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SPATIAL ORGANIZATION OF THE SOIL MACROFAUNA COMMUNITY OF AN OAK FOREST IN THE STEPPE ZONE OF UKRAINE

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Background. Environmental impact assessments and the development of measures for the protection and sustainable use of ecosystems should take into account that not only steppe ecosystems but also forest, marsh, salt marsh and meadow ecosystems are referenced for the steppe zone. A comparative approach requires the study of reference ecosystems to understand how much a particular ecosystem has been transformed or how far it is from natural patterns in the restoration process. The soil macrofaunal community of the forest ecosystem of the right bank of the Samara River can be considered a reference for many forest ecosystems in the region. The aim of this study was to identify patterns of spatial organization of the soil macrofaunal community of an oak forest on the right bank of the Samara River.

Materials and Methods. A study was conducted in a deciduous woodland located in an oak forest on the right bank of the Samara River. The study area was divided into 5 transects, each consisting of 20 sampling points with a 2 m distance between rows. The samples of the soil macrofauna were taken from a single block of soil that was 25×25×30 cm deep and removed quickly. Vascular plant species lists were recorded for each 2×2 m subplot. The soil penetration resistance and electrical conductivity were measured. Soil faunal trophic activity was assessed by means of a bait lamina test.

Results and Discussion. The spatial structure of the community is complex in terms of hierarchy. The driver of the broad-scale component of spatial variation in the community is the properties of the topsoil, mainly the density of the litter. Vegetation cover forms a broad component of the spatial variation in soil macrofauna. An important factor in structuring ecological space is the location of trees. The pure spatial pattern is represented by broad-, medium-, and fine-scale components.

Conclusion. The soil macrofaunal community of an oak forest on the slope of the right bank of a steppe river has a high level of abundance and taxonomic and ecological diversity. The spatial distribution of trees forms a broad-scale component of variation in the soil macrofaunal community, and herbaceous cover forms a medium-scale component. The fine-scale component of community variation is due to neutral factors.

Keywords: diversity, spatial ecology, hierarchical organization, pattern, community ordination, procrust analysis, environmental impact assessment

INTRODUCTION

Soil is a medium for a wide variety of biological objects (Jezierska-Tys *et al.*, 2020). Soil animals perform important ecological functions, contributing to soil formation processes and intersystem linkages. According to J. Tsaryk (2021), interecosystem linkages maintain the integrity of ecological systems from the consortium to the biosphere. The connections between consortia and ecosystems of different hierarchical levels that form the biosphere are not well understood (Tsaryk, 2021). Soil animals can provide valuable information for assessing ecological regimes in soils and are commonly used for soil diagnostics (Schloter *et al.*, 2003). It is important to note that different groups of animals perceive soil as a habitat differently (Pollierer *et al.*, 2021). For instance, small animals such as soil protozoa or some nematodes live in a film of water that covers the soil particles and therefore perceive soil as no different from water. These animals are referred to as geohydrobiota. Slightly larger animals, such as soil mites, enchytraeids, nematodes, collembola, proturans and diplurans, inhabit soil cracks. They reside on the surface of soil particles and do not require special adaptations to move through the soil. These animals, along with others of similar size, are referred to as geoatmobionts. M. P. Kozlovsky's research revealed the bioindication capacities of phytonematode communities in terrestrial ecosystems (Kozlovskyi, 2009). The Collembola communities in floodplain forests are sensitive to hydrological regime and tree stand age (Sterzyńska *et al.*, 2014). Soil animals that are larger than 2 mm are referred to as macrofauna. The vast majority of these animals are larger than the size of soil particles, so they have to develop certain adaptations to move in the soil or use galleries of soil passages created by other animals. The representatives of the soil macrofauna perceive the soil as a whole, so they are the best for the purposes of zoological soil diagnostics (Maslikova, 2018).

The issue of zoological soil diagnostics has been a under scholarly discussion for some time (Gilarov, 1965), but this topic requires further consideration. Identifying the factors that affect soil animals at different spatial levels is important (Martins da Silva *et al.*, 2012). Soil animals are significantly restricted in their ability to move (Collis-George, 1959). The imaginal stages of insect development have considerable potential for dispersal, but larvae that emerge from eggs cannot spread over a significant distance on their own (Truman, 2019). Other representative soil animals that are entirely soil-dwelling are also severely limited in their migratory ability. Therefore, soil animals are sensitive to specific habitat conditions, and the structure of their communities is influenced by various factors (Kudureti *et al.*, 2023). These include specific soil and vegetation features, the history of the animal population, ecological interactions and neutral factors. Understanding the patterns of formation of soil macrofaunal communities is the basis for the application of zoological indications and zoological diagnostics in general practice.

The following types of substance cycling and energy flow are represented in ecosystems in the steppe zone of Ukraine: steppe, forest, meadow, salt marsh and swamp. Environmental impact assessments and the development of measures for the protection and sustainable use of ecosystems should take into account that not only steppe ecosystems but also forest, marsh, salt marsh and meadow ecosystems are the reference for the steppe zone. The natural forest ecosystems in the steppe zone are composed of watershed-ravine and valley-terrace landscapes. Forests within the watershed-ravine landscape are located in steppe ravine, where they form so-called bayraks. Genetically close to them are the forests on the slopes of the right banks of steppe rivers, called prystinas. The animal community of ravine forests has attracted attention in the context of solving problems related to zoological soil diagnostics. Soil macrofauna can be used to indicate the level of anthropogenic transformation of urban areas (Kunakh *et al*., 2021; Yorkina *et al.*, 2019; Yorkina & Budakova, 2020) and for the diagnosis of reclaimed land (Kunakh *et al.*, 2024). The comparative approach requires the study of reference ecosystems to understand the extent to which a particular ecosystem has been transformed or how far it is from natural patterns in the process of its recovery. The community of soil macrofauna in the forest ecosystem on the right bank of the Samara River can be considered a reference for many forest ecosystems in the region. The aim of this study was to reveal the spatial organization patterns of the soil macrofaunal community of an oak forest on the right bank of the Samara River

MATERIALS AND METHODS

Sampling methods. In May 2010, a study was conducted in a deciduous woodland (0.04 ha) located in an oak forest (48°45′N, 35°25′E) on the right bank of the Samara River (Dnipropetrovsk region, Ukraine). The study area was divided into 5 transects, each consisting of 20 sampling points with a 2 m distance between rows. The longest side of the polygon was situated along the steepest slope of the relief with an inclination of 9°. Soil macrofauna refers to invertebrates that are visible to the naked eye (Warren & Zou, 2002). These include geobionts, large soil invertebrates that permanently inhabit the soil, and geophiles, organisms that live in the soil only for particular phases of their lives (Gholami *et al.*, 2016). The samples were taken from a single block of soil that was 25×25×30 cm deep and removed quickly. Prior to taking the soil samples, a quadrat was fixed onto the soil surface. The soil macrofauna was manually collected from the soil samples, sorted, and stored in 4% formaldehyde (Mathieu *et al.*, 2004). Soil faunal trophic activity was assessed by means of a bait lamina test (Rozen *et al.*, 2010).

