Spatial organization of the soil macrofauna community in a floodplain forest

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Abstract. Soil fauna is an important functional component of terrestrial ecosystems. Several hierarchical levels of spatial organization of pedobionts communities can be distinguished: point level, ecosystem level and landscape level. Of particular importance is the ecosystem level of spatial organization where the results of interaction between soil animals and soil and plant environmental factors, as well as the results of the influence of factors of neutral nature are expressed to the greatest extent. The aim of the work is to test the hypothesis that the spatial patterns of soil macrofauna at the ecosystem level can be explained by ecomorphs. Soil animals were sampled in floodplain ecosystems in the Dnieper River valley. Animals were sampled according to a regular grid with recording of local coordinates of sampling points. At the same points, soil properties were measured and geobotanical descriptions of vegetation were made. Phytoindication assessment of environmental factors was carried out on the basis of vegetation descriptions. The soil animal community is represented by high taxonomic and ecological diversity. The spatial distribution of soil macrofauna is not random and is a consequence of environmental factors and causes of a neutral nature. The ratio of these factors varies depending on the scale level. The fine-scale level is represented by factors of neutral nature. Medium- and broad-scale components are determined by soil and vegetation factors. The main spatial patterns of variation in the soil animal community correlate with the ecomorphic features of the animals. The ecomorphic approach allows interpreting the information on the spatial organization of pedobionts communities.

1. Introduction

The species composition of communities according to niche theory can be explained by environmental variables [1, 2]. Abiotic environmental factors act as ecological filters selecting those species appropriate to specific habitat conditions [3]. Abiotic and biotic drivers can generate spatial patterns of the community [4]. According to neutral theory, dispersal limitation and ecological drift are important factors in shaping soil communities [5–9]. The structuring of communities is influenced by non-environmental factors such as dispersal and other population processes [10]. The probability of colonizing some space depends on the dispersal potential [11]. Ecological drift is the result of random fluctuations in the abundance of species [5]. The dispersal limitation and ecological drift are able to produce spatial patterns in the community structure, which can be revealed by spatial filters [12]. The ratio of the importance of environmental and neutral factors in community structuring can vary considerably. The importance of environmental factors compared to those of neutral nature increases as the spatial scale increases,
which is explained by the coverage of greater environmental heterogeneity [13–17]. The leading role of dispersal limitation as an assembly process leads to the fact that community composition and species distribution can be spatially structured independently of the variability of environmental properties [18, 19]. A fraction of community variation that is spatially structured but not explained by environmental factors is called a pure spatial component. The pure spatial component represents the role of a dispersion limitation only when all significant environmental variables were accounted for [20].

Environmental factors, such as soil property gradients and vegetation composition, have a major influence on the distribution of soil organisms [21–24]. The ecological selection shapes the structure of the soil community [25, 26]. Biotic forces, such as competition and predation, as well as abiotic ones, shape the soil biota [27]. The control of soil macrofauna communities can be from the bottom due to resource shortages or from the top by predators [28, 29]. Soil and vegetation factors are important in structuring the communities of soil macrofauna at the level of beta diversity. The distribution of soil pore sizes, soil microclimate, structure of roots and above-ground vegetation determine the fine-scale distribution of soil fauna [30, 31]. The vegetation structure and quality of above-ground litter affect soil macrofauna communities [32]. The quality and quantity of food of soil macrofauna depends on the plants [33]. The production of aboveground litter depends on the nature of the vegetation [32]. The diversity of plants stimulates the diversity of soil fauna due to the fact that soil animals additionally use forest litter of different origin and different chemical composition [34]. The spatial distribution of plant root systems also causes the formation of spatial patterns of soil macrofauna [35, 36]. The vegetation density and litter height have a positive effect on the abundance of soil animals [37]. Herbaceous vegetation promotes the abundance and species richness of soil-dwelling animals, such as earthworms. Plant biomass and primary production have a positive effect on the abundance of soil fauna, which may not depend on plant diversity. [38]. The effect of above-ground vegetation on soil animals is due to the fact that plants change the microclimate near them, cooling the soil in the shade of their leaves [33]. The vegetation structure determines the diversity of microhabitats and the living conditions of macroinvertebrates [32]. The earthworms respond with increased abundance to shading effects, lower soil temperatures, and higher soil moisture in the vicinity of trees [39]. Species diversity of stands stimulates the diversity of the soil macrofauna community by creating a variety of small-scale microhabitats [40]. The most important factors in the organization of the spatial structure of the soil macrofauna of forest ecosystems are the density and diversity of tree stands [41].

