FOLIA OECOLOGICA – vol. 50, no. 1 (2023), doi: 10.2478/foecol-2023-0002

The role of soil and plant cover as drivers of soil macrofauna of the Dnipro River floodplain ecosystems

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Abstract

Kunakh, O., Zhukova, Y., Yakovenko, V., Zhukov, O., 2023. The role of soil and plant cover as drivers of soil macrofauna of the Dnipro River floodplain ecosystems. *Folia Oecologica*, 50 (1): 16–43.

Floodplain ecosystems are hotspots of biological diversity and perform important ecosystem functions in the landscape. The key to understanding the sustainability of ecosystem function is knowledge of the relationships between ecosystem components. The article reveals the role of morphological and physical properties of soil, as well as phytoindication of environmental factors as drivers of biological diversity of soil macrofauna of protected ecosystems of the Dnipro River floodplain. The studies were conducted in the forest floodplain ecosystems of the "Dnipro-Orilskiy" Nature Reserve. The studies of morphological properties of soils allowed us to identify the representatives of two reference groups: Fluvisol and Gleysol. The soil physical property data were subjected to principal component analysis, which extracted four principal components whose eigenvalues exceeded unity and described 79.9% of the variation in traits. The principal components of variation in soil physical properties and phytoindication assessments of environmental factors were used as predictors of the community structure of soil macrofauna. These predictors were able to explain 29.6% of the community variation. Physical soil properties are most important as a driver of soil macrofauna. The morphological properties of the soil and phytoindicator assessments are able to explain a much smaller part of the community variation. The pure influence of the predictors is small, indicating that they interact significantly in influencing soil animals. The results obtained have implications for the development of optimal strategies for floodplain ecosystem management and biodiversity conservation.

Keywords

biodiversity, landscape management, nature conservation, phytoindication, temporal dynamics, zoological diagnostics

Introduction

Floodplain ecosystems play an important role in the functioning of landscapes (Thoms, 2003). Ecosystems located in river valleys perform important ecological functions. They stabilize the intensity of floods, thus protecting the adjacent areas, contribute to the process of self-purification of water and provide the preservation of many unique species of plants and animals (Naiman et al., 2005). A knowledge of the relationship between soil cover, vegetation, and animal communities is essential to understanding the processes of floodplain ecosystem functioning. Floodplain soils are azonal, whose development is closely related to the surrounding geospatial variations and

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the nature of the rivers (Rodrigo-Comino et al., 2021). The high level of vertical and horizontal heterogeneity of floodplain soils is due to the variability of properties of alluvial sediments, sedimentation regime, age of formation, intensity and duration of floods (Kercheva et al., 2017). The physical properties of alluvial soils are subject to considerable spatial variability. Geostatistical analysis showed that the spatially dependent stochastic component is dominated by the nugget effect. Analysis and interpretation of the spatial variability of alluvial soils is an important prerequisite for the application of precision agriculture in floodplain landscapes (Iqbal et al., 2005). The soil morphological properties reflect the genesis of soils and are formed over time, which is commensurate with the duration of the most important soil-forming processes (Mansyur et al., 2019; Veneman and Bodine, 1982).

Riparian forests are the most diverse and productive in nature (Capon and Dowe, 2007). In the steppe zone, floodplains of rivers occupy a small part of the whole territory (Goncharenko et al., 2020), but they provide a place of concentration of regional biodiversity and diversity of soil cover (Globevnik et al., 2020). The floodplain ecosystems are very dynamic, since they are affected by floods (Talbot et al., 2018). These systems function under conditions of varying water (Bouska et al., 2020; Doering et al., 2021), salt (Didukh et al., 2015; Dubyna et al., 2020) and air regimes (Kolesnikova et al., 2016) and the impact of erosion processes of varying intensity (Arnaud-Fassetta et al., 2009; Hohensinner et al., 2022). The specificity of the species composition of plant communities in floodplain forests can be maintained only with regular flooding (Glaeser and Wulf, 2009). The anthropogenic impact on any component of the landscape catena is reflected in the dynamics of floodplain ecosystems (Gritsan et al., 2019). The floodplain ecosystems are sensitive to changes and processes that are in other parts of the landscape and in a broad sense are a mirror of the landscape as a whole (Tockner et al., 2010). The floodplain ecosystems form a mosaic of biotic cover, which depends on external influences and on the interaction of soil, vegetation and soil biota (Stanford et al., 2005). The elements of the habitat mosaic have a different time of existence after emergence and may disappear naturally or as a result of catastrophic events (Simioni et al., 2019). Solving the problem of managing floodplain ecosystems that are under anthropogenic influence is possible based on an understanding of the interactions between the various biotic components of ecosystems and soil cover (Schindler et al., 2016; Vári et al., 2022). The important role in procedures of development of optimum management strategies is played by protected floodplain ecosystems, which can be considered as a reference pattern of interaction between various components of an ecosystem (Kiedrzyńska et al., 2015; Serra-Llobet et al., 2022).

Floodplain ecosystems have an important economic value (Gren et al., 1995). However, the dynamic nature of floodplains creates conditions when opportunities for human economic activity are severely limited. Such locations become natural reserves of biological diversity (Schindler et al., 2013). To effectively use the resources of floodplain ecosystems, consensus solutions must be implemented and biodiversity must be incorporated into management activities to maximize the provision of ecosystem services and potential human benefits (Schindler et al., 2016). The application of these results to landscape management issues is what attracts particular attention to soil macrofauna. Typically, the soil macrofauna is not a popular target for biodiversity conservation. When selecting species for protection, an emotional component plays an important role. Red lists of rare and endangered species include mainly mammals, birds, butterflies, large beetles. In the Red book of Ukraine from the soil macrofauna only one species of earthworm is presented (Pindrus, 2009), one species of Chilopoda (Tarashuko, 2009) there are no species of spiders, woodlice. However, the high functional potential of soil animals should be noted, which is of interest for their protection (Ayuke, 2010; Sofo et al., 2020). The maintenance of a high level of abundance and species diversity of soil animal communities allows the promotion of the functions performed by them (Asfaw and Zewudie, 2021; Zulu et al., 2022).

Soil macrofauna affects the dynamics of soil physical properties and provides the formation of soil structure, which affects the living conditions of soil biota and plants (Filser et al., 2016; Tiunov, 2000; Tiunov and Scheu, 1999). The number of species, population abundance and biomass of soil macrofauna are declining in a range of ecosystems from nature reserves to managed agro-ecosystems. The main reason for this decline is the reduction of available organic matter and essential elements in the soil of the agroecosystem (Pokarzhevskii and Krivolutskii, 1997). Knowledge of the mechanisms that shape the dynamics of soil macrofauna community diversity and the factors that influence communities contributes significantly to understanding the patterns of functioning and sustainability of floodplain ecosystems (Barrios, 2007; Pauli et al., 2010). The diversity of animal communities depends on the history (Mougi and Nishimura, 2009; Tanner et al., 1996), influence of environmental filters (Lososová et al., 2015), and factors of a neutral nature (Illian and Burslem, 2007; Legendre et al., 2009; Pollierer et al., 2021). The environmental filters of soil macrofauna communities are driven by features of soil properties and soil regimes (Kunakh et al., 2021; Zhukov et al., 2019). The variability of soil chemical properties determines habitat properties and the availability of nutrients to animals and chemical elements that form the protective structures of pedobionts (Rosa et al., 2015; Umerova et al., 2022; Yorkina et al., 2018; Zhukov et al., 2019). An important aspect of the influence on soil animals is the physical properties of the soil (Zhukov et al., 2018). They affect the ability and energy requirements for animals to move through the soil. The physical properties of the soil also regulate the aeration regime (Gebauer et al., 1996), the water regime (Zhukov et al., 2021), and the salinity regime (Xu et al., 2019; Yu et al., 2014). These regimes directly affect soil animals (Korobushkin et al., 2019; Pereira et al., 2019).

The role of history in the formation of biodiversity patterns of soil macrofauna communities is very

difficult to trace. This is due to the fact that the temporal patterns have a hierarchical multiscale structure (Bondarev et al., 2022; Zhukov et al., 2021; Zhukov et al., 2019). The dynamic nature of the floodplain leads to the highly variable durations of species-specific habitat. The complexity of the dynamics of processes over time is superimposed on the lack of series of data on the composition of the soil animal communities of sufficient duration. Therefore, it is possible to assume the effectiveness of such an approach, when the relationship of the soil macrofauna community in space within a limited time slice with variables having a certain temporal cyclicity, can be proxied by the influence on the community of a process that is commensurate in temporal dynamics with the controlling factor. This approach proceeds from the assumption that the connection between the factor and the community may have formed in a temporal pattern that corresponds to the rhythm of the controlling factor. If the temporal patterns of the factors do not correspond to the community dynamics, then the influence of such factors has the character of noise, and no connection with the community can be fixed. In this regard, the possible factors which influence the soil animal community can be ranked according to their "characteristic" time dynamics (Pokarzhevskii, 1996).

The morphological features of soils are very conservative and their variability reflects the genesis of soils, which comprises considerable time intervals, which run into hundreds and thousands of years (Stockmann et al., 2014). The physical properties of soils may be closely related to morphological features and have the same temporal rhythm of variability (Lin, 2011). Or they may change very rapidly and be characterized by rhythmic processes from a few days to months or years (Alletto et al., 2015; Gritsan et al., 2019; Hu et al., 2018). The rhythm of ecological processes, commensurate in time with the dynamics of the plant community, correspond to the phytoindicator assessments of environmental factors (Didukh, 2011). Thus, we can hypothesize that the assessment of the influence of different sets of predictors on the soil macrofauna community can model the role of ecological drivers in the hierarchy of temporal patterns. Therefore, the aim of this article was to investigate the role of soil morphological and physical properties and phytoindication assessments of environmental factors as drivers of biological diversity of soil macrofauna of protected ecosystems of the Dnipro River floodplain.

Materials and methods

Study sites

The studies were conducted in the forest floodplain ecosystems of the "Dnipro-Orilskiy" Nature Reserve (Fig. 1). The "Dnipro-Orilskiy" Nature Reserve was founded in 1990 (Bondarev et al., 2022). The area of the reserve is 3,766 ha, of which water bodies occupy 203 ha. Intense changes in the relief on the territory of the reserve occurred after the construction of the Dnipro hydropower dam in 1932. The water level here was raised by 1.5–2 m, which corresponds to an average level of 49.7 m above sea level. During World War II, the dam was destroyed in 1941, which returned the water level to its previous state. After the dam was raised in 1950, and after the beginning of construction of the second unit of Dnieper hydropower

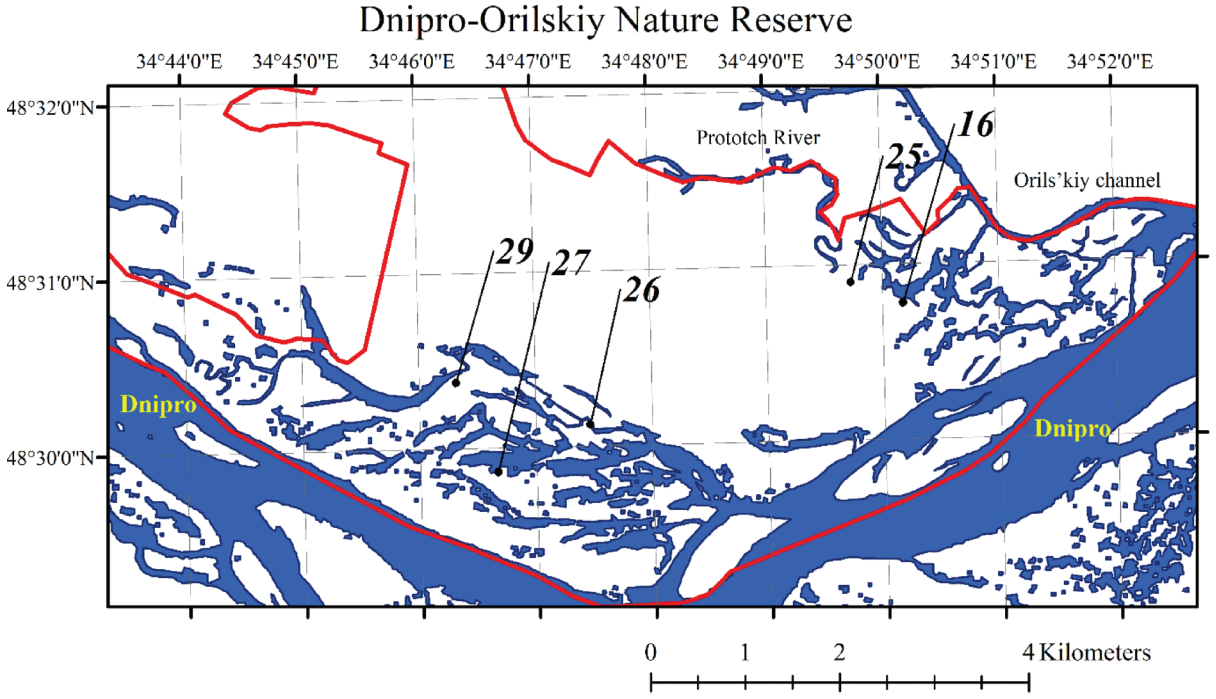

Fig. 1. Locations of sampling sites in the floodplain ecosystems of the Dnipro-Orilskiy Nature Reserve. 16, 25, 26, 27, and 29 are sampling sites; the red line shows the boundaries of the reserve.

plant in the 1960s and the construction of Dniprodzerzhinska (Kamianska) HPP, the water level was raised to 51.4 m above the sea level. Thus, after the construction of the cascade of Dnipro reservoirs, the total rise in the level of the Dnipro River in the territory of the "Dnipro-Orilskiy" Nature Reserve, compared with the natural, was 3.0–3.5 m, which led to the inundation of part of the floodplain, changes in the configuration of the banks and the area of water bodies. The intensity and duration of floods also decreased.