Vegetation survey and plant variables. Vascular plant species lists were recorded for each 2×2 m subplot. Visual estimates of species cover were made using the nine-degree Braun-Blanquet scale (Westhoff & Van Der Maarel, 1978). The projective cover of plant species was recorded at ground level, at the understorey (up to 2 m height), and at the canopy (above 2 m height). Species-level identification was possible for all quadrats. The analyses excluded seedlings and saplings of woody species. Within the plot, all woody stems ≥1 cm in diameter at breast height were measured and mapped. The stands of the oak forest were represented by *Quercus robur* L., *Fraxinus excelsior* L. and *Acer campestre* L. The second stratum was represented by *Ulmus minor* Mill., *Morus nigra* L., and *Pyrus communis* L. *Acer platanoides* L. and *Robinia pseudoacacia* L. were sometimes observed. Shrubs included *Acer tataricum* L., *Crataegus fallacina* Klokov, and *Euonymus verrucosus* Scop. The herbage was dominated by *Viola mirabilis* L., with plants such as *Alliaria petiolata* (M.Bieb.) Cavara et Grande, *Ballota nigra* L., *Geum urbanum* L., *Erigeron canadensis* L., and *Stellaria media* (L.) Vill.

From the syntaxonomic perspective, vegetation can be identified as follows:
Class *Carpino-Fagetea* Passarge in Passarge et G. Hofmann 1968
Ordo *Alno-Fraxinetalia excelsioris* Passarge et G. Hofmann 1968
Union *Alnion incanae* Pawáowski 1928
Ass. *Violo odoratae-Fraxinetum (excelsioris)* Nazarenko et Kuzemko 2011

Soil variables. The soil of Luvic Chernozem (Siltic, Hyperhumic, Pachic) was formed on the slopes of a gully in forests under natural forest vegetation. In addition to precipitation, soils receive water from surface runoff from surrounding areas (Gorban *et al.*, 2020; Yakovenko, 2017; Yakovenko & Zhukov, 2021). Soil penetration resistance was measured in the field using a hand penetrometer (Eijkelkamp) at 5 cm intervals to a depth of 50 cm. The device has an average measurement error of ±8 %. A cone with a cross-sectional dimension of 2 cm^2 was used for the measurements. The soil penetration resistance was measured once at each point. The electrical conductivity of the soil *in situ* was measured using the HI 76305 sensor from Hanna Instruments, Woonsocket, R. I., in conjunction with the portable device HI 993310.

Statistical analysis. Redundancy analysis (RDA) was applied to the analysis of variance for both herb layer and soil macrofauna species composition (Rao, 1964). Prior to analysis, the percentage cover of plant species or the abundance of animal species underwent Hellinger transformation to avoid problematic Euclidean distances used in the RDA (Legendre & Gallagher, 2001). The variables soil mechanical impedance, soil electrical conductivity, and litter layer thickness were log-transformed. First, we tested the significance of the RDA global model. Next, we used the geographic coordinates of the sampling locations to generate a set of orthogonal eigenvector-based spatial variables (dbMEMs), each representing a pattern of a particular scale within the extent of the sampling area (Borcard & Legendre, 2002). The significance of the soil models was tested using the Monte Carlo permutation test (9999 permutations). To inspect the spatial scaling of community variation in detail, the scalogram approach was applied (Legendre & Legendre, 2012). To achieve this, two sets of RDA analyses were conducted, each using one of the dbMEM variables as a predictor. The first set of RDA analyses used raw (Hellinger-transformed) species data as a response variable, while the second set used residuals of the environmental model, in which forward-selected environmental variables acted as predictors (Chudomelová, Zelený, 2017). From each RDA, we extracted R^2_{adj} for individual dbMEMs and plotted them into juxtaposed bar plots (Chang *et al.*, 2013). All the statistical analyses were conducted in R (v. 3.5.0., R Foundation for Statistical Computing, Vienna, AT) using the following packages: vegan (v. 2.5-2, https://CRAN.R-project.org/package=vegan) for multivariate analysis and for the computation of global and partial Moran's I (Oksanen *et al.*, 2018) and adespatial (v. 0.3-2. https://CRAN.R-project.org/package=adespatial) for forward selection and for the generation of spatial filters (Dray *et al.*, 2018).

RESULTS

Soil macrofauna. Manual examination of the soil samples revealed that the community included 42 species of soil macrofauna (**Table 1**). Additional recording methods identified the presence of 56 species. The abundance of soil macrofauna was 331.8±43.6 ind./m^2. Earthworms were the dominant group of invertebrates, accounting for 41.1% of the total number of communities. Earthworms were represented by 5 epigeic, endogeic and anecic species (**Table 1**). The abundance of the epigeic species *Dendrobaena octaedra* (Savigny, 1826) was 6.08±1.04 ind./m^2. The group of endogeic earthworms included three species: *Aporrectodea caliginosa trapezoides* (Duges, 1828), *Aporrectodea rosea* (Savigny, 1826), and *Octolasion lacteum* (Oerley, 1885). This group was the most numerous among the earthworms in the community. The abundance of the anecic species *Octodrilus transpadanus* (Rosa, 1884) was 6.72±1.09 ind./m^2.