A significant portion of the variation explained by soil properties in an Eastern European poplar-willow forest in the floodplain of the River Dniipro was spatially structured. The large-scale component of community variation was shown to be induced by stands that modified herbaceous vegetation structure at soil properties. Calcium-rich herbaceous plants strongly influenced the spatial placement of soil animals [42]. Soil and plant factors play an important role in structuring soil macrofauna communities of the Dniipro river arena terrace. The sensitivity of communities to environmental factors changes in space and is spatially structured. Specific spatial patterns of community sensitivity are distinguished for different ecological factors [43]. The spatial variation of soil macrofauna was fractionated into three components: broad-scale, medium-scale, and fine-scale. The broad-scale component depended on vegetation cover, the medium-scale component depended on soil properties, and the fine-scale component depended on vegetation and soil properties. For litter-dwelling animals, the most characteristic spatial patterns were at the broad-scale and medium-scale levels. For endogeic and anecic animals, the most significant spatial patterns were observed at the fine-scale level [44].
2. Research aim and objectives
The aim of our study was to reveal the role of plant and soil factors in the spatial organization of the soil macrofauna community of the floodplain ecosystem.

We tested the following hypotheses:
(i) plant, soil, and neutral factors act at different spatial levels;
(ii) topsoil properties and soil properties in the profile affect different spatial patterns of soil macrofauna;
(iii) soil animals modify the soil as a result of soil-forming activities, which causes new spatial patterns in the variability of vegetation, soil, and soil macrofauna properties.

3. Material and methods
3.1. Study area
The study was carried out in the elm oak forest in the floodplain of the Dnipro River (Dniprovsko-Orilsky Nature Reserve, Ukraine) (48.50° N 34.77° E). The soil properties measurement, description of plants, and collection of soil macrofauna were performed in 105 locations, which were located on a regular grid. The locations were 3×3 meter squares. The squares were adjacent to each other, forming a polygon. The description of plants was performed within each square, and the measurement of soil properties and sampling of soil animals were performed in the center of each square.

3.2. Description of soil morphology
The study of the soil profile morphology was performed in accordance with the guidelines of the field description of soils FAO [45]. Genetic type of soil profile was determined according to Rozanov [46]. The classification of soils was performed according to IUSS Working Group WRB [47]. The soils classification position according to WRB was Fluvic Gleysol (Arenic, Ochric) and Fluvic Mollic Gleysol (Loamic, Humic).

3.3. Sampling methods
The polygon consisted of 7 transects. Each transect was made up of 15 sampling points. The distance between rows within the polygon was 3 m. 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) [48]. 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.

3.4. Plant community description
The vegetation description was performed at polygon consisted of 105 sampling points (relevés). The points were located along 7 transects with 15 sampling points each. The distance between points in the transect as well as the distance between transects was 3 m. The adjacent sampling points were in close proximity to each other. Vascular plant species lists were recorded for each 3×3 m sampling point, along with a visual assessment of species coverage using a Braun-Blanquet scale [49]. The projective cover of plant species was measured at soil level, understory (up to 2 m in height), and canopy (above 2 m in height). Seedlings and seedlings of tree species were subsequently excluded from the analysis. A phytoindication of environmental factors was performed based on the Didukh [50].
3.5. Soil properties measurement
The soil penetration resistance was measured in the field using the Eijkelkamp manual penetrometer, to a depth of 100 cm at 5 cm intervals. The average error of the measurement results of the device is ± 8%. Measurements were made with a cone with a cross section of 1 cm². At each measurement point, the soil penetration resistance was performed in only one replication. The aggregate structure was evaluated by Savinov’s dry sieving method. The percentage content of such fractions was established: <0.25, 0.25–0.5, 0.5–1, 1–2, 2–3, 3–5, 5–7, 7–10, >10 mm, and plant roots. The bulk density of the soil was estimated by the Kachinskiy method, soil moisture by the weight method.