Sampling design

Five sampling plots were located in the different parts of the floodplain landscape: #16 and #25 (the floodplain of the Protich River, which is a left tributary of the Dnipro River), ##26, 27, 29 (the floodplain of the Dnipro River) (Fig. 1). The numbering of sampling plots is given in accordance with the article Gritsan et al. (2019). The sampling plots each consisted of 7 transects. Each transect was consisted of 15 sampling points (Fig. 2). The distance between the nearest sampling points was 3 m. At each of the 105 sampling points, 0.25 × 0.25 m soil cores were taken to extract the soil macrofauna. Soil macrofauna was defined as an invertebrate group found within terrestrial soil samples which has more than 90% of its specimens in such samples visible to the naked eye (macroscopic organisms) (Warren and Zou, 2002; Lavelle et al., 2003; Gholami, 2016). Geobionts (large soil invertebrates that permanently inhabit the soil) and geophiles (organisms that live in the soil only for particular phases of their lives) (Krivolutsky, 1992; Gholami et al., 2016) were assessed. Samples consisted of single blocks of soil, 25 × 25 × 30 cm3 deep, dug out quickly. A quadrat was fixed on the soil surface prior to taking the soil samples. The litter macrofauna was manually collected from the soil samples. The soil macrofauna were sorted and the animals were stored in 4% formaldehyde (Mathieu et al., 2004).

The sampling plot #16 was established on May 12, 2018 in the floodplain of the Protich River (48°30'56''N, 34°49'22''E), which is a left tributary of the Dnipro River (Fig. 1). The sampling site is located on its largest side along the largest local elevation gradient from the floodplain lake to the foot of the sandy hill of the arena terrace, extending somewhat beyond the floodplain. The habitat type according to EUNIS (European Nature Information System): G1.223 Southeast European *Fraxinus – Quercus – Alnus forests*. The soil classification position according to WRB (World reference base for soil resource): Fluvic Calcic Mollic Gleysol (Loamic, Humic).

The sampling plot #25 was established on May 9, 2018 in the floodplain of the Protich River (48°30'51''N, 34°49'04''E), which is a left tributary of the Dnipro River. The habitat type according to EUNIS: G1.1112 Eastern European poplar-willow forests. The soil classification position according to WRB: Gleyic Pantofluvic Fluvisol (Loamic, Protocalcic, Humic, Nechic).

The sampling plot #26 was established on May 15, 2016 in the floodplain of the Dnipro River (48°30'06''N, 34°47'18''E). The habitat type according to EUNIS: G1.225 Sarmatic riverine [*Quercus*] forests. The soil classification position according to WRB: Gleyic Pantofluvic Fluvisol (Arenic, Ochric, Thaptoochric).

The sampling plot #27 was established on May 12, 2017 in the floodplain of the Dnipro River (48°29'24"N, 34°46'37"E). The habitat type according to EUNIS: G1.225 Sarmatic riverine [*Quercus*] forests. The soil classification position according to WRB: Gleyic Pantofluvic Fluvisol (Loamic, Protocalcic, Humic, Thaptohumic). The soil classification position in an additional soil section #28: Gleyic Pantofluvic Fluvisol (Loamic, Humic, Thaptoochric).

The sampling plot #29 was established on May 16, 2020 in the floodplain of the Dnipro River

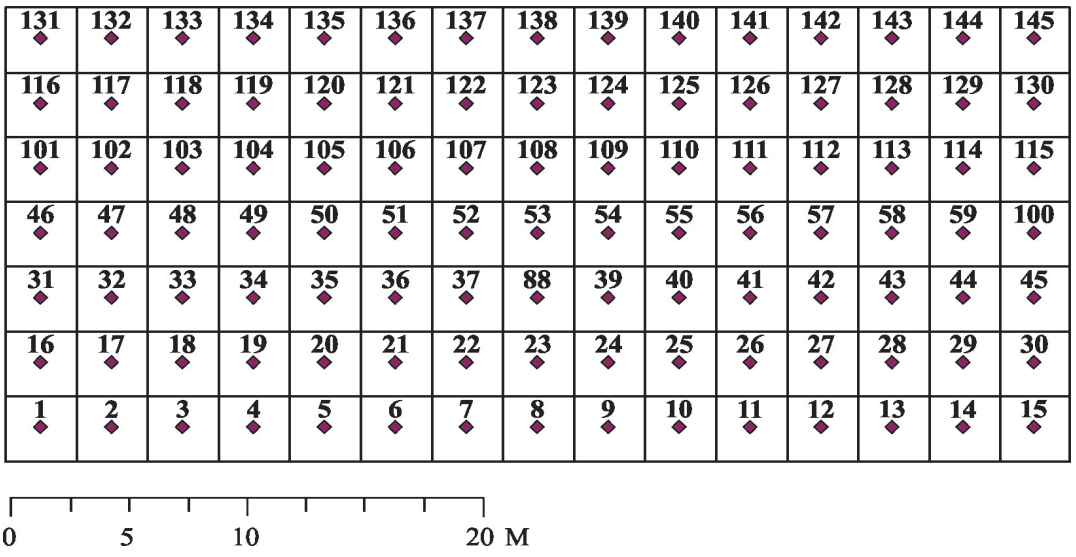

Fig. 2. Scheme of the location of sampling points within the sampling plots. X-axis and Y-axis are local coordinates, meters. The extraction of soil cores and measurement of soil properties were performed at the sampling points. The vegetation was recorded in squares of 3 by 3 meters with the centroid at the sampling point.

(48°30'15"N, 34°26'47"E). The habitat type according to EUNIS: G1.225 Sarmatic riverine [Quercus] forests. The soil classification position according to WRB: Gleyic Pantofluvic Fluvisol (Arenic, Ochric). The soil classification position in an additional soil section #30: Fluvic Mollic Gleysol (Loamic, Humic).

Measurement of environmental indicators

The soil morphology was described in accordance with the FAO soil field description methodology, the genetic type of the soil profile was determined according to B. Rozanov (Rozanov, 2004), and the soil classification was given according to the IUSS Working Group WRB 2015 (WRB, 2015).

The soil penetration resistance was measured in the field using a hand-held Eijkelkamp penetrometer to a depth of 100 cm with an interval of 5 cm. The average error of the measurement results of the device was ±8%. The measurement was made with a cone with a cross-sectional size of 2 cm^2. Within each sampling point, the soil penetration resistance was measured in a single repetition.

An HI 76305 sensor (Hanna Instruments, Woodsocket, RI) was used to measure the electrical conductivity of the soil in situ. This sensor works together with a portable HI 993310 tester. The tester evaluates the total electrical conductivity of the soil, i.e. the combined conductivity of air, water and soil particles. The measurement results of the device are presented in units of soil salt concentration, i.e., g l^{-1}. The comparison of HI 76305 measurements with laboratory data allowed us to estimate the unit conversion factor as 1 dS m^{-1} = 155 mg l^{-1} (Pennisi and van Iersel, 2002).

The soil aggregate structure was evaluated by the method of dry sieving according to Savinov (Savinov, 1936). The volume weight of the soil and the gravimetric water content in the soil were determined according to Karpachevsky (2005). The method by Kachinsky is described by L.O. Karpachevsky (2005) in his monograph „Ecological soil science".

The phytoindication assessment of environmental factors was performed on the basis of geobotanical descriptions of vegetation at sampling points with a size of 3 by 3 meters. The projective cover of plants was estimated by eyesight in gradations of 10, 20, ..., 90, 100% (Voronov, 1973). Edaphic and climatic factors can be assessed using phytoindication scales (Didukh, 2011). The edaphic phytoindication scales include the soil water regime (Hd), the variability of humidity (fH), the soil aeration regime (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 (thermal regime, Tm), humidity (Om), crioclimate (Cr) and the continentality of climate (Kn). The light scale (Lc) is an indicator of the microclimate. The phytoindication assessment of environmental factors was performed by the ideal indicator method (Buzuk, 2017). Phytoindication of environmental factors was made on the basis of information about the projective cover of the herbaceous layer.

Statistical methods

The relationship between soil morphological traits was evaluated using multiple correspondence analysis. The soil physical property data were subjected to principal component analysis. The mentioned statistical analyses and calculation of descriptive statistics were performed in the software STATISTICS (*Statistics. Data Analysis Software System*, 2014). The evaluation of alpha, beta, and gamma diversity of soil macrofauna communities was performed using the package *entropart* (Marcon and Hérault, 2015) for a language and environment for statistical computing *R* (R Core Team, 2020). A canonical correspondence analysis was used to ordinate the soil macrofauna community using the package *ade4* (Dray and Dufour, 2007). The partitioning of the community data variation with respect to the explanatory tables of ecological properties was performed with the help of the package *vegan* (Oksanen et al., 2018). Indicator value analysis of soil macrofauna species was performed with the help of the package *indicspecies* (Cáceres, 2013).

Results

Soil morphology

The studies of morphological properties of soils in the Dnipro River floodplain allowed us to identify the representatives of two reference groups: Fluvisols and Gleysols (Table 1). By granulometric composition, the soils were sandy or sandy loam (Arenic) or loamy (Loamic). The Humic qualifier refers to soils that contain soil organic carbon in the fines fraction ≥1%, calculated as a weighted average to a depth of 50 cm from the mineral soil surface. The Ochric classifier refers to soils that contain ≥0.2% soil organic carbon (weighted average) in a layer 0–10 cm deep from the mineral soil surface. The calcic horizon is characterized by the presence of secondary calcium carbonate detected by the hydrochloric acid test. The Protosalic properties are related to soil solution carbonates precipitated in the soil. Diagnosis of Protocalcic properties is based on their persistence and a fairly marked amount in the soil. Nechic denotes the presence of uncovered films of mineral dust or sand grains in a darker base at a depth ≤ 5 cm from the surface of the mineral soil. The qualifiers Thaptoochric and Thaptohumic denote the presence of buried horizons of appropriate color.