Table 1. **Taxonomic diversity and abundance of soil macrofauna**

Taxon	Abundance, mean ± s.e., ind./m^2
Annelidae	
Oligohaeta	
Haplotaxida	
Lumbricidae	
Aporrectodea caliginosa trapezoides (Duges, 1828)	26.08±2.90
Aporrectodea rosea (Savigny, 1826)	20.32±2.52
Dendrobaena octaedra (Savigny, 1826)	6.08±1.04
Octodrilus transpadanus (Rosa, 1884)	6.72±1.09
Octolasion lacteum (Oerley, 1885)	77.12±3.91
Arthropoda	
Arachnida	
Araneae	
Agelenidae	
Tegenaria lapicidinarum Spassky, 1934	+
Dysderidae	
Harpactea rubicunda (C. L. Koch, 1838)	+
Linyphiidae	
Megalephyphantes pseudocollinus Saaristo 1997	+
Liocranidae	
Agroeca brunnea (Blackwall, 1833)	+
Lycosidae	
Pardosa lugubris (Walckenaer 1802)	19.68±1.85
Trochosa terricola Thorell 1856	+
Opiliones	
Phalangiidae	
Zacheus lupatus (Eichwald, 1830)	5.92±1.06
Odiellus bieniaszi (Kulczynski 1909)	+

Continued Table 1

Chilopoda	
Geophilomorpha	
Geophilidae	
Geophilus proximus C.L.Koch 1847	19.20±2.02
Pachymerium ferrugineum (C. L. Koch 1835)	16.32±3.18
Lithobiomorpha	
Lithobiidae	
Lithobius (*Monotarsobius*) *curtipes* C. L. Koch 1847	18.08±1.76
Scolopendromorpha	
Cryptopidae	
Cryptops hortensis (Donovan 1810)	2.88±0.73
Diplopoda	
Julida	
Julidae	
Megaphyllum sjaelandicum (Meinert, 1868)	3.20±0.64
Polydesmida	
Polydesmidae	
Schizoturanius dmitrievi (Timotheew 1899)	1.92±0.52
Insecta	
Coleoptera	
Cantharidae	
Malthodes (*Malthodes*) *marginatus* (Latreille 1806)	0.48±0.36
Carabidae	
Badister (*Badister*) *bullatus* (Schrank 1798)	5.12±1.04
Brachinus (*Brachinus*) *crepitans* (Linnaeus, 1758)	4.64±0.89
Carabus (*Tachypus*) *cancellatus* Illiger 1798	+
Harpalus (*Pseudoophonus*) *rufipes* (De Geer, 1774)	+
Panagaeus cruxmajor L.	+
Pterostichus oblongopunctatus (Fabricius 1787)	+
Pterostichus (*Morphnosoma*) *melanarius* (Illiger, 1798)	15.52±2.38
Chrysomelidae	
Chrysolina (*Fastuolina*) *fastuosa* (Scopoli 1763)	2.40±0.57
Curculionidae	
Otiorhynchus (*Choilisanus*) *raucus* (Fabricius, 1777)	2.56±0.59
Elateridae	
Ampedus (Ampedus) balteatus (Linnaeus 1758)	3.20±0.64
Athous (Athous) haemorrhoidalis (Fabricius 1801)	5.92±1.08
Cardiophorus rufipes (Goeze, 1777)	0.96±0.38
Prosternon tessellatum (Linnaeus 1758)	0.16±0.16

Continued Table 1

Melolonthidae	
Amphimallon solstitiale (Linnaeus 1758)	6.24±1.06
Holochelus (*Miltotrogus*) *vernus* (Germar 1823)	5.44±1.00
Silphidae	
Nicrophorus humator (Gleditsch 1767)	+
Oiceptoma thoracica (Linnaeus, 1758)	+
Silpha (*Silpha*) *carinata* Herbst, 1783	+
Dendroxena quadrimaculata (Scopoli 1772)	2.40±0.57
Staphylinidae	
Lathrobium rufescens Motschulsky, 1860	0.96±0.38
Staphylinus erythropterus Linnaeus, 1758	3.04±0.63
Tenebrionidae	
Crypticus quisquilius (Linnaeus 1761)	+
Cylindronotus (*Nalassus*) *brevicollis* Kuster, 1850	0.80±0.35
Diptera	
Stratiomyidae	
Chloromyia formosa (Scopoli, 1763)	3.20±0.64
Tabanidae	
Tabanus bromius Linnaeus 1758	2.56±0.59
Homoptera	
Cicadidae	
Cicadetta montana (Scopoli, 1772)	0.16±0.16
Lepidoptera	
Noctuidae	
Agrotis segetum (Denis & Schiffermüller, 1775)	3.20±0.64
Microcoryphia	
Machilidae	
Charimachilis ukraniensis Stach 1958	0.32±0.23
Raphidioptera	
Raphidiidae	
Xanthostigma xanthostigma (Schummel 1832)	0.32±0.23
Malacostraca	
Isopoda	
Oniscoidae	
Armadillidium nasutum Budde-Lund 1885	11.20±1.83
Trachelipodidae	
Protracheoniscus topczievi Borutzkii 1975	0.32±0.32
Trachelipus rathkii (Brandt 1833)	20.00±1.85

End of the Table 1

Mollusca	
Gastropoda	
Pulmonata	
Clausiliidae	
Cochlodina (*Cochlodina*) *laminata* (Montagu 1803)	0.16±0.16
Gastrodontidae	
Zonitoides (*Zonitoides*) *nitidus* (O. F. Muller 1774)	1.12±0.41
Hygromiidae	
Euomphalia strigella (Draparnaud 1801)	2.24±0.56
Patulidae	
Discus (*Discus*) *ruderatus* (W. Hartmann 1821)	3.68±0.68

The abundance of spiders was 19.68±1.85 ind./m^2. Manual sampling revealed one species of *Pardosa lugubris* (Walckenaer 1802). The use of Barber traps allowed the identification of a much larger number of spider species in this ecosystem. The germplasms Opiliones were represented by two species: *Zacheus lupatus* (Eichwald, 1830) and *Odiellus bieniaszi* (Kulczynski 1909). Centipedes were represented by three species, *Geophilus proximus* C. L. Koch 1847, *Pachymerium ferrugineum* (C. L. Koch 1835), and *Lithobius (Monotarsobius) curtipes* C. L. Koch 1847, but millipedes were represented by two species, *Megaphyllum sjaelandicum* (Meinert, 1868) and *Schizoturanius dmitrievi* (Timotheew 1899). Additionally, in the oak forest, a scolopendra *Cryptops hortensis* (Donovan 1810) was found with an abundance of 2.88±0.73 ind./m^2.

