify the relevant patterns, a detailed large-scale survey of the territory must be made.

It is worth taking into account the indicator differential entropy. This indicator reflects the sensitivity of beta-diversity of the community to the impact of external factors. Most often, attention is paid to the spatial characteristics of the soil properties (Jackson, Caldwell, 1993, 1996; Reza et al., 2016) or separate species (Gongalsky et al., 2009) or the community of living organisms (Gongalsky et al., 2008). Differential entropy characterizes the relationship between environmental factors and the community. Spatial structuring of differential entropy indicates that the community sensitivity to environmental factors is not uniform in space (Figs 5, 6).

In the framework of the MDM approach, the effects of the model can be expressed as changes in entropy. Entropy can be partitioned within and between sites, species and models, and changes in entropy can be attributed to model predictors (De'ath, 2012). We have found that soil macrofauna species vary in sensitivity to action of edaphic and vegetation factors. Similarities in these reactions serves as a basis for the classification of species. A significant group

of species is insensitive to the action of both edaphic (16 species) and vegetation factors (16 species). 12 species within the community are not sensitive to the action of both edaphic and vegetation factors. It can be assumed that these species are sensitive to these ecological factors on other spatial levels or that interspecies interaction plays an important role in the organization of the community represented by these species.

Conclusion

We found that edaphic and vegetation factors play an important role in structuring the soil macrofauna community on the level of beta diversity. The sensitivity of the community to environmental factors varies in space and is spatially structured. For edaphic and vegetation factors, specific spatial patterns of community sensitivity are allocated. Beta diversity may be due to the fact that the species of soil macrofauna community also vary in the degree of sensitivity to various environmental factors. A considerable part of the community is represented by the species indifferent to the impact of ecological factors within the studied spatial scale.

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