The multiple correspondence analysis indicated the relationship of soil properties in the studied soil types (Fig. 3). The soils marginal in their properties were represented in sampling sites 16, 25, and 26. The soils that were transitional in their properties were represented in sampling sites 27 and 29. The Pro-

Table 1. Classification position of soils according to World reference base for soil resources (WRB) and qualitative qualifiers of soils

Sampling site	Soil profile	WRB classification	Granulometric composition		Humus layer		Mineralogy		Buried layers	
			Loamic	Arenic	Humic	Ochric	Protocalcic	Nechic	Thaptoochric	Thaptohumic
16	16	Fluvic Calcic Mollic Gleysol	+	–	+	–	–	–	–	–
25	25	Gleyic Pantofluvic Fluvisol	+		+	–	+	+	–	–
26	26	Gleyic Pantofluvic Fluvisol	–	+	–	+	–	–	+	–
27	27	Gleyic Pantofluvic Fluvisol	+	–	+	–	+	–	–	+
	28	Gleyic Pantofluvic Fluvisol	+	–	+	–	–	–	+	–
29	29	Gleyic Pantofluvic Fluvisol	–	+	–	+	–	–	–	–
	30	Fluvic Mollic Gleysol	+	–	+	–	–	–	–	–

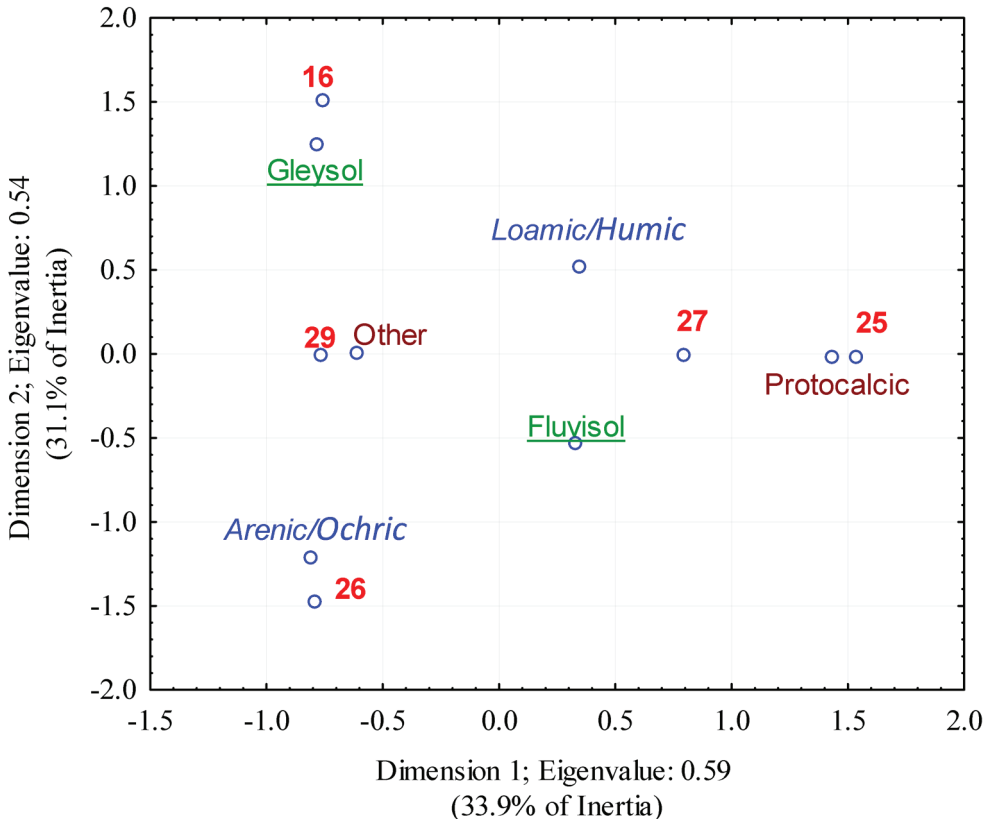

Fig. 3. Multiple correspondence analysis of sampling sites, soil types, and qualifiers of soil properties. Sampling sites – 16, 25, 26, 27, 29; soil types – Fluvisol and Gleysol, Humus layer/Granulometric composition – Loamic/Humic, Arenic/Ochric; Mineralogy – Protocalcic and Other.

tocalcic property was represented in the soils in sampling sites 25 and 27. The soils of sampling sites 16 and 29 were classified as Gleysols. Accordingly, all other soils were referred to Fluvisols. The soils of sampling sites 26 and 29 had the property Arenic, while the remaining soils had the property Loamic. The diagram also allowed us to evaluate the relationship between the properties. Thus, the soils with Arenic property never possessed Protocalcic property, while the soils with Loamic property could possess this property. Also, the Loamic and Protocalcic properties were more common in fluvisols, whereas the Arenic property was more common in gleysoils.

Soil properties

The soil physical property data (Appendix 1) were subjected to principal component analysis (Table 2), which extracted four principal components whose eigenvalues exceeded unity. The first four principal components described 79.9% of the variation in traits. The principal component 1 described 46.3% of the variation and reflected a unidirectional change in the soil penetration resistance along the profile. Thus, the positive PC1 scores indicated soils with the high compactness within the entire profile, and the negative scores, on the contrary, indicated the soils with low compactness within the profile. In

Table 2. Results of principal component analysis of variation of soil properties

Variables	PC1, λ=15.3, 46.3%	PC2, λ=4.9, 14.9%	PC3, λ=3.7, 11.3%	PC4, λ=2.4, 7.4%
Soil penetration resistance (on depth, cm)				
0–5	0.54	0.48	–0.31	–0.54
5–10	0.53	0.43	–0.41	–0.49
10–15	0.60	0.34	–0.51	–0.22
15–20	0.56	–	–0.66	–
20–25	0.67	–	–0.58	0.30
25–30	0.71	–	–0.55	0.27
30–35	0.80	–	–0.45	0.20
35–40	0.85	–	–0.35	–
40–45	0.88	–0.11	–0.26	–
45–50	0.93	–0.11	–0.10	–
50–55	0.94	–0.10	–	–
55–60	0.93	–0.15	–	–
60–65	0.92	–0.17	0.22	–0.10
65–70	0.90	–0.17	0.28	–0.12
70–75	0.89	–0.17	0.30	–0.11
75–80	0.88	–0.19	0.33	–0.12
80–85	0.87	–0.17	0.37	–0.15
85–90	0.86	–0.18	0.39	–0.16
90–95	0.85	–0.17	0.39	–0.15
95–100	0.85	–0.17	0.39	–0.13
Other soil properties				
Electrical conductivity, dSm/m	–	0.45	0.39	–
Litter depth (cm)	–0.32	–	–	–
Soil wetness (%)	0.43	0.29	–0.49	–0.34
Soil bulk density (g $cm^{-3)}$	–0.27	–0.29	0.14	–0.56
Aggregate fraction (mm)				
> 10	–	0.82	0.30	–
7–10	–	0.90	0.19	–
5–7	–	0.74	0.18	0.23
3–5	0.66	–	0.13	0.42
2–3	0.70	–0.37	0.15	0.44
1–2	–0.16	–0.84	–0.28	–
0.5–1	–0.55	–0.66	–0.25	–
0.25–0.5	–0.58	–0.53	–0.28	–0.38
<0.25	–0.41	–	–	–0.63

soils with high compactness, the forest litter depth and soil bulk density were usually lower, and the moisture content was usually higher. The positive PC1 scores indicated an increase in the proportion of aggregate fractions of 2–5 mm and a decrease in the proportion of aggregate fractions of <0.25–2 mm. The principal component 2 described 14.9% of the trait variability. The positive scores of this principal component indicated an increase in the soil penetration resistance at 0–15 cm depth and with a concomitant decrease in the penetration resistance at 40 cm depth and deeper. The principal component 2 was sensitive to the variability in electrical conductivity, moisture, and soil bulk density. The positive PC2 scores indicated an increase in the proportion of aggregate fractions larger than 5 mm and a decrease in the proportion of aggregate fractions of 0.25–3 mm. The principal component 3 described 11.3% of the trait variation and indicated the opposite dynamics of the soil penetration resistance variability at 0–50 cm depth (the negative principal component scores) and 60 cm and deeper (the positive principal component scores). The principal component 3 was sensitive to the variability in electrical conductivity, soil moisture, and soil bulk density. The positive PC3 scores indicated an increase in the proportion of aggregate fractions larger than 2 mm and a decrease in the proportion of aggregate fractions between 0.25 and 2 mm. The principal component 4 described 7.4% of the trait variation and indicated the opposite dynamics of the soil penetration resistance variability at depths of 0–15 cm and 60–100 cm (the negative principal component scores) and 20–35 cm (the positive principal component scores). The principal component 3 was sensitive to the variability of soil moisture and soil bulk density. The positive PC4 scores indicated an increase in the proportion of aggregate fractions of size 2–7 mm and a decrease in the proportion of aggregate fractions of size <0.25–0.5 mm.

The vegetation cover and phytoindication of ecological regimes

There were 109 vascular plant species recorded within the surveyed floodplain ecosystems (Appendix 2). Among them 15 species (13.8%) were Phanerophytes, 16 species (17.7%) were Nanophanerophytes, 47 species (43.1%) were Hemicryptophytes, 19 species (17.4%) were Therophytes and 12 species (11.0%) were Geophytes. The phytoindication of ecological regimes was performed on the basis of information about species composition of communities and projective cover of plants (Table 3). The floodplain ecosystems studied were found to have a moisture regime that ranged from a favorable for subxerophytes to submesophytes. The regime of moisture variability was favorable for hydrocontrastophobes. The soil acidity regime was favorable for subacidophiles, and the trophicity regime was favorable for mesotrophs. The soil carbonate content was favorable for acarbonatophiles, and the nitrogen content was favorable for nitrophiles. The soil aeration regime was favorable for aerophiles. The light regime was favorable for sub-heliophytes (plants of light forests and shrubberies, or high herbaceous communities; lower layers are in the shade). The climatic scales assessed conditions for the landscape as a whole, and the regular variability of these scales should be seen as the result of their correlation with scales that are sensitive to soil properties.

Soil macrofauna

The abundance of the soil macrofauna community ranged from 135.9 ± 21.1 to 332.0 ± 34.9 ind. m^{-2} (Appendix 3). Earthworms were the dominant community group, represented by five species, among which Aporrectodea caliginosa trapezoides (Duges, 1828) and Aporrectodea rosea (Savigny, 1826) were found in all ecosystems studied. The predatory Chilopoda was represented by six species, among which Lithobius (Lithobius) forficatus (Linnaeus, 1758) was found in all studied ecosystems. The saprotrophic Diplopoda was represented by three species. Soil insects, which were represented by the imaginal and larval phases, were diverse. The woodlouse Trachelipus rathkii (Brandt, 1833) was found in all ecosystems. Six species of mollusks were recorded. Their abundance was relatively low. The mollusk Cochlicopa lubrica (O.F. Muller, 1774) was consistently found.

Alpha diversity of the soil macrofauna community was 8.8 species and was between 8.6 and 8.9 species in 95% of cases (Fig. 4). Gamma community diversity was 75 species and 95% of the cases ranged from 70.7 to 77.3 species. Beta diversity was 8.55 and 95% of the cases ranged from 8.1 to 8.9.

Soil macrofauna community ordination

For further analysis, we used information on species that occurred more than 10 times. There were 45 such species. According to the results of the preliminary detrended correspondence analysis, the length of the largest axis was 3.4, so the canonical correspondence analysis was the most adequate alternative as an ordination procedure. The first four canonical axes were statistically significant (Table 4). The soil and plant predictors were able to explain 29.6% of the community variation (F = 11.2, p < 0.001). The differences between soils in morphological traits were able to explain 11.3% of the macrofauna community variation (F = 11.3, p < 0.001), while the pure morphological component, when excluding the combined influence of soil and plant variation, was able to explain 1.9% of the community variation (F = 5.3, p < 0.001). The soil physical properties described 23.7% of community variation (F = 41.8, p < 0.001), while the pure component induced by the physical properties, when excluding the combined effects of the variation in soil morphological properties and plant properties, was able to explain 9.4% of community variation (F = 17.4, p < 0.001). The plant properties, which are represented by the phytoindication assessments of environmental factors, were able to explain 10.1% of community variation (F = 5.9, p < 0.001), while the pure component induced by the plant properties was able to explain 1.3% of community variation (F = 1.8,

Table 3. Phytoindicator assessment of ecological factors for individual sampling sites: 16, 25, 26, 27, 29 (mean ± standard error)

Ecological factor*	16	25	26	27	29
Hd	8.80 ± 0.06	7.29 ± 0.08	8.89 ± 0.06	8.50 ± 0.06	9.12 ± 0.08
fH	4.42 ± 0.04	4.11 ± 0.06	4.67 ± 0.06	4.71 ± 0.05	4.76 ± 0.06
Rc	7.77 ± 0.02	8.36 ± 0.04	8.04 ± 0.03	7.73 ± 0.03	7.89 ± 0.02
Sl	6.13 ± 0.05	6.35 ± 0.04	6.36 ± 0.06	5.96 ± 0.05	6.55 ± 0.04
Ca	8.15 ± 0.06	8.28 ± 0.04	8.42 ± 0.06	7.86 ± 0.05	8.04 ± 0.04
Nt	8.38 ± 0.04	7.73 ± 0.04	8.65 ± 0.05	8.39 ± 0.05	8.37 ± 0.04
Ae	5.80 ± 0.02	5.90 ± 0.01	5.98 ± 0.02	6.05 ± 0.02	5.85 ± 0.02
Tm	9.76 ± 0.04	9.10 ± 0.06	9.66 ± 0.06	9.93 ± 0.04	9.80 ± 0.04
Om	12.21 ± 0.03	12.34 ± 0.03	12.15 ± 0.04	11.64 ± 0.03	12.01 ± 0.03
Kn	10.84 ± 0.04	10.90 ± 0.04	10.95 ± 0.04	11.01 ± 0.04	11.01 ± 0.04
Cr	8.61 ± 0.06	8.58 ± 0.05	8.45 ± 0.07	8.65 ± 0.07	8.94 ± 0.06
Lc	7.51 ± 0.03	8.05 ± 0.03	7.48 ± 0.02	7.64 ± 0.03	7.49 ± 0.03

* indicates: Hd, 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, thermal climate; Om, climate aridity-humidity; Kn, continentality of climate; Cr, cryoregime (average temperature of the coldest month); Lc, light regime.