Ground beetles (Carabidae) are a large and diverse group of insects. They were represented by both larval and imaginal phases. Leaf beetles (Chrysomelidae) were represented by the larvae *Chrysolina* (*Fastuolina*) *fastuosa* (Scopoli 1763), and snout beetles (Curculionidae) were represented by the larvae *Otiorhynchus* (*Choilisanus*) *raucus* (Fabricius, 1777). The larvae of click beetles (Elateridae) were represented by 4 species, among which the typical inhabitant of oak forest soils, *Athous* (*Athous*) *haemorrhoidalis* (Fabricius 1801), dominated. The larvae of Melolonthidae have a C-shaped shape and are represented by two species, *Amphimallon solstitiale* (Linnaeus 1758) and *Holochelus* (*Miltotrogus*) *vernus* (Germar 1823). The larvae of Silphidae were represented by 4 species, among which *Dendroxena quadrimaculata* (Scopoli 1772) was found in the manual analysis of soil samples with an abundance of 2.40±0.57 ind./m^2. Staphylinidae was represented by two species, among which *Staphylinus erythropterus* Linnaeus 1758 predominated in abundance. The larvae of the darkling beetles (Tenebrionidae) were represented by two species, namely, *Crypticus quisquilius* (Linnaeus 1761) and *Cylindronotus* (*Nalassus*) *brevicollis* Kuster, 1850.

The soil macrofauna also included the litter inhabitants *Chloromyia formosa* (Scopoli, 1763). The soil layer was inhabited by larvae of the horse fly (Tabanidae) *Tabanus bromius* Linnaeus 1758 and larvae of Cicadidae *Cicadetta montana* (Scopoli, 1772). The soil larvae of the butterfly *Agrotis segetum* (Denis & Schiffermüller, 1775) are herbivorous. The abundances of *Charimachilis ukraniensis* Stach 1958 and the larvae of *Xanthostigma xanthostigma* (Schummel 1832) were sporadically recorded. There were numerous groups of woodlice, represented by 3 species. High abundances of this genus were detected in the woodlice *Trachelipus rathkii* (Brandt 1833) and *Armadillidium nasutum* Budde-Lund 1885. The woodlice *Protracheoniscus topczievi* Borutzkii 1975 was occasionally found. Molluscs were represented by 4 species, among which *Discus* (*Discus*) *ruderatus* (W. Hartmann 1821) predominated.

Soil properties. The depth of the litter layer was 3.04±0.06 cm, and 95 % of the litter layers ranged from 2.03 to 4.20 cm (**Table 2**). The soil electrical conductivity was 0.54±0.02 dS/m, and in 95 % of the cases, it ranged from 0.24 to 0.90 dS/m. The projected vegetation cover was 31.80±1.27 %, and 95 % of the total vegetation cover was in the range of 15–60 %. The bait-lamina test was 8.83±0.24, with a variation in 95 % of cases in the range of 5–14. The depth of the litter was negatively correlated with the vegetative cover and the electrical conductivity of the soil but was positively correlated with the bait-lamina test results (**Fig. 1**). The electrical conductivity of the soil was positively correlated with the vegetative cover and negatively correlated with the bait-lamina test. The projective cover was negatively correlated with the bait-lamina test. The soil penetration resistance was the lowest in the upper soil layer and monotonically increased with depth. A local maximum coefficient of variation of the soil penetration resistance was observed at a depth of 20–25 cm.

Table 2. **Descriptive statistics of the environmental parameters**

Indicator	Mean ± S.E.	2.5 % persentil	97.5 % persentil	CV, %
Environmental indicators				
Litter layer, cm	3.04±0.06	2.03	4.20	18.65
Soil electrical conductivity, dS/m	0.54±0.02	0.24	0.90	33.16
Projected vegetation cover, %	31.80±1.27	15.00	60.00	39.95
Bait-lamina test	8.83±0.24	5.00	14.00	26.70
Soil penetration resistance in the soil layer, cm in MPa				
0–5	1.71±0.03	1.10	2.40	17.96
5–10	2.38±0.03	1.80	3.00	14.64
10–15	2.84±0.06	1.90	4.00	19.73
15–20	3.45±0.08	2.00	5.20	23.70
20–25	3.95±0.10	2.20	5.80	25.40
25–30	4.38±0.08	2.80	6.00	19.14
30–35	4.47±0.08	2.87	6.00	18.64
35–40	4.64±0.08	3.20	6.17	16.59
40–45	5.04±0.08	3.60	7.00	16.18
45–50	5.12±0.08	3.41	6.80	16.58