3.6. Statistical analysis
Canonical correspondence analysis (CCA) was used for analysis of the variance soil macrofauna species composition. Soil mechanical impedance, soil electrical conductivity, litter layer thickness, moisture and soil bulk density were log transformed. The significance of CCA global model was first tested. The geographic coordinates of sampling locations were used to generate a set of orthogonal eigenvector-based spatial variables (dbMEMs), each of them representing a pattern of particular scale within the extent of the sampling area [11]. All 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 the multivariate analysis and for the computation of global and partial Moran’s I. [51], adespatial (v. 0.3-2. https://CRAN.R-project.org/package=adespatial) for the forward selection and for the generation of spatial filters [52].

4. Results
The soil macrofauna community included 46 species with a total abundance of 293.9±38.84 ind./m² (table 1). The earthworms were the most abundant group of soil animals and were represented by the 3 species. The abundance of earthworm cocoons was 16.91±2.44 ind./m². Endogeic species (Melolontha melolontha, Isomira murina, Serica brunnea) were also highly abundant. The group of epigeic animals was diverse and abundant.

Table 1: Taxonomic diversity and abundance (ind./m²) of the soil animals.

| Taxon | Mean±st.error |
|-------|---------------|
| Annelidae | |
| Oligochaeta | |
| Haplotaxida | |
| Lumbricidae | |
| Aporrectodea caliginosa trapezoids (Duges, 1828) | 71.92±4.13 |
| Aporrectodea rosea (Savigny, 1826) | 0.30±0.21 |
| Dendrobaena octaedra (Savigny, 1826) | 4.42±0.70 |
| Lumbricidae sp. sp. | 16.91±2.44 |
| Arthropoda | |
| Arachnida | |
| Araneae | |
| Lycosidae | |
| Xerolycosa miniata (L.C. Koch, 1834) | 9.60±1.29 |
| Chilopoda | |
| Geophilomorpha | |
| Geophilidae | |
| Taxon | Mean±st.error |
|-------|---------------|
| Geophilus proximus C.L.Koch 1847 | 9.60±1.10 |
| Pachymerium ferrugineum (C.L.Koch 1835) | 8.08±1.72 |
| Lithobiomorpha | |
| Lithobiidae | |
| Lithobius (Monotarsobius) aeruginosus L. Koch 1862 | 0.30±0.21 |
| Lithobius (Monotarsobius) curtipes C.L. Koch 1847 | 2.44±0.56 |
| Diplopoda | |
| Julida | |
| Megaphyllum rossicum (Timothew, 1897) | 6.86±1.10 |
| Insecta | |
| Coleoptera | |
| Carabidae | |
| Amara familiaris (Duftschmid, 1812) | 27.58±2.49 |
| Amara similata (Gyllenhal, 1810) | 1.98±0.64 |
| Calathus (Calathus) fuscipes (Goeze, 1777) | 2.90±0.99 |
| Calosoma (Calosoma) inquisitor (Linne 1758) | 0.46±0.26 |
| Harpalus (Pseudoophonus) griseus Panzer, 1796 | 0.15±0.15 |
| Chrysomelidae | |
| Chrysolina (Fastuolina) fastuosa (Scopoli 1763) | 1.07±0.39 |
| Curculionidae | |
| Otiorhynchus (Cryphiphorus) ligustici (Linnaeus 1758) | 4.88±1.04 |
| Elateridae | |
| Agriotes (Agriotes) lineatus (Linnaeus 1767) | 1.98±0.52 |
| Agrypnus murinus (Linnaeus 1758) | 0.76±0.33 |
| Athous (Athous) haemorrhoidalis (Fabricius 1801) | 9.14±1.28 |
| Cardiophorus rufipes (Goeze, 1777) | 8.99±1.26 |
| Prosternon tessellatum (Linnaeus 1758) | 1.52±0.46 |
| Silphidae | |
| Dendroxena quadrimaculata (Scopoli 1772) | 0.15±0.15 |
| Staphylinidae | |
| Drusilla canaliculata (Fabricius, 1787) | 0.46±0.26 |
| Othis punctulatus (Goeze 1777) | 0.30±0.21 |
| Platyrhacrus (Platyrhacrus) fulvipes (Scopoli 1763) | 0.76±0.33 |
| Tenebrionidae | |
| Cylindronotus (Nalassus) brevicollis Kuster, 1850 | 0.15±0.15 |
| Helops coeruleus (Linnaeus 1758) | 0.30±0.21 |
| Isomira murina (Linnaeus 1758) | 16.76±1.57 |
| Opatrum sabulosum (Linnaeus 1761) | 0.15±0.15 |
| Melolonthidae | |
| Amphimallon solstitiale (Linnaeus 1758) | 6.25±0.93 |
| Melolontha melolontha (Linnaeus 1758) | 33.68±3.10 |
| Polyphylla (Polyphylla) fullo (Linnaeus 1758) | 3.35±0.88 |
| Serica brunnea (Linnaeus 1758) | 11.43±1.40 |
| Dermaptera | |
| Forficulidae | |
| Forficula auricularia Linnaeus 1758 | 2.13±0.65 |
| Diptera | |
### Table 1 – continued from previous page