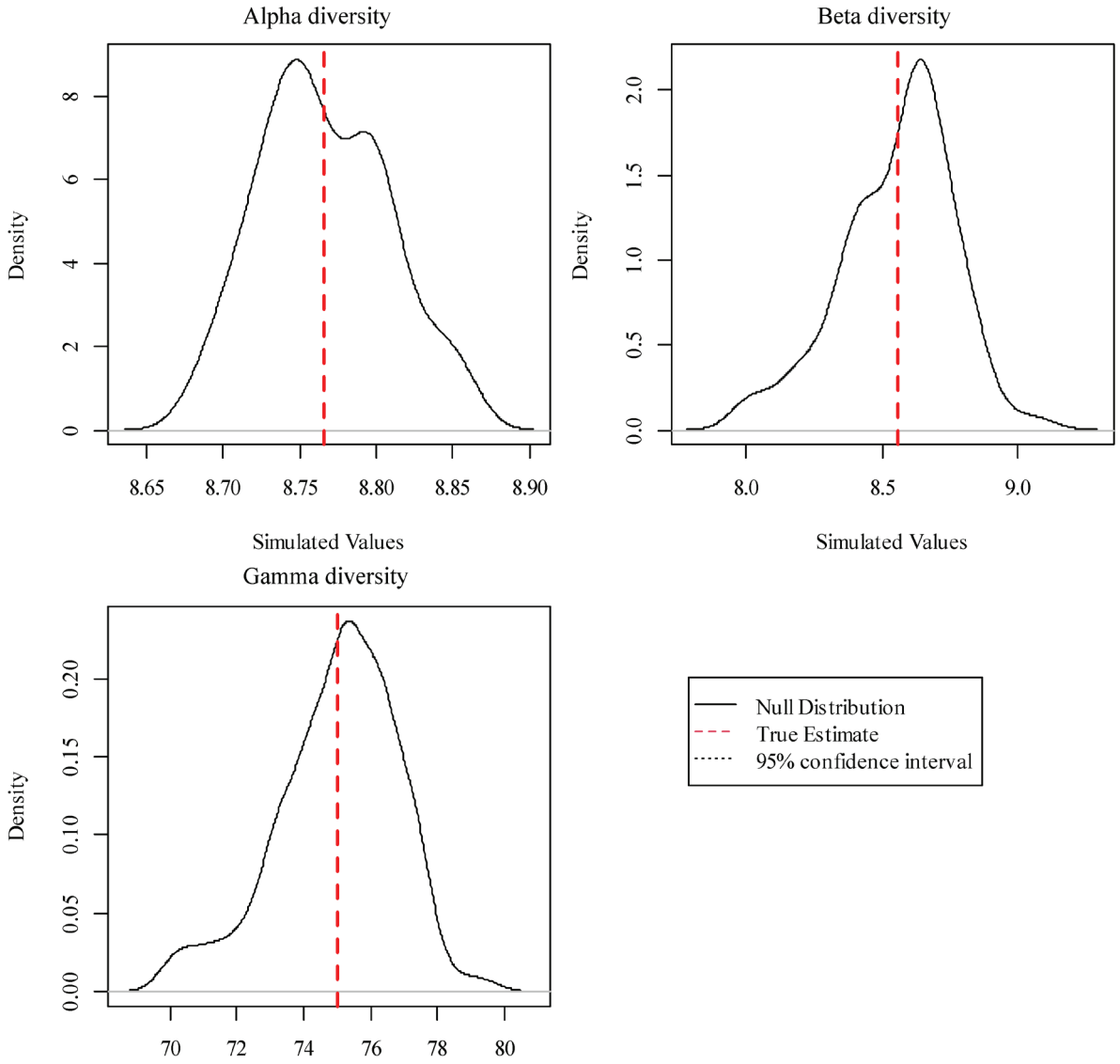

Fig. 4. Alpha, beta, and gamma diversity of soil macrofauna communities.

Table 4. Species scores on the canonical axes

Species	CCA1, $_{Radj}^{2}$=10.2% F = 73.2, p < 0.001	CCA2, $_{Radj}^{2}$ = 7.1% F = 50.8, p < 0.001	CCA3, $_{Radj}^{2}$ = 6.7% F = 47.8, *p* < 0.001	CCA4, $_{Radj}^{2}$ = 2.1% F = 15.4, *p* < 0.001
Agriotes lineatus	0.06	–1.04	0.79	–0.04
Agrotis segetum	–0.77	0.12	0.08	–0.09
Agrypnus murinus	0.76	0.55	0.02	–0.55
Amara familiaris	0.49	–1.24	0.72	–0.08
Amara similata	0.44	1.25	0.85	0.14
Ampedus balteatus	–0.31	–0.77	–2.67	0.27
Amphimallon solstitiale	0.36	1.18	0.55	–0.12
Aporrectodea rosea	–1.23	0.28	0.13	0.18
Aporrectodea trapezoides	0.47	0.41	0.12	0.02
Asilidae sp.1	–0.81	–0.64	–0.21	–0.43
Athous haemorrhoidalis	0.39	–0.24	–0.20	–0.08
Cardiophorus rufipes	0.36	–1.01	0.28	–0.09
Cepaea vindobonensis	0.32	–1.36	0.75	–0.14
Chrysolina fastuosa	0.23	–0.68	0.48	0.66
Cochlicopa lubrica	–0.11	–0.03	–0.04	0.78
Dendrobaena octaedra	0.60	0.64	0.07	–0.53
Dendroxena quadrimaculata	0.80	1.06	–0.04	–0.97
Enchytraeus sp. 1	–1.42	0.27	–0.25	–0.22
Forficula auricularia	0.40	–0.95	0.65	–0.05
Geophilus proximus	0.22	0.28	0.33	0.57
Isomira murina	0.21	–0.80	–0.98	0.03
Lithobius aeruginosus	0.27	0.61	–0.31	–0.67
Lithobius curtipes	0.07	0.56	0.14	–0.54
Lumbricidae sp.	0.44	–1.18	0.65	–0.28
Megaphyllum rossicum	–0.62	–0.56	0.52	–0.27
Megaphyllum sjaelandicum	–1.02	–0.03	0.33	0.06
Melolontha melolontha	0.42	–0.23	0.05	0.16
Octodrilus transpadanus	–0.22	–0.01	–1.65	–0.15
Othius angustus	1.10	0.95	0.00	–0.77
Otiorhynchus ligustici	0.13	–0.81	0.40	–0.19
Pachymerium ferrugineum	–0.21	–0.94	0.51	–0.27
Pardosa lugubris	–1.42	0.14	0.06	–0.55
Platydracus fulvipes	–0.21	–0.94	0.62	–0.11
Polydesmus inconstans	–1.33	0.31	0.35	0.30
Polyphylla fullo	0.48	–0.63	0.30	–0.24
Prosternon tessellatum	0.18	0.09	0.42	1.16
Pterostichus ovoideus	0.67	1.06	–0.16	–0.93
Rhagio scolopaceus	–1.19	–0.65	0.46	–0.45
Rhipidia uniseriata	–0.30	–0.30	–2.46	0.08
Serica brunnea	0.07	–0.80	–1.23	0.08
Tabanus bromius	–0.10	–0.03	–0.87	–0.29
Thereva nobilitata	–0.97	–0.35	–0.32	0.00
Tipula lunata	0.38	0.41	–0.57	0.51
Trachelipus rathkii	0.38	0.04	0.22	–0.04
Xerolycosa miniata	0.43	–0.78	0.50	0.37

$p < 0.001$) when excluding the combined effects of soil morphological and physical property variability.

The canonical axis 1 differentiated the communities of sampling site (sampling plot) 26 from all others (Fig. 5). The high principal component 4 and low principal component 3 scores were specific to the conditions of sampling site 26. High aeration, high carbonate and nitrogen compounds were also a feature of this sampling site. The negative scores of species on axis 1 indicate that these species preferred the living conditions observed in sampling site 26. Such species include *Pardosa lugubris*, *Polydesmus inconstans*, *Enchytraeus* sp., *Rhagio scolopaceus* (larvae), *Aporrectodea rosea*, *Megaphyllum sjaelandicum* and *Thereva nobilitata* (larvae).

The canonical axis 2 differentiates the soil macrofauna communities of sampling site 25 (positive scores) and sampling site 29 (negative scores). The positive scores of the axis are indicated by high PC 2 values, higher thermoclimate values and soil nitrogen content. The negative scores of the canonical axis 2 are marked by higher PC1 values and a higher level of soil solution salinity. Such species as *Pterostichus ovoideus, Dendroxena quadrimaculata, Othius angustus, Dendrobaena octaedra, Lithobius aeruginosus,* and *L. curtipes* occurred more frequently within sampling site 25. Sampling site 29 was preferred by species such as *Cardiophorus rufipes* (larvae), *Amphimallon solstitiale* (larvae), *Agriotes lineatus* (larvae), *Amara similata* (larvae), *A. familiaris* (larvae) and *Cepaea vindobonensis.*

The canonical axes 1 and 2 showed a complex of differences that are generally characteristic of Fluvisols and Gleysols. Fluvisols had the Arenic property more frequently, and Gleysols had the Loamic property more frequently. Fluvisols had a more alkaline soil solution reaction, and Gleysols had a more acidic soil solution reaction.

The community of sampling site 25 can be differentiated from other communities along canonical axis 3. The negative values of principal components 1 and 2, increased light regime, and soil acidity were characteristic of sampling site 25. This sampling site was characterized by the presence of Protocalcic and Loamic properties. Sampling site 25 was preferred by species such as *Ampedus balteatus* (larvae), *Rhipidia uniseriate* (larvae), *Serica brunnea* (larvae), *Octodrilus transpadanus, Isomira murina* (larvae) and *Tabanus bromius* (larvae).

The canonical axis 4 differentiates the soil macrofauna community of sampling site 27 from all others. This community was characterized by the increased values of principal component 3 and soil aeration, as well as lower salinity of soil solution and carbonate content in the soil. Species such as Prosternon tessellatum (larvae), C*ochlicopa lubrica, Geophilus proximus, Chrysolina fastuosa* (larvae)*, Tipula lunata* (larvae), and *Polydesmus inconstans* were more common in sampling site 27.

Indicator value analysis of soil macrofauna species

The analysis of indicator values allowed us to identify more accurately the relationship between soil types and categorical soil properties and soil macrofauna species (Table 5). Only one species *(Cochlicopa lubrica)* was indifferent to sampling site type. Species such as *Agrypnus murinus* (larvae), *Dendrobaena octaedra, Dendroxena quadrimaculata, Lithobius aeruginosus, Othius angustus, and Pterostichus ovoideus* were unique indicators of sampling site 16. The unique indicators of sampling site 25 were such species as *Ampedus balteatus* (larvae), *Octodrilus transpadanus, Rhipidia uniseriate* (larvae). The unique indicators of sampling site 26 were such species as Asilidae sp. (larvae), *Enchytraeus* sp., *Pardosa lugubris.* No unique indicators of sampling site 27 were identified. The indicator species of this sampling site are also indicators of sampling sites 26 or 29, less frequently in combinations with other sampling sites. The unique indicator species of sampling site 26 were *Agriotes lineatus* (larvae), *Amara familiaris* (larvae), *Amara similata* (larvae), *Amphimallon solstitiale* (larvae), *Cardiophorus rufipes* (larvae), *Cepaea vindobonensis, Forficula auricularia, Otiorhynchus ligustici* (larvae) and *Polyphylla fullo* (larvae).