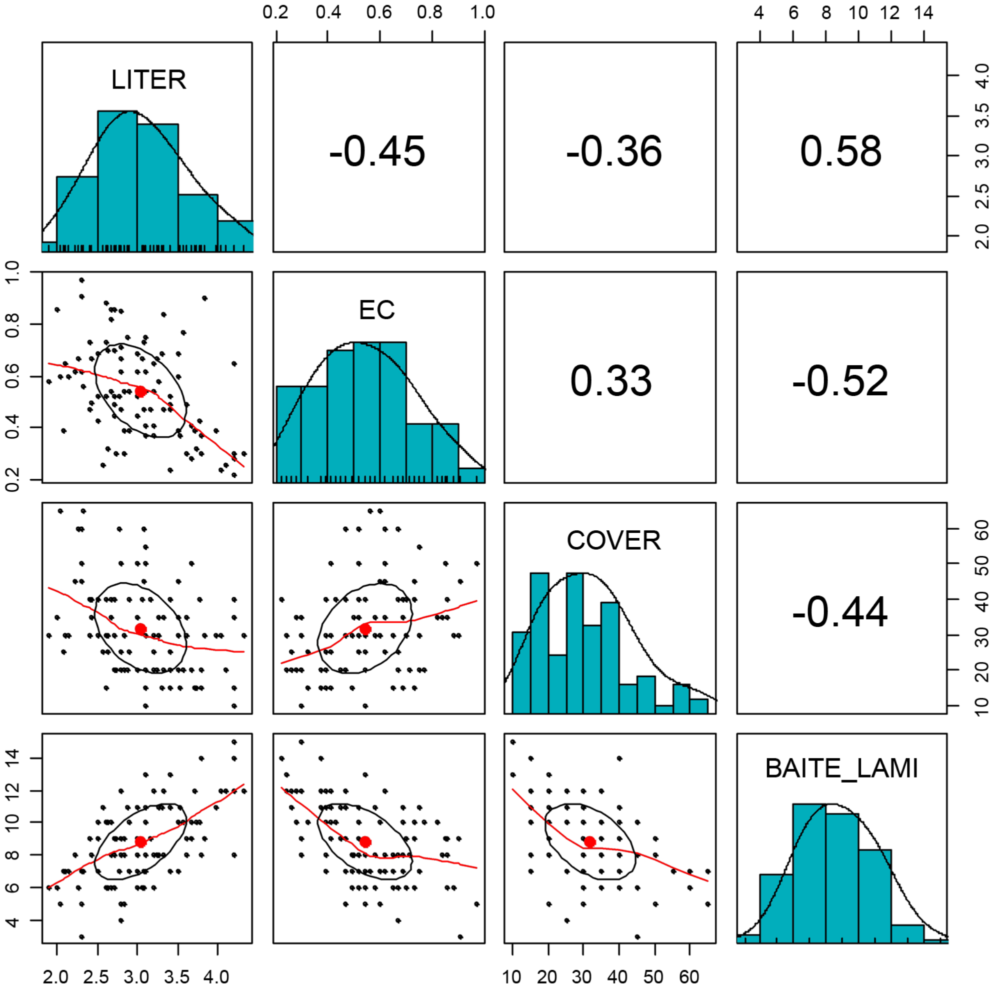

Fig. 1. Correlations between environmental indicators. Histograms of the distribution of indicators are shown on the diagonal. The upper right half-square shows Pearson's correlation coefficients, while the lower left half-square shows scatter plots and correlation ellipses

Influence of spatial variables on soil macrofauna. The species found in at least 5 samples were used for further analysis. There were 34 such species. The detrend analysis showed that the length of the longest ordination axis was 2.5, which exceeded the conditional critical level of 2. Therefore, we used canonical correspondence analysis as the ordination procedure. The spatial variables explained 33.8 % of the variation in the community (*F* = 2.1, *P* = 0.001) (**Fig. 2**). The spatial variables at different scales contribute to the explained variation in the community, and we can distinguish between broad-, medium-, and fine-scale components (**Fig. 3**). The broad-scale components included spatial variables 1–8, which were able to explain 12.9 % of the variation in the community (*F* = 2.1, *P* = 0.001). The medium-scale components included spatial variables 11, 12, 16, 23, and 26, which explained 4.8% of the variation in the community

($F = 2.0$, $P = 0.001$). The fine-scale component was described by spatial variable 40 and was able to explain 0.6% of the variation in the community ($F = 1.6$, $P = 0.05$). Canonical analysis of the correspondence of the soil macrofaunal community with spatial variables as predictors allowed us to extract six statistically significant axes. These axes can be labelled with soil invertebrate species (**Table 3**).

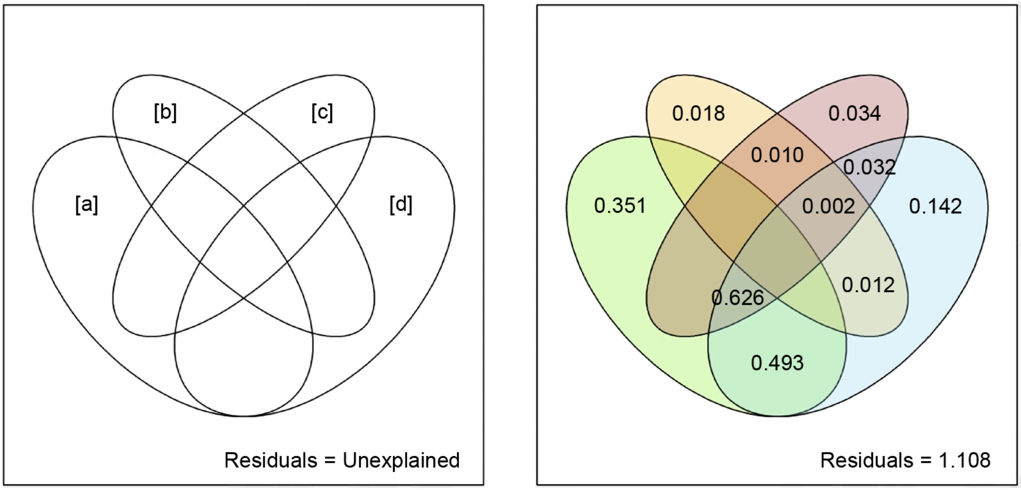

Fig. 2. Variance partitioning between spatial, topsoil, profile soil, and plant explanatory variables. [a] – variation captured by spatial (dbMEM) variables corresponds to the pure spatial component; [b] – variation explained solely by topsoil variables (soil electrical conductivity, forest litter depth, soil water content, soil bulk density, aggregate fraction composition in the soil layer 5 cm deep from the surface); [c] – variation explained solely by soil penetration resistance variables measured to a depth of 1 meter at intervals of every 5 cm; [d] – explained solely by plant variables. The intersection of the ellipses corresponds to the variations explained by the respective sources together. All the variance fractions shown are significant at $P < 0.001$

Table 3. **Correlations between soil macrofaunal species and spatial canonical axes. The three species with the highest and lowest correlation coefficients with the canonical axes are presented**

Sign	CCA1 $F = 19.9$, $P = 0.001$	CCA2 $F = 12.4$, $P = 0.001$	CCA3 $F = 12.1$, $P = 0.001$	CCA4 $F = 10.5$, $P = 0.001$	CCA5 $F = 9.4$, $P = 0.001$	CCA6 $F = 8.1$, $P = 0.007$
+	*E. strigella*	*Ch. fastuosa*	*Sch. dmitriewi*	*L. rufesceus*	*C. rufipes*	*D. quadrimaculata*
	B. bullatus	*C. rufipes*	*S. erythropterus*	*O. raucus*	*L. rufesceus*	*T. bromius*
	A. balteatus	*T. bromius*	*P. melanarius*	*A. segetum*	*Ch. formosa*	*E. strigella*
–	*H. vernus*	*A. haemorrhoidalis*	*D. octaedra*	*Z. nitidus*	*D. ruderatus*	*A. solstitialis*
	Ch. formosa	*C. hortensis*	*Z. nitidus*	*Sch. dmitriewi*	*B. crepitans*	*C. rufipes*
	Sch. dmitriewi	*E. strigella*	*D. quadrimaculata*	*C. rufipes*	*A. segetum*	*Z. nitidus*

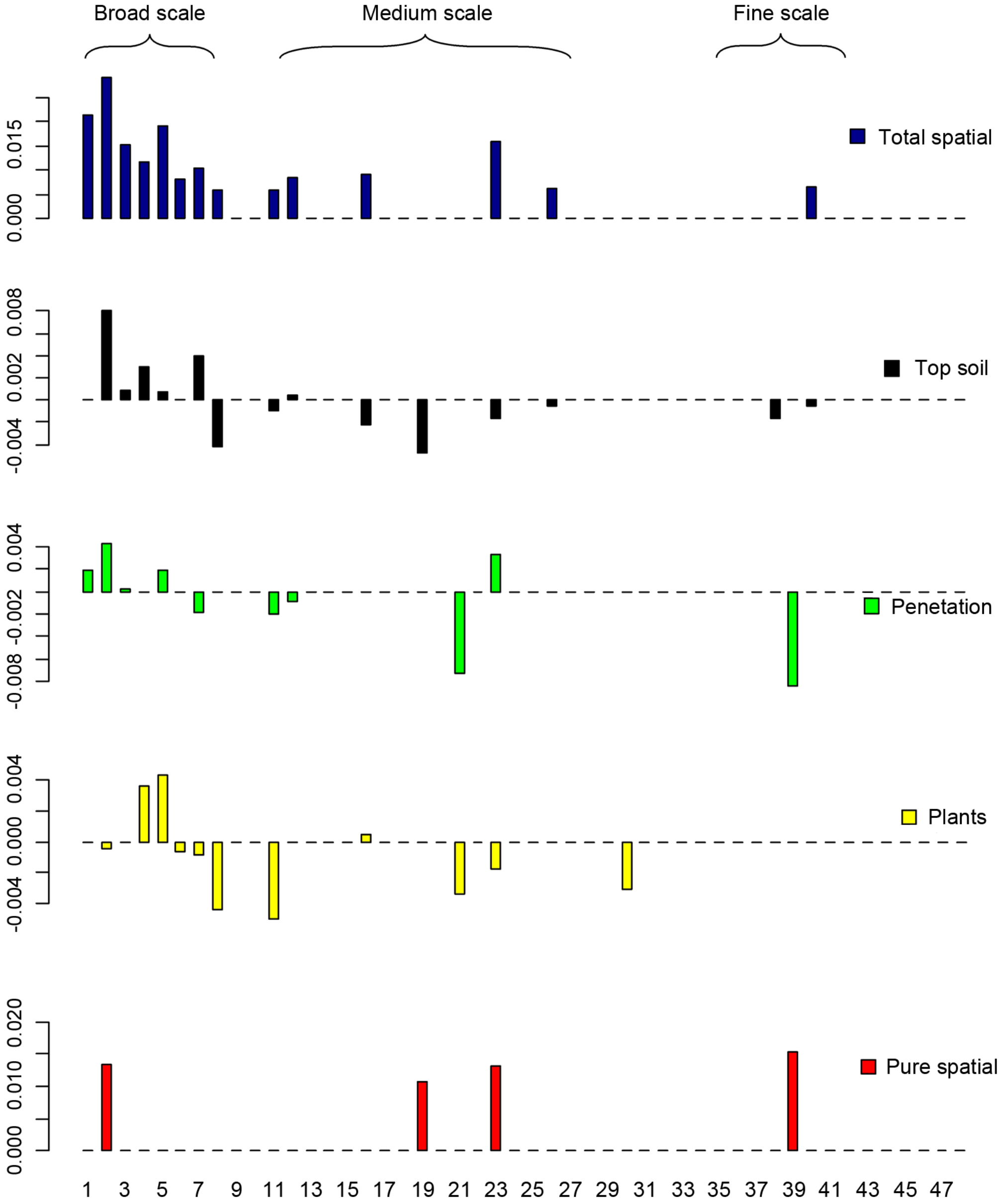

Fig. 3. Scalograms illustrating the scaling of spatial structure variation in the soil macrofaunal community data (no variables such as covariates, blue bars) and the residuals of the spatial models (red bars), topsoil models (black bars), soil penetration models (green bars) and plant models (yellow bars). The value of R^2_{adj} is the variation explained by individual dbMEM variables for spatially structured variation and pure spatial models and the differences between the variations explained by the spatial models and the variations explained by the topsoil, profile soil and plant models. The dbMEMs are decreasingly ordered according to the scale of spatial patterns, where the *x*-axis represents the number of dbMEMs

Partitioning of the soil macrofauna variation. The environmental characteristics of the topsoil together explained 6.7% of the variation in the community (F = 2.8, P = 0.001). Accounting for surface soil properties reduced the variation explained by spatial variables to 28.3 % (F = 1.8, P = 0.001). The properties of the upper soil layer contributed significantly to the formation of a large-scale spatial pattern of community variability. The transformation of the community under the influence of surface soil properties (**Fig. 1**) was due to species such as *Lathrobium rufesceus*, *Euomphalia strigella*, *Zonitoides nitidus*, *Pterostichus melanarius*, and *Dendrobaena octaedra*.

The soil penetration resistance explained 12.0 % of the variation in the community (F = 2.3, P = 0.001). Accounting for soil penetration resistance reduced the variation explained by spatial variables to 27.7 % (F = 1.9, P = 0.001). The transformation of the macrofaunal community under the influence of soil compactness was due to species such as *Cardiophorus rufipes*, *Schizothuranius dmitriewi*, *Agrotis segetum*, *Tabanus bromius*, and *Zonitoides nitidus*. Soil penetration resistance hides medium- and fine-scale spatial patterns: isolating the effect of soil compactness allows for the identification of spatial patterns at these scale levels.

Vegetation cover was able to explain 3.9 % of the variation in the community (F = 1.2, P = 0.007). Accounting for vegetation cover reduced the variation explained by spatial variables to 28.9% (F = 1.7, p < 0.001). The transformation of the community under the influence of vegetation occurred due to species such as *Cardiophorus rufipes, Dendroxena quadrimaculata*, *Lathrobium rufesceus*, *Schizothuranius dmitriewi*, and *Otiorhynchus raucus*. Separating the influence of vegetation cover allowed us to additionally identify the presence of broad- and medium-scale components of variation in the soil macrofaunal community. The influence of vegetation has a clearly defined broad-scale component of variation, which differs in frequency characteristics from the broad-scale components of the influence of topsoil properties and soil penetration resistance.

The pure spatial component explained 16.1 % of the community variation (F = 1.5, P < 0.001). The differences between the total spatial variation and the net spatial variation of the community are mainly due to species such as *Cardiophorus rufipes, Schizothuranius dmitriewi, Staphylinus erythropterus, Brachinus crepitans, Chloromyia formosa*, and *Dendroxena quadrimaculata*. The canonical analysis of the correspondence of the pure spatial component of the community variation revealed only one CCA-axis, which was statistically significant (F = 7.8, P = 0.005). *Badister bullatus*, *Ampedus balteatus*, *Chrysolina fastuosa*, and *Megaphyllum sjaelandicum* had the strongest positive correlations with this axis, and *Pachimerium ferrugineum*, *Lathrobium rufesceus*, *Holochelus vernus*, and *Schizothuranius dmitriewi* had the strongest negative correlations.