The canonical axis 2 differentiates the soil macrofauna communities of sampling site 25 (positive scores) and sampling site 29 (negative scores). The positive scores of the axis are indicated by high PC 2 values, higher thermoclimate values and soil nitrogen content. The negative scores of the canonical axis 2 are marked by higher PC1 values and a higher level of soil solution salinity. Such species as *Pterostichus ovoideus, Dendroxena quadrimaculata, Othius angustus, Dendrobaena octaedra, Lithobius aeruginosus,* and *L. curtipes* occurred more frequently within sampling site 25. Sampling site 29 was preferred by species such as *Cardiophorus rufipes* (larvae), *Amphimallon solstitiale* (larvae), *Agriotes lineatus* (larvae), *Amara similata* (larvae), *A. familiaris* (larvae) and *Cepaea vindobonensis.*

The canonical axes 1 and 2 showed a complex of differences that are generally characteristic of Fluvisols and Gleysols. Fluvisols had the Arenic property more frequently, and Gleysols had the Loamic property more frequently. Fluvisols had a more alkaline soil solution reaction, and Gleysols had a more acidic soil solution reaction.

The community of sampling site 25 can be differentiated from other communities along canonical axis 3. The negative values of principal components 1 and 2, increased light regime, and soil acidity were characteristic of sampling site 25. This sampling site was characterized by the presence of Protocalcic and Loamic properties. Sampling site 25 was preferred by species such as *Ampedus balteatus* (larvae), *Rhipidia uniseriate* (larvae), *Serica brunnea* (larvae), *Octodrilus transpadanus, Isomira murina* (larvae) and *Tabanus bromius* (larvae).

The canonical axis 4 differentiates the soil macrofauna community of sampling site 27 from all others. This community was characterized by the increased values of principal component 3 and soil aeration, as well as lower salinity of soil solution and carbonate content in the soil. Species such as *Prosternon tessellatum* (larvae), *Cochlicopa lubrica, Geophilus proximus, Chrysolina fastuosa* (larvae), *Tipula lunata* (larvae), and *Polydesmus inconstans* were more common in sampling site 27.

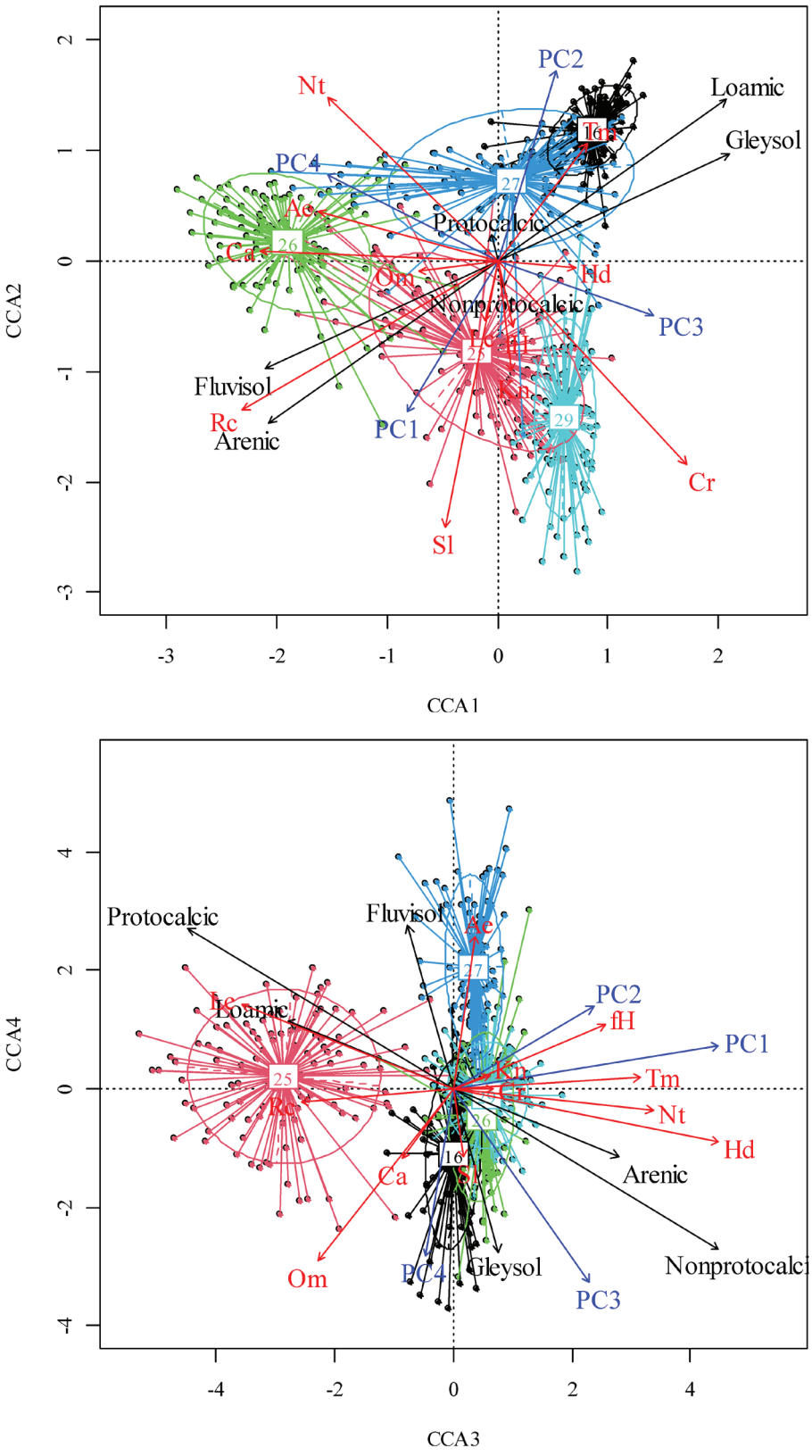

Fig. 5. Location of sampling sites in the CCA axis space. Soils: 16 – Fluvic Calcic Mollic Gleysol (Loamic, Humic); 25 – Gleyic Pantofluvic Fluvisol (Loamic, Protocalcic, Humic, Nechic); 26 – Gleyic Pantofluvic Fluvisol (Arenic, Ochric, Thaptoochric); 27 – Gleyic Pantofluvic Fluvisol (Loamic, Protocalcic, Humic, Thaptohumic); 29 – Gleyic Pantofluvic Fluvisol (Arenic, Ochric). Environmental factors: Hd – 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 – thermal climate; Om – climate aridity-humidity; Kn – continentality of climate; Cr – crioregime (average temperature of the coldest month); Lc – light regime. PC 1–4 extracted after principal component analysis of the variation in soil parameters.

Indicator value analysis of soil macrofauna species

The analysis of indicator values allowed us to identify more accurately the relationship between soil types and categorical soil properties and soil macrofauna species (Table 5). Only one species (*Cochlicopa lubrica*) was indifferent to sampling site type. Species such as *Agrypnus murinus* (larvae), *Dendrobaena octaedra, Dendroxena quadrimaculata, Lithobius aeruginosus, Othius angustus*, and *Pterostichus ovoideus* were unique indicators of sampling site 16. The unique indicators of sampling site 25 were such species as *Ampedus balteatus* (larvae), *Octodrilus transpadanus, Rhipidia uniseriate* (larvae). The unique indicators of sampling site 26 were such species as Asilidae sp. (larvae), *Enchytraeus* sp., *Pardosa lugubris*. No unique indicators of sampling site 27 were identified. The indicator species of this sampling site are also indicators of sampling sites 26 or 29, less frequently in combinations with other sampling sites. The unique indicator species of sampling site 26 were *Agriotes lineatus* (larvae), *Amara familiaris* (larvae), *Amara similata* (larvae), *Amphimallon solstitiale* (larvae), *Cardiophorus rufipes* (larvae), *Cepaea vindobonensis, Forficula auricularia, Otiorhynchus ligustici* (larvae) and *Polyphylla fullo* (larvae).

18 species were indifferent to soil type (40.0% of the total number of species in the analysis). The Fluvisol indicators were 12 species (26.7%) and the Gleysol indicators were 15 species (33.3%). The species indifferent to soil granulometric composition were 15 species (33.3%). The Arenic/Ochric properties indicators were 22 species (48.9%) and the Loamic/Humic properties indicators were 11 species (24.4%). The species indifferent to soil mineralogy were 10 species (22.2%). Indicators of Protocalcic properties were 7 species (15.6%), and indicators of the absence of this property were 28 species (62.2%).

Discussion

Three sets of parameters were used to explain the variability of the soil macrofauna community of floodplain soils. These are morphological characteristics of soils, physical properties of soils, and phytoindication assessments of environmental factors. Each of these groups of factors has different spatial and temporal dynamics. The chosen set of predictors of the soil macrofauna community reflects various spatial and temporal patterns of the dynamics of ecological conditions. The intrinsic time of variability of the physical properties of the soil has a duration of days, months, years. The intrinsic time of variability of phytoindication assessments of environmental factors has duration of some years or decades. The intrinsic time of variability of morphological properties of soil has duration of some years,dozens of years, centuries.

The soil types and soil morphological properties can also be indicated by soil macrofauna species. The basis of the soil animal community consists of earthworms, so their role as indicators is of particular interest. Our results show that the indicator of Fluvisols is the endogean earthworm *A. rosea*, and the indicators of Gleysols are the endogean earthworm *A. trapezoides* and the epigean *D. octaedra*. The complexes of soil type indicators are ecologically diverse. Species that have a similar ecological optimum are combined into ecological groups (Shelford, 1912). Different species from the same ecological group can belong to different life forms and occupy different ecological niches, so the ecological niche is characterized not only by an optimum, but also by an ecological range. Obviously, those of the species whose ecological optimum is within specific ecological conditions are the best indicators. Fluvisol indicators include both epigeic species (*Agrotis segetum* (larvae), *Pardosa lugubris*, *Polydesmus inconstans*, *Rhipidia uniseriate* (larvae), *Thereva nobilitata* (larvae), *Megaphyllum sjaelandicum*) and endogeic species (*Ampedus balteatus* (larvae), *Prosternon tessellatum* (larvae), *Rhagio scolopaceus* (larvae), *Serica brunnea* (larvae), *Enchytraeus* sp.). The same is true for Gleysols, whose indicators include both epigean species (*Amara familiaris*, *Dendroxena quadrimaculata, L. aeruginosus, Lithobius curtipes, Othius angustus (larvae), Pterostichus ovoideus, Tipula lunata* (larvae), *Trachelipus rathkii*) and endogeic species (larval stages of *Agrypnus murinus, Athous haemorrhoidalis, Melolontha melolontha, Polyphylla fullo*).

The ecological groups of soil animal species can adapt to certain environmental conditions, which as a consequence of the activity of elementary soil processes are reflected in the morphology of the soil profile. The species that are indicators of the granulometric composition of soils or the presence of a carbonate horizon were identified. The identified indicator values of species correspond to their known ecological features. For example, the ground beetle *Amara familiaris* prefers sandy soils (Thiele, 1977). The beetle *Amara similata* prefers damp areas, riverbanks and water meadows (Chapman, 2014). This species is part of the group that indicates pioneer sandbars (van Looy et al., 2005). *A. lineatus* larvae were found to prefer soils with higher water holding capacity (Staudacher et al., 2013), as well as soils rich in organic matter (Jakubowska et al., 2018). This species prefers soils with high bulk density (Benefer et al., 2012). In our study, sandy soils were found to be the ones with higher density than loam soils. The larvae of *Amphimallon solstitiale* prefer floodplain sandy soils (Medvedev, 1952). Also inhabitants of sandy soils are the larvae of *Cardiophorus rufipes* (Dolin, 1978). The mollusk *C. vindobonensis* is associated with dry, sunny, calcareous habitats (Pokryszko et al., 2004), but in river valleys it is usually found in floodplains closer to the river bed on alluvial deposits (Mierzwa, 2009).