DISCUSSION

Forest soils and litter support a diverse range of animal communities that depend directly or indirectly on dead organic matter for habitat and food. The composition of the community can be influenced by biotic or abiotic factors that vary with changes in habitat structure and resource availability related to the spatial structure of the forest (Pollierer *et al.*, 2021). It is important to note that community composition may be affected by various factors. The impact of soil macrofauna on various soil properties and regimes is significant; therefore, the most important pedobionts are considered to be ecosystem engineers (Bottinelli *et al.*, 2015; Jones *et al.*, 1994; Lavelle *et al.*, 1997). The influence of macrofauna on the structural conditions of soils in different natural zones is complex. The activity of soil animals promotes soil aggregation processes (Blanchart, 1992; Frazão *et al.*, 2019; Fujimaki *et al.*, 2010; Jongmans *et al.*, 2001) and is one of the main factors in the formation of soil pore space (Capowiez *et al.*, 2015; Pérès *et al.*, 2010; van Vliet *et al.*, 1993). Animals have a significant impact on the morphological properties of the soil structure in soils with a high number of invertebrate communities (Castellanos-Navarrete *et al.*, 2012; Phillips & FitzPatrick, 1999; Piron *et al.*, 2012) and on the formation of the microstructure of surface organo-mineral horizons (Frouz *et al.*, 2007; Jongmans *et al.*, 2003; Sanborn & Pawluk, 1989; Zanella *et al.*, 2018). The degree and nature of the impact of animals on soil structure are dependent on the ecological and taxonomic composition and abundance of macrofaunal communities (Bottinelli *et al.*, 2015). The structure of macrofaunal communities in the steppe zone of Ukraine is determined by ecological conditions, which are formed depending on the relief, water regime and spatial organization of plant communities (Zhukov *et al.*, 2019). The ecological conditions of natural forests determine the formation of a corresponding complex of soil invertebrates that differ from the complex of steppe black soil animals in terms of species composition, population density, spatial distribution and dynamics of animal activity during the vegetation period (Zhukov *et al.*, 2018).

The studied community has high species diversity and abundance. The ecological diversity of soil animals is also noteworthy. Earthworms are the key component of the community. One effective methodological approach to studying local biodiversity is investigating the importance of key species in its formation (Tsaryk *et al.*, 2019). Endogeic earthworms dominate in terms of abundance and species diversity. The community is represented by *A. rosea*, which is a typical inhabitant of zonal steppe communities.

The traditional name for the soil of wall oak forests is forest chernozem. This name emphasizes the connection of this forest soil with steppe zonal chernozem soils. This connection can also be traced at the level of the soil animal community. The dominant earthworm species is *O. lacteum*. This species is relatively moisture-loving, but its main feature is calciphilicity. In general, calciphilic species are significantly represented in the community. This group included *M. sjaelandicum*, *A. nasutum*, and all molluscs. The numerous and diverse group of calcophilic species indicates the importance of calcium compounds in the soil formation process of the studied soil, which is a condition for the formation of a water-resistant soil aggregate structure. The earthworm *A. trapezoides* is a very common species in the region. It is ecologically close to *A. rosea*, so they often occur together in communities. However, the earthworm *A. trapezoides* is more hygrophilous, while *A. rosea* is able to tolerate short-term conditions of very dry soil.

The epigeic species *D. octaedra* and the anecic species *O. transpadanus* are very sensitive to the state of the forest litter (Simmons et al., 2015), so they are markers of forest-type nutrient cycling. Other litter dwellers, such as spiders, molluscs, millipedes, adult insects and larvae, are widely represented in the community. The burrowing species *O. transpadanus* is also sensitive to the state of the soil cover in general. The creation of a gallery of soil channels requires considerable energy, so their existence is critical for maintaining the population of burrowing earthworm species (Gavinelli *et al.*, 2018). The highly structured state of forest soil creates favourable conditions for burrowing worms (Capowiez *et al.*, 2014), which in turn are an important driver of the soil formation process. Structured soil provides a variety of conditions, resulting in a diverse endogean species pool. The insect larvae are also diverse and abundant. Among them are species that move in the soil along existing passages (larvae of Elateridae) or that have a C-shaped body and move in the soil while in a soil capsule. This adaptation is important for survival under conditions of moisture deficit. The moisture regime of steppe forests is more favourable than that of steppe ecosystems, but in the second half of summer, there is a deficit of moisture in steppe forests. Therefore, the ecological diversity of the soil macrofaunal community ensures its functional stability throughout the vegetation season.

Spatial organization is a marker of ecological connectivity in a community (Daigle *et al.*, 2020). The state of the above-ground cover (forest floor and vegetation) and topsoil as well as variations in soil properties in the soil profile are factors of spatial structuring of the community. These factors demonstrate spatial structure, but a certain component of their influence does not depend on spatial regularity. Ecological factors are not completely independent but are largely correlated with each other. Obviously, the spatial variability of soil properties affects the structure of vegetation cover, and relief features affect both the variability of soil properties and the spatial organization of vegetation. Depending on the microrelief features, forest litter and moisture are redistributed, which is also a driver of the spatial organization of soil macrofauna. This finding is confirmed by the fact that the spatial variability of the soil macrofaunal community can be decomposed into six components, which are indicated by six canonical axes. These axes are mainly correlated with the abundance of epigeic species. The epigeic component is represented by significant species diversity, but the abundance of individual species is lower than that of endogeic species. Endogeic species are very abundant and are the functional basis of the community.