The larvae of *Melolontha melolontha* prefer loamy soils (Medvedev, 1952). The earthworm *Octodrilus transpadanus* is anecic, building an extensive system of soil galleries (Gorres and Amador, 2010; Ruiz and Or, 2018). Burrows cannot persist for long periods of time in sandy soil, so these earthworms prefer loamy soils. Soil depth is one of the most important factors explaining the distribution of earthworm communities, especially for

Table 5. The relationship between species and soil types and soil properties (only statistically significant associations are shown at the level of $p < 0.05$)

Species	Sampling site					Soil		Granulometry		Mineralogy	
	16	25	26	27	29	Fluvisol	Gleysol	Arenic	Loamic	Non Protoc.	Protocalcic
Agriotes lineatus	0	0	0	0	1	–	–	1	0	1	0
Agrotis segetum	1	0	1	1	0	1	0	1	0	1	0
Agrypnus murinus	1	0	0	0	0	0	1	–	–	–	–
Amara familiaris	0	0	0	0	1	0	1	1	0	1	0
Amara similata	0	0	0	0	1	–	–	1	0	1	0
Ampedus balteatus	0	1	0	0	0	1	0	–	–	0	1
Amphimallon solstitiale	0	0	0	0	1	–	–	1	0	1	0
Aporrectodea rosea	0	0	1	1	0	1	0	–	–	–	–
Aporrectodea trapezoides	1	0	0	1	1	0	1	–	–	–	–
Asilidae sp.	0	0	1	0	0	–	–	1	0	–	–
Athous haemorrhoidalis	1	1	0	0	1	0	1	0	1	–	–
Cardiophorus rufipes	0	0	0	0	1	–	–	1	0	1	0
Cepaea vindobonensis	0	0	0	0	1	–	–	1	0	1	0
Chrysolina fastuosa	0	0	0	1	1	–	–	–	–	–	–
Cochlicopa lubrica	–	–	–	–	–	–	–	–	–	–	–
Dendrobaena octaedra	1	0	0	0	0	0	1	0	1	1	0
Dendroxena quadrimaculata	1	0	0	0	0	0	1	0	1	1	0
Enchytraeus sp.	0	0	1	0	0	1	0	1	0	–	–
Forficula auricularia	0	0	0	0	1	–	–	1	0	1	0
Geophilus proximus	1	0	0	1	1	–	–	–	–	1	0
Isomira murina	0	1	0	0	1	–	–	–	–	0	1
Lithobius aeruginosus	1	0	0	0	0	0	1	0	1	1	0
Lithobius curtipes	1	0	1	0	0	0	1	–	–	1	0
Lumbricidae sp.	0	0	0	0	1	0	1	1	0	1	0
Megaphyllum rossicum	0	0	1	0	1	–	–	1	0	1	0
Megaphyllum sjaelandicum	0	0	1	1	0	1	0	1	0	1	0
Melolontha melolontha	1	0	0	1	1	0	1	0	1	1	0
Octodrilus transpadanus	0	1	0	0	0	–	–	0	1	0	1
Othius angustus	1	0	0	0	0	0	1	0	1	1	0
Otiorhynchus ligustici	0	0	0	0	1	–	–	1	0	1	0
Pachymerium ferrugineum	0	0	1	0	1	–	–	1	0	1	0
Pardosa lugubris	0	0	1	0	0	1	0	1	0	1	0
Platydracus fulvipes	0	0	1	0	1	–	–	1	0	1	0
Polydesmus inconstans	0	0	1	1	0	1	0	1	0	–	–
Polyphylla fullo	0	0	0	0	1	0	1	1	0	1	0
Prosternon tessellatum	0	0	0	1	1	1	0	–	–	–	–
Pterostichus ovoideus	1	0	0	0	0	0	1	0	1	1	0
Rhagio scolopaceus	0	0	1	0	1	1	0	1	0	1	0
Rhipidia uniseriata	0	1	0	0	0	1	0	0	1	0	1
Serica brunnea	0	1	0	0	1	1	0	–	–	0	1
Tabanus bromius	1	1	1	0	1	–	–	–	–	0	1
Thereva nobilitata	0	1	1	0	0	1	0	1	0	–	–
Tipula lunata	1	1	0	1	0	0	1	0	1	0	1
Trachelipus rathkii	1	0	0	1	1	0	1	–	–	1	0
Xerolycosa miniata	0	0	0	1	1	–	–	–	–	1	0

Protoc., Protocalcic.

anecic species (Bouché, 1977; Phillipson et al., 1976). In floodplain forests, soil depth is largely determined by stream dynamics, resulting in erosion and sedimentation processes. Sandy soils usually have a thin humus horizon, whereas sandy loam soils have a much larger humus horizon (Bullinger-Weber et al., 2007; Salomé et al., 2011).

The list of species that are indicators of sandy soils largely repeats the list of species that indicate soils with no carbonate horizon. This is consistent, since the carbonate content and texture of soils are closely correlated. The number of the indicator species of carbonate horizon is very low. The larvae of *Ampedus balteatus* inhabit rotten wood or forest litter (Dolin, 1978), therefore, the indicator role of the carbonate horizon may be as a consequence of the peculiarities of the influence of soil conditions on the vegetation cover. These larvae prefer sandy soils (Lönnberg and Jonsell, 2012), so they are widely distributed in floodplain ecosystems. Our results indicate that this species is an indicator of Protocalcic horizon in sandy and sandy loam floodplain soils. The earthworm *Octodrilus transpadanus* is also an indicator of Protocalcic horizon. Increased calcium content in the soil is a factor in soil structure (Wuddivira and Camps-Roach, 2007). In turn, soil structure is necessary to maintain the earthworm burrow system (Sharma et al., 2017), and calcium is necessary for the normal digestive process of earthworms (Hodson et al., 2015; Horn et al., 2003).

The floodplain soils are young and dynamic, but the duration of the process of their genesis is measured in centuries (Shrestha et al., 2014; Wade et al., 2020). The dynamism of floodplain soils is caused by the variability of the main soil-forming factors under flooding conditions that regularly occur. The duration of floods in the floodplain of the Dnipro River was 30–40 days, and in the floodplains of tributaries of the Dnipro River flooding was up to 10 days every spring (Belgard, 1950). Due to construction of a series of dams in the Dnipro River channel, the water regime of the river has changed dramatically (Bondarev et al., 2022). Much of the floodplain was permanently flooded, and in the remaining part of the floodplain the intensity and duration of floods significantly decreased. The flood regime resulted in constant variability of floodplain soils' relief, alluvial material was regularly redeposited. The variability of the level of soil water led to leaching of salts from the soil profile (Botros et al., 2009). The deposits of organic matter were constantly evacuated during floods. Alluvial soils in zones of frequent flooding contain significantly less total organic carbon than soils in zones of no or moderate flooding. The absence of forest litter in zones of frequent flooding contributes to a decrease in the supply of organic matter to the surface horizons and gradually leads to soil depletion (Saint-Laurent et al., 2016). Extreme conditions, which were formed in the presence of regular floods, were a strong ecological filter that limited the spread of a significant number of plant species. In floodplain soils with intense floods, the species diversity of plant communities was significantly lower than in floodplains with shorter flood duration. Thus, the morphological characteristics of soils reflect their essential features, which are the result of the interaction of the main soil-forming factors: relief, soil-forming material, climate, communities of living organisms and time (Dokuchaev, 1883; Florinsky, 2012; Jenny, 1941; Jones et al., 2006).

The physical properties of soil depend on the factors of soil formation (Jenny, 1941). However, they are characterized by significant dynamism in space and time. The variability of soil physical properties is represented by temporal patterns with varying periodicity: from a few years to a few days or hours. Physical properties vary between different soils. There is also considerable variability of physical properties within the same ecosystem, which is induced by relief heterogeneity within the ecosystem, the influence of plants and animals. The variability of water content in alluvial soils at the ecosystem scale is determined by soil texture, topography, and the position of the water table. The characteristics of variability are driven by other soil factors such as soil structure, microrelief, preferred water pathways, plant root system features, and rock content (Orfánus et al., 2016).

Plant communities are subject to successional dynamics. The duration of successional changes of plant community is centuries (Clements, 1936; Horn, 1974). In floodplain ecosystems the intensity of dynamic phenomena in vegetation cover is very significant (Benjankar et al., 2011; Richards et al., 2002). Nevertheless, the nature of interrelation of plants and ecological processes allows using plants for indication of ecological regimes (Halarewicz et al., 2021; Yakovenko et al., 2019). Obviously, such an approach is sensitive to the ecological factors, the rhythm of which is consistent with the dynamics of the plant community. The species composition of plant phytocenoses and changes in the quantitative composition of individual taxa are useful indicators for studying and monitoring environmental changes. Similar results were obtained for direct and phytoindication methods of estimating nitrogen content in soil. For other ecological properties, direct and phytoindication estimates differed greatly. Therefore, the authors recommend researchers to prefer the direct measurements of environmental properties (Halarewicz et al., 2021). Obviously, direct and phytoindication estimates characterize different aspects of the dynamics of environmental properties. The direct measurement reflects the specific time slice at the moment of measuring the property. The phytoindication assessment characterizes the regime of environmental properties over a certain time interval, which is commensurate with the duration of stages of successional dynamics of the plant community.

About 1/3 of the variability of the soil macrofauna community was found to be explained by the soil and plant predictors. The unexplained variance could be completely random, due to the action of unmeasured factors in the study, the action of measured factors at the ecosystem level, or be the result of causes of a neutral nature. Among the sets of measured environmental factors considered, the soil physical properties are the most important driver of changes in the soil macrofauna community. The soil morphological traits and phytoindication scales are also able to explain some proportion of the community variation, but the larg-

est part of this influence is correlated with the influence of physical properties. The result obtained can be interpreted in a temporal context. The community is most sensitive to the influence of environmental factors that change over a few days to a few months or years. The ecological processes that continue over a longer period of time also affect the soil macrofauna community, but to a much lesser extent.

The principal components analysis was used to extract the integral characteristics of soil physical properties. This approach made it possible to significantly reduce the dimensionality of the feature space and solve the problem of multicollinearity. However, the principal components reflect the most significant trends in the covariance of the initial variables for the sample as a whole. In this approach, the intra-ecosystem variability of soil physical properties is taken into account to the extent that it manifests itself at the inter-ecosystem level. Thus, it can be assumed that some of the explained variance can be increased by considering the effects of soil physical properties at the ecosystem level. Moran's Eigenvector Maps and related methods for the spatial multiscale analysis of ecological data can be used to model the effects of neutral or unreported environmental factors (Blanchet et al., 2008; Dray et al., 2006).

The features of the coherent influence of the physical properties of the soil and environmental factors that were identified by phytoindication can be meaningfully interpreted. The most important driver that affects the soil macrofauna community is the aeration regime and the content of calcium compounds in the soil. This influence is coordinated with the variability of soil physical properties. The formation of soil structure depends significantly on the presence of calcium in the soil. A soil structure, represented by aggregates and intra-aggregate and inter-aggregate pore space (Yakovenko, 2017; Yakovenko and Zhukov, 2021), is considered the main indicator of soil physical condition and is associated with a variety of ecological functions (Dexter, 2004; Horn et al., 1994; Jozefaciuk, 2009; Umerova et al., 2022). In turn, the soil aggregate structure is able to provide an optimal respiratory regime for soil biota (Six et al., 2004). The patterns of profile variability of soil penetration resistance characterize the availability of soil space for plant roots and soil animals to penetrate. For many plants, a soil penetration resistance value of 3 MPa is the limiting value that roots can overcome. If the value of the resistance exceeds the threshold value, root growth is severely limited or becomes impossible. The maximum radial pressure values for anecic and endogeic earthworms are 0.13 MPa and 0.195 MPa, respectively (Ruiz and Or, 2018). The construction of soil galleries by animals is a very energy-consuming process. The opposite feature should also be noted: the constructed galleries should have some durability, which ensures their sufficient duration of existence to be used for movement by animals. Low soil compactness corresponds to loose soils, in which soil galleries cannot exist for a long time and their renewal becomes energetically unprofitable. Soil compactness is characterized by both density and soil penetration resistance. Therefore, these indicators are information-valuable predictors of soil macrofauna community structure.

The results indicate that moisture and aeration of floodplain soils have opposite effects on soil fauna, which is natural since water and air compete for soil pore space, and the higher the soil moisture, the less air available for respiration in the soil. Thus, wetter soils create unfavorable breathing conditions for soil animals. Also importantly, the moisture regime marks the most important gradient of soil macrofauna community variability (CCA1). The next most important gradient (CCA2) marks the trophicity factor. The CCA3 is also noted to be marked by a phytoindicative indicator of moisture variability, which closely depends on the flooding regime. This result is fully consistent with the ideas of O. L. Belgard (Belgard, 1971, 1950) on the typology of steppe floodplain forests. In the framework of this approach, the level of moisture, trophicity, and floodplain intensity are considered as the main structuring gradients. Our results indicate that these structuring factors also act at the level of soil macrofauna.

Conclusion

The representatives of two reference groups of soils: Fluvisol and Gleysol were identified in the floodplain of the Dnipro River in the Dnipro-Orilsky Nature Reserve. There were 109 vascular plant species and 75 soil macrofauna species recorded within the surveyed floodplain ecosystems. The indicators of soil types and morphological properties are ecologically diverse complexes of soil macrofauna species. The endogean earthworm *A. rosea* is indicator of Fluvisols, and the endogean earthworm *A. trapezoides* and the epigean *D. octaedra* are indicators of Gleaysols. Morphological characteristics of soils, physical properties of soils, and phytoindication estimates of environmental factors were able to explain about 1/3 of the variation in the soil macrofauna community of floodplain ecosystems. The physical properties of soils are the most important driver of variation in the soil macrofauna community. The morphological features of soils and phytoindication scales are also capable of explaining some of the community variation, but most of this influence correlates with the influence of physical properties.

Acknowledgements

The authors are grateful to the staff of the "Dniprovsko-Orilsky" Nature Reserve for their support and assistance with this research. We thank Paul Bradbeer for checking the English text and the two anonymous reviewers for helping us to improve earlier versions of this paper.

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Received July 8, 2022
Accepted October 29, 2022

Appendix 1. Descriptive statistics of soil physical properties for individual sampling sites: 16, 25, 26, 27, 29 (mean ± standard error, N = 105).

Properties	16	25	26	27	29
Soil penetration resistance, MPa (on depth, cm)					
0–5	0.76 ± 0.02	0.65 ± 0.01	0.97 ± 0.03	1.83 ± 0.01	1.29 ± 0.02
5–10	0.81 ± 0.02	0.87 ± 0.01	1.17 ± 0.03	2.10 ± 0.05	1.50 ± 0.04
10–15	0.81 ± 0.02	0.95 ± 0.01	1.54 ± 0.05	1.96 ± 0.05	1.46 ± 0.03
15–20	0.86 ± 0.02	1.37 ± 0.02	2.04 ± 0.06	1.86 ± 0.04	1.45 ± 0.02
20–25	0.81 ± 0.03	1.25 ± 0.02	2.54 ± 0.06	1.97 ± 0.04	1.51 ± 0.03
25–30	0.79 ± 0.02	1.40 ± 0.02	3.03 ± 0.07	2.29 ± 0.05	1.85 ± 0.04
30–35	0.75 ± 0.02	1.52 ± 0.03	3.47 ± 0.10	2.55 ± 0.07	2.44 ± 0.05
35–40	0.81 ± 0.02	1.48 ± 0.03	3.74 ± 0.12	2.96 ± 0.09	3.07 ± 0.08
40–45	1.04 ± 0.03	1.72 ± 0.04	4.33 ± 0.13	3.34 ± 0.10	3.83 ± 0.10
45–50	1.32 ± 0.03	1.78 ± 0.04	4.84 ± 0.13	3.77 ± 0.08	5.02 ± 0.11
50–55	1.79 ± 0.05	1.83 ± 0.03	5.36 ± 0.14	4.17 ± 0.07	6.18 ± 0.13
55–60	2.21 ± 0.05	2.04 ± 0.03	5.91 ± 0.14	4.30 ± 0.07	7.36 ± 0.13
60–65	2.52 ± 0.05	2.29 ± 0.05	6.24 ± 0.16	4.38 ± 0.07	8.10 ± 0.11
65–70	2.86 ± 0.08	2.46 ± 0.05	6.56 ± 0.14	4.61 ± 0.05	8.70 ± 0.10
70–75	3.03 ± 0.09	2.59 ± 0.04	6.73 ± 0.16	4.76 ± 0.04	9.05 ± 0.09
75–80	3.18 ± 0.07	2.91 ± 0.05	6.71 ± 0.16	4.81 ± 0.04	9.40 ± 0.06
80–85	3.44 ± 0.09	2.88 ± 0.06	6.54 ± 0.16	4.89 ± 0.03	9.64 ± 0.03
85–90	3.50 ± 0.09	2.95 ± 0.07	6.59 ± 0.16	4.93 ± 0.02	9.88 ± 0.02
90–95	3.58 ± 0.08	3.01 ± 0.06	6.53 ± 0.18	4.95 ± 0.02	9.94 ± 0.01
95–100	3.69 ± 0.09	3.08 ± 0.05	6.70 ± 0.19	4.96 ± 0.01	9.96 ± 0.01
Other soil properties					
Electrical conductivity (dSm m^{-2})	0.54 ± 0.06	0.14 ± 0.01	0.13 ± 0.01	0.25 ± 0.02	0.22 ± 0.01
Litter depth (cm)	2.40 ± 0.07	3.14 ± 0.05	2.04 ± 0.14	2.10 ± 0.03	2.43 ± 0.04
Soil wetness (%)	5.18 ± 0.27	14.08 ± 0.26	16.32 ± 0.44	30.48 ± 0.58	17.19 ± 0.29
Bulk density (g cm^{-3})	1.07 ± 0.01	1.13 ± 0.01	0.91 ± 0.01	1.02 ± 0.01	1.12 ± 0.00
Aggregate fraction, mm (in %)					
> 10	23.11 ± 0.67	0.63 ± 0.06	13.27 ± 0.57	21.42 ± 0.75	14.40 ± 0.42
7–10	10.39 ± 0.20	4.10 ± 0.14	7.94 ± 0.20	10.75 ± 0.21	7.77 ± 0.11
5–7	11.93 ± 0.22	8.77 ± 0.18	10.34 ± 0.21	12.08 ± 0.17	9.97 ± 0.08
3–5	18.12 ± 0.26	14.17 ± 0.27	23.60 ± 0.40	19.19 ± 0.28	21.60 ± 0.18
2–3	14.36 ± 0.21	15.85 ± 0.20	28.04 ± 0.48	14.61 ± 0.23	23.47 ± 0.26
1–2	8.40 ± 0.23	19.53 ± 0.31	13.55 ± 0.49	8.44 ± 0.22	11.94 ± 0.17
0.5–1	2.37 ± 0.08	19.14 ± 0.43	1.25 ± 0.09	1.90 ± 0.09	3.82 ± 0.10
0.25–0.5	5.03 ± 0.30	13.15 ± 0.40	1.55 ± 0.12	5.08 ± 0.31	3.94 ± 0.15
<0.25	6.29 ± 0.39	4.67 ± 0.13	0.44 ± 0.04	6.53 ± 0.39	3.19 ± 0.18

Appendix 2. Plant species list for individual sampling sites (16, 25, 26, 27, 29).

Raunkiaer life form	Species	16	25	26	27	29
Ph	*Acer campestre* L.	–	–	+	–	–
	Acer negundo L.	+	+	+	+	+
	Fraxinus excelsior L.	+	–	–	+	–
	Gleditsia triacanthos L.	–	+	–	–	–
	Malus sylvestris (L.) Mill.	–	–	–	+	–
	Morus alba L.	–	+	–	–	–
	Morus nigra L.	–	–	+	–	–
	Populus alba L.	–	+	–	–	–
	Populus nigra L.	+	–	+	–	–
	Pyrus communis L.	+	+	+	+	+
	Quercus robur L.	+	+	+	+	+
	Salix alba L.	+	–	–	–	–
	Tilia cordata Mill.	–	+	–	–	–
	Ulmus laevis Pall.	+	+	+	+	+
	Ulmus minor Mill.	+	+	–	–	–
nPh	*Acer tataricum* L.	+	+	–	–	–
	Amorpha fruticosa L.	+	+	+	+	+
	Berberis vulgaris L.	+	+	–	–	–
	Caragana frutex (L.) C. Koch	–	–	–	–	+
	Cornus sanguinea L.	+	–	–	+	–
	Crataegus fallacina Klokov	–	–	–	–	+
	Crataegus monogyna Jacq.	+	–	–	–	–
	Crataegus rhipidophylla Gand.	–	+	+	+	–
	Euonymus europaeus L.	+	+	+	+	+
	Euonymus verrucosus Scop.	–	+	–	+	+
	Frangula alnus Mill.	+	+	+	+	+
	Parthenocissus quinquefolia (L.) Planch.	+	–	–	+	–
	Rhamnus cathartica L.	+	+	–	+	+
	Rosa majalis Herrm	–	–	–	+	–
	Rubus caesius L.	+	–	+	+	+
	Sambucus nigra L.	+	+	+	+	+
HKr	*Agrostis stolonifera* L.	–	–	+	–	–
	Alliaria petiolata (M.Bieb.) Cavara et Grande	+	+	+	+	+
	Anchusa officinalis L.	–	+	–	+	–
	Anthriscus sylvestris (L.) Hoffm.	+	+	+	+	+
	Arctium lappa L.	+	–	+	+	+
	Arctium minus (Hill) Bernh.	–	–	+	–	–
	Asparagus officinalis L.	–	+	+	–	+
	Ballota nigra L.	–	–	+	+	–
	Brachypodium sylvaticum (Huds.) P.Beauv.	+	–	–	–	+
	Calystegia sepium (L.) R.Br.	+	–	+	+	+
	Carduus crispus L.	–	–	–	+	–
	Carex acuta L.	–	–	–	+	+
	Carex caryophyllea Latourr.	–	–	+	–	–
	Carex colchica J.Gay	–	–	+	–	–
	Carex pilosa Scop.	+	–	–	–	–
	Carex vulpina L.	–	–	–	+	+

Appendix 2. Continued

Raunkiaer life form	Species	16	25	26	27	29
	Chelidonium majus L.	+	+	+	–	+
	Cynoglossum officinale L.	+	–	–	–	+
	Erigeron acris L.	–	–	+	–	–
	Erysimum aureum M.Bieb.	–	–	–	–	+
	Festuca drymeja Mert. & W.D.J. Koch	–	–	+	–	+
	Geranium robertianum L.	+	+	+	+	+
	Geum urbanum L.	+	+	+	+	+
	Glechoma hederacea L.	+	+	+	+	+
	Leonurus cardiaca L.	+	–	+	–	–
	Leonurus quinquelobatus Gilib.	–	+	+	+	+
	Lithospermum officinale L.	–	–	–	–	+
	Lycopus europaeus L.	–	–	–	–	+
	Lysimachia nummularia L.	–	–	+	+	+
	Milium effusum L.	–	–	–	+	–
	Myosotis laxa subsp. caespitosa (Schultz) Hyl. ex Nordh.	–	–	+	–	–
	Poa angustifolia L.	–	–	+	–	–
	Poa nemoralis L.	+	–	+	+	+
	Ranunculus repens L.	–	–	–	+	–
	Scrophularia nodosa L.	+	–	+	+	–
	Silene baccifera (L.) Roth	+	+	–	–	+
	Silene latifolia Poir.	–	–	–	–	+
	Solidago canadensis L.	–	–	–	+	–
	Symphytum officinale L.	+	+	+	–	+
	Taraxacum campylodes G.E.Haglund	–	–	–	+	–
	Taraxacum serotinum (Waldst ex Kit) Roir	–	–	+	–	–
	Trifolium repens L.	–	–	–	+	–
	Urtica dioica L.	+	+	+	+	+
	Veronica chamaedrys L.	–	–	–	+	+
	Vicia cracca L.	–	–	+	+	–
	Vincetoxicum rossicum (Kleop.)Barbar.	–	–	+	–	–
	Viola odorata L.	–	–	+	+	–
T	*Ambrosia artemisiifolia* L.	–	–	+	–	–
	Anthriscus cerefolium (L.) Hoffm.	+	+	+	+	+
	Atriplex micrantha C. A. May	–	–	+	–	+
	Bidens tripartita L.	–	–	+	+	–
	Cardamine parviflora L	–	–	+	+	–
	Descurainia sophia L	–	–	+	–	–
	Diplotaxis muralis (L.) DC.	–	–	+	–	–
	Erigeron annuus (L.) Desf.	–	–	–	+	–
	Erigeron canadensis L.	–	–	+	–	–
	Erodium cicutarium (L.) L'Hér.	+	–	–	–	–
	Galium aparine L.	+	+	+	+	+
	Lactuca serriola L.	–	–	+	+	+
	Lapsana communis L.	–	–	–	–	+
	Polygonum aviculare L.	–	–	–	–	+
	Raphanus raphanistrum L.	–	–	+	–	–
	Sonchus oleraceus L.	–	–	–	+	–

Appendix 2. Continued

Raunkiaer life form	*Species*	16	25	26	27	29
	Stellaria media (L.) Vill	+	+	+	+	+
	Vicia tetrasperma (L.) Schreb.	–	–	+	+	+
	Viola arvensis Murr.	–	–	–	+	+
G	*Alopecurus pratensis* subsp. *arundinaceus* (Poir.) Husn.	–	–	+	+	+
	Aristolochia clematitis L.	–	+	+	+	+
	Calamagrostis epigeios (L.) Roth	–	–	+	–	+
	Convallaria majalis L.	+	+	–	+	+
	Convolvulus arvensis L.	–	+	–	–	–
	Elymus repens (L.) Gould	–	–	+	+	+
	Humulus lupulus L.	+	+	–	–	–
	Iris pseudacorus L.	–	–	–	+	–
	Lamium album L.	+	–	–	–	–
	Poa pratensis L.	–	–	+	+	–
	Polygonatum odoratum (Mill.) Druce	–	+	–	–	–
	Sonchus arvensis L.	–	–	–	+	–

Appendix 3. Taxonomy diversity and abundance of the soil macrofauna for individual sampling sites: 16, 25, 26, 27, 29 (mean ± standard error, ind. m^{-2}, N = 105).