The spatial structure of the community is also complex in terms of hierarchy. The broad-, medium-, and fine-scale components of community variation can be distinguished. The driver of the broad-scale component of spatial variation in the community is the properties of the topsoil, mainly the density of the litter. Usually, forest litter is a factor in the formation of fine- or medium-scale components of community variation (Kunakh *et al.*, 2023). Litter can form clusters that differ significantly in their environment for soil epigeic animals from areas with lower litter density or no litter. On the slope of the riverbank, more significant movements of forest litter are possible under the influence of gravity. The locations of forest litter accumulation are cracks on the soil surface, which are typical in conditions of significant erosion. The general trend of forest litter accumulation is a top-down movement, which determines the formation of a broad-scale component of environmental variation, according to which the structure of the soil macrofaunal community changes mainly due to its epigeic component. Notably, the redistribution and accumulation of forest litter are caused by gravitational forces and relief heterogeneity, which are also correlated with changes in soil profile properties (Tutova *et al.*, 2023). This correlation explains a certain connection between the variation in surface and profile soil properties, as well as the fact that profile variation in penetration resistance also significantly contributes to the formation of a broad-scale component of spatial patterns of soil macrofauna. The influence of soil penetration resistance on extraction allows the identification of medium- and fine-scale components of variation in animal communities. The formation of spatial patterns of soil compactness can be assumed to have an independent endogenous component that is not in line with the general pattern of spatial variability of other soil properties and vegetation cover and thus is a source of misinformation. Pedoturbation due to fractured slope soils and under the influence of soil-wind phenomena can be the reasons for the formation of specific spatial patterns of soil penetration resistance at the medium- and fine-scale levels (Emshanov, 1999).

Vegetation cover forms a broad component of the spatial variation in soil macrofauna. An important factor in structuring ecological space is the location of trees. The spatial patterns generated by trees can be identified on a broad scale compared to the size of the experimental site. The extraction of the vegetation component allows the identification of the presence of additional broad- and medium-scale components. This phenomenon can be explained as a consequence of endogenous vegetation structuring processes, which are independent or sometimes have the opposite effect as the overall spatial pattern. The broad-scale impact can be explained by the spatial organization of the stand, and the medium-scale impact is due to the effect of the herbaceous cover.

The pure spatial pattern is represented by broad-, medium-, and fine-scale components. The pure broad-scale spatial component may be the result of the influence of the spatial arrangement of trees, which requires additional research involving mapping the distribution of tree trunks and projective crown cover. Thus, it can be assumed that the pure spatial broad-scale component represents the variability of the community structure under the influence of unmeasured stand properties. The medium-scale component may be due to the influence of unmeasured soil properties, such as the soil aggregate structure. The detailed-scale component may be the result of neutral factors related to the peculiarities of animal distribution within the territory.

CONCLUSION

The soil macrofaunal community of an oak forest on the slope of the right bank of a steppe river has a high level of taxonomic and ecological diversity. The study revealed that the community included 56 species of soil macrofauna. The abundance of soil macrofauna was 331.8±43.6 ind./m^2. The soil macrofaunal community exhibits spatial patterns that are influenced by soil and vegetation properties. The spatial variables were able to explain 33.8 % of the variation in the community. The spatial variables at different scales contribute to the explained variation in the community, and we can distinguish between broad-, medium-, and fine-scale components. The broad-scale components were able to explain 12.9 % of the variation in the community. The redistribution of forest litter under the influence of gravity along the riverbank slope creates a broad spatial structure of soil macrofauna, which includes mainly epigean species. The spatial distribution of trees forms a broad-scale component of soil macrofaunal community variability, while herbaceous cover forms a medium-scale component. The medium-scale spatial variables explained 4.8 % of the variation in the community. The fine-scale component of community variability is due to neutral factors, which were able to explain 0.6 % of the variation in the community. The results of the study can be used for monitoring the biodiversity of forest ecosystems in the steppe zone and for assessing the consequences of the armed aggression of the Russian Federation against Ukraine.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

Human Rights: this article does not contain any studies with human subjects performed by any of the authors.

Animal studies: all international and national guidelines for the care, maintenance and use of laboratory animals were followed.

AUTHOR CONTRIBUTIONS

Conceptualization, [O.Z.]; methodology, [O.K.]; investigation, [O.K., O.Z.]; data analysis, [O.Z.]; writing – original draft preparation, [O.K., O.Z.]; writing – review and editing, [O.K.]; visualization, [O.Z.]; supervision, [O.K.]; project administration, [O.K.]; funding acquisition, [–]. All authors have read and agreed to the published version of the manuscript.

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ПРОСТОРОВА ОРГАНІЗАЦІЯ УГРУПОВАННЯ ҐРУНТОВОЇ МАКРОФАУНИ ДУБОВОГО ЛІСУ В СТЕПОВІЙ ЗОНІ УКРАЇНИ

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Вступ. Оцінюючи вплив на довкілля та розробляючи заходи з охорони і раціонального використання екосистем, варто пам'ятати, що для Степової зони референтними є не лише степові екосистеми, а й лісові, болотні, солончакові та лучні. Порівняльний підхід потребує вивчення референтних екосистем, щоб зрозуміти, наскільки трансформована та чи інша екосистема або наскільки вона далека від природних зразків у процесі відновлення. Угруповання ґрунтової макрофауни лісової екосистеми правого берега р. Самара можна розглядати як референтне для багатьох лісових екосистем регіону. Мета статті – виявити закономірності просторової організації угруповання ґрунтової макрофауни дубового лісу на правому березі р. Самара.

Матеріали та методи. Дослідження проводили в листяному лісовому масиві, розташованому в діброві на правому березі р. Самара. Територія дослідження була розділена на 5 трансект, кожна з яких складалася з 20 точок відбору зразків із відстанню між рядами 2 м. Зразки ґрунтової макрофауни відбирали з однієї ділянки ґрунту розміром 25×25×30 см, яку швидко викопували. Списки видів судинних рослин були записані для кожної ділянки розміром 2×2 м. Вимірювали опір проникненню та електропровідність ґрунту. Трофічну активність ґрунтової фауни оцінювали за допомогою пластинчастого тесту з приманкою.

Результати й обговорення. Просторова структура угруповання є складною в ієрархічному аспекті. Драйвером широкомасштабного компонента просторової мінливості угруповання є властивості верхнього шару ґрунту, головно, щільність підстилки. Рослинний покрив формує широкий компонент просторової мінливості ґрунтової макрофауни. Важливим чинником структурування екологічного простору є розташування дерев. Чистий просторовий патерн представлений широко-, середньо- та дрібномасштабними компонентами.

Висновок. Угруповання ґрунтової макрофауни дубового лісу на схилі правого берега степової річки має високий рівень чисельності, таксономічного й екологічного різноманіття. Просторовий розподіл дерев формує широкомасштабний компонент мінливості угруповання ґрунтової макрофауни, а трав'яний покрив – середньомасштабний. Дрібномасштабний компонент мінливості угруповання зумовлений нейтральними факторами.

Ключові слова: різноманіття, просторова екологія, ієрархічна організація, патерн, ординація угруповань, прокрустовий аналіз, оцінка впливу на довкілля

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