Taxon	16	25	26	27	29
Annelidae					
Oligohaeta					
Haplotaxida					
Lumbricidae					
Aporrectodea caliginosa trapezoides (Duges, 1828)	131.05 ± 8.35	8.84 ± 1.73	9.45 ± 1.73	74.51 ± 7.05	61.41 ± 4.02
Aporrectodea rosea (Savigny, 1826)	0.46 ± 0.34	7.47 ± 1.52	64.46 ± 4.25	21.03 ± 3.06	0.30 ± 0.21
Dendrobaena octaedra (Savigny, 1826)	19.50 ± 1.73	–	1.07 ± 0.45	2.90 ± 0.60	4.11 ± 0.69
Eiseniella tetraedra tetraedra (Savigny, 1826)	–	0.15 ± 0.15	–	–	–
Lumbricidae sp. sp. (Cocoon)	–	–	1.37 ± 0.44	–	21.79 ± 1.32
Octodrilus transpadanus (Rosa, 1884)	6.10 ± 1.13	16.00 ± 1.21	2.90 ± 0.71	–	–
Tubificida					
Enchytraeidae					
Enchytraeus sp.	0.46 ± 0.26	5.03 ± 1.19	15.70 ± 2.07	0.46 ± 0.26	–
Arthropoda					
Arachnida					
Araneae					
Gnaphosidae					
Gnaphosidea sp. sp.	–	–	–	0.15 ± 0.15	–
Lycosidae					
Hygrolycosa rubrofasciata (Ohl., 1865)	0.15 ± 0.15	–	–	–	–
Pardosa lugubris (Walckenaer 1802)	0.15 ± 0.15	0.76 ± 0.33	7.47 ± 0.87	–	–
Xerolycosa miniata (L.C. Koch, 1834)	–	–	–	3.05 ± 0.62	8.84 ± 1.24
Thomisidae					
Xysticus sp.	–	–	–	0.30 ± 0.30	–
Chilopoda					
Geophilomorpha					
Geophilidae					
Geophilus proximus C.L.Koch 1847	13.56 ± 2.11	–	6.10 ± 1.00	24.84 ± 1.90	14.93 ± 1.55
Pachymerium ferrugineum (C.L.Koch 1835)	0.91 ± 0.42	0.46 ± 0.34	3.05 ± 0.75	–	7.77 ± 1.53
Lithobiomorpha					
Lithobiidae					
Lithobius (Lithobius) forficatus (Linnaeus 1758)	19.05 ± 1.19	3.81 ± 0.67	4.72 ± 0.72	0.15 ± 0.15	1.07 ± 0.39
Lithobius (Lithobius) lucifugus L. Koch 1862	13.87 ± 0.69	–	6.55 ± 0.80	1.52 ± 0.46	2.13 ± 0.53
Lithobius (Monotarsobius) aeruginosus L. Koch 1862	1.22 ± 0.47	–	–	–	–
Lithobius (Monotarsobius) curtipes C.L. Koch 1847	–	0.76 ± 0.40	–	–	–
Diplopoda					
Julida					
Julidae					
Megaphyllum rossicum (Timotheew, 1897)	0.30 ± 0.21	–	17.37 ± 0.75	0.30 ± 0.21	15.39 ± 0.30
Megaphyllum sjaelandicum (Meinert, 1868)	1.22 ± 0.42	1.07 ± 0.39	26.67 ± 1.46	8.23 ± 0.78	5.49 ± 0.74
Polydesmida					
Paradoxosomatidae					
Polydesmus inconstans Latzel 1884	–	–	6.40 ± 0.88	2.59 ± 0.58	–
Insecta					
Coleoptera					
Carabidae					

Appendix 3. Continued

Taxon	16	25	26	27	29
Amara (Amara) tibialis (Paykull 1798)	–	–	–	1.22 ± 0.42	–
Amara familiaris (Duftschmid, 1812)	–	–	–	–	29.71 ± 2.53
Amara similata (Gyllenhal, 1810)	–	–	–	–	2.90 ± 0.68
Amara sp. (larv.)	–	–	0.15 ± 0.15	–	–
Calathus (Calathus) fuscipes (Goeze, 1777)	–	–	–	–	1.37 ± 0.72
Calosoma (Calosoma) inquisitor (Linne 1758)	–	–	–	–	0.46 ± 0.26
Carabidae sp. 1 (larv.)	–	–	–	0.61 ± 0.30	–
Carabidae sp. 2 (larv.)	–	0.15 ± 0.15	–	0.46 ± 0.26	–
Carabus (Pachystus) hungaricus scythus Motschulsky, 1847	–	0.15 ± 0.15	–	–	–
Harpalus (Harpalus) affinis (Schrank 1781)	–	–	–	0.30 ± 0.21	–
Harpalus (Harpalus) amplicollis Ménétriés 1848	–	–	–	0.15 ± 0.15	–
Harpalus (Pseudoophonus) griseus Panzer, 1796	–	–	–	–	0.15 ± 0.15
Pterostichus (Phonias) ovoideus (Sturm 1824)	–	–	–	0.30 ± 0.21	–
Pterostichus (Pseudomaseus) anthracinus (Illiger, 1798)	3.35 ± 0.83	–	–	–	–
Chrysomelidae					
Chrysolina (Fastuolina) fastuosa (Scopoli 1763)	–	0.15 ± 0.15	0.15 ± 0.15	0.61 ± 0.30	1.52 ± 0.51
Curculionidae					
Otiorhynchus (Cryphiphorus) ligustici (Linnaeus 1758)	0.61 ± 0.30	0.91 ± 0.42	1.83 ± 0.50	0.15 ± 0.15	9.14 ± 0.92
Elateridae					
Adrastus limbatus (Fabricius 1776)	1.52 ± 0.46	–	–	–	–
Agriotes (Agriotes) lineatus (Linnaeus 1767)	–	–	0.30 ± 0.21	0.15 ± 0.15	1.37 ± 0.44
Agrypnus murinus (Linnaeus 1758)	1.52 ± 0.46	–	–	0.15 ± 0.15	0.30 ± 0.21
Ampedus (Ampedus) balteatus (Linnaeus 1758)	–	1.83 ± 0.50	–	–	–
Athous (Athous) haemorrhoidalis (Fabricius 1801)	7.62 ± 1.21	5.18 ± 1.05	0.61 ± 0.30	2.44 ± 0.56	11.58 ± 1.33
Cardiophorus rufipes (Goeze, 1777)	0.46 ± 0.26	0.76 ± 0.33	0.30 ± 0.21	0.46 ± 0.26	7.47 ± 0.78
Prosternon tessellatum (Linnaeus 1758)	0.46 ± 0.26	–	0.46 ± 0.26	3.66 ± 0.69	1.68 ± 0.48
Silphidae					
Dendroxena quadrimaculata (Scopoli 1772)	5.03 ± 0.95	–	–	–	0.15 ± 0.15
Staphylinidae					
Drusilla canaliculata (Fabricius, 1787)	–	–	–	–	0.46 ± 0.26
Othius angustus angustus Stephens 1833	3.05 ± 0.75	–	–	–	–
Othius punctulatus (Goeze 1777)	–	–	–	–	0.30 ± 0.21
Platydracus (Platydracus) fulvipes (Scopoli 1763)	0.15 ± 0.15	–	1.22 ± 0.42	0.15 ± 0.15	2.74 ± 0.73
Staphylininae sp. sp.	–	–	–	0.61 ± 0.30	–
Tenebrionidae					
Cylindronotus (Nalassus) brevicollis Kuster, 1850	–	–	–	–	0.15 ± 0.15
Helops coeruleus (Linnaeus 1758)	0.46 ± 0.26	–	–	–	0.30 ± 0.21
Isomira murina (Linnaeus 1758)	0.61 ± 0.37	17.83 ± 2.20	0.15 ± 0.15	0.46 ± 0.26	17.6 ± 1.60
Opatrum sabulosum (Linnaeus 1761)	–	–	–	–	0.15 ± 0.15
Melolonthidae					
Amphimallon solstitiale (Linnaeus 1758)	–	0.46 ± 0.26	0.15 ± 0.15	–	6.55 ± 0.96
Melolontha melolontha (Linnaeus 1758)	20.88 ± 1.15	7.62 ± 1.04	2.90 ± 0.60	16.46 ± 1.16	32.46 ± 1.25
Polyphylla (Polyphylla) fullo (Linnaeus 1758)	1.52 ± 0.46	0.46 ± 0.26	0.61 ± 0.30	–	4.72 ± 0.84
Serica brunnea (Linnaeus 1758)	0.61 ± 0.30	26.21 ± 1.21	1.22 ± 0.47	0.46 ± 0.26	17.37 ± 1.09
Dermaptera					
Forficulidae					

Appendix 3. Continued

Forficula auricularia Linnaeus 1758	0.30 ± 0.21	0.15 ± 0.15	0.30 ± 0.21	–	5.03 ± 0.90
Therevidae					
Taxon	16	25	26	27	29
Thereva nobilitata (Fabricius 1775)	–	2.90 ± 0.64	6.25 ± 0.77	1.07 ± 0.39	1.37 ± 0.44
Asilidae					
Asilidae sp. 1	–	0.30 ± 0.21	1.22 ± 0.42	–	0.46 ± 0.26
Limoniidae					
Rhipidia (Rhipidia) uniseriata Schiner, 1864	–	3.66 ± 1.00	–	–	–
Rhagionidae					
Rhagio scolopaceus (Linnaeus 1758)	–	–	4.42 ± 0.73	–	1.83 ± 0.50
Stratiomyidae					
Chloromyia formosa (Scopoli, 1763)	1.37 ± 0.49	–	–	–	–
Tabanidae					
Tabanus bromius Linnaeus 1758	3.20 ± 0.73	5.18 ± 0.82	2.13 ± 0.53	0.30 ± 0.21	1.83 ± 0.50
Tipulidae					
Tipula (Lunatipula) lunata Linnaeus 1758	14.32 ± 1.35	11.12 ± 0.92	–	16.15 ± 1.83	1.37 ± 0.49
Empididae					
Empis (Kritempis) livida Linnaeus 1758	–	–	–	–	0.15 ± 0.15
Lepidoptera					
Noctuidae					
Agrotis segetum (Denis & Schiffermüller, 1775)	12.65 ± 2.16	4.57 ± 1.05	40.53 ± 3.64	10.82 ± 1.34	6.25 ± 1.14
Malacostraca					
Isopoda					
Trachelipodidae					
Trachelipus rathkii (Brandt 1833)	16.76 ± 0.70	1.83 ± 0.50	5.33 ± 0.74	9.90 ± 0.76	17.37 ± 0.44
Mollusca					
Gastropoda					
Pulmonata					
Cochlicopidae					
Cochlicopa lubrica (O.F. Muller 1774)	0.15 ± 0.15	0.15 ± 0.15	0.30 ± 0.21	0.91 ± 0.36	0.30 ± 0.21
Gastrodontidae					
Zonitoides (Zonitoides) nitidus (O.F. Muller 1774)	–	–	0.30 ± 0.30	–	–
Helicidae					
Cepaea (Austrotachea) vindobonensis (C. Pfeiffer 1828)	–	–	0.15 ± 0.15	–	1.98 ± 0.52
Succineidae					
Succinella oblonga (Draparnaud 1801)	–	–	0.15 ± 0.15	–	–
Valloniidae					
Vallonia pulchella (O.F. Muller 1774)	–	–	–	–	0.15 ± 0.15
Vitrinidae					
Vitrina pellucida (O.F. Muller 1774)	–	–	–	0.30 ± 0.21	–
Community abundance	304.6 ± 31.6	135.9 ± 21.1	244.4 ± 28.6	208.3 ± 27.2	332.0 ± 34.9