| Taxon                        | Mean±st.error |
|------------------------------|---------------|
| Therevidae                   |               |
| *Thereva nobilitata* (Fabricius 1775) | 0.61±0.30     |
| Asilidae                     |               |
| Asilidae sp.1                | 0.30±0.21     |
| Rhagionidae                  |               |
| *Rhagio scolopaceus* (Linnaeus 1758) | 0.76±0.33     |
| Tabanidae                    |               |
| *Tabanus bromius* Linnaeus 1758 | 1.07±0.39     |
| Tipulidae                    |               |
| *Tipula (Lunatipula) lunata* Linnaeus 1758 | 0.30±0.30     |
| Empididae                    |               |
| *Empis (Kritempis) livida* Linnaeus 1758 | 0.15±0.15     |
| Lepidoptera                  |               |
| *Agrotis segetum* (Denis & Schiffermüller, 1775) | 7.16±1.40     |
| Malacostraca                 |               |
| Isopoda                      |               |
| *Trachelipodida*             |               |
| *Trachelipus rathkii* (Brandt 1833) | 11.28±1.18    |
| Mollusca                      |               |
| *Cochlicopidae*              |               |
| *Cochlicopa lubrica* (O.F. Muller 1774) | 0.15±0.15     |
| Helicidae                    |               |
| *Cepaea (Austrotachea) vindobonensis* (C. Pfeiffer 1828) | 4.27±0.95     |
| Valloniidae                  |               |
| *Vallonia pulchella* (O.F. Muller 1774) | 0.15±0.15     |

The detrended correspondence analysis found that the largest axis had a length of 2.3, which exceeds the conditional limit of 2, so a canonical correspondence analysis was chosen as the ordination procedure. The spatial variables were able to explain 39.6% of the variation in the soil macrofauna community \(F = 2.8, p < 0.001\). Topsoil characteristics were able to explain 8.8% of community variation \(F = 1.8, p < 0.001\). The soil penetration resistance characteristics in the soil profile were able to explain 10.6% of the variation in the soil macrofauna community \(F = 1.7, p < 0.001\). Vegetation features were able to explain 10.9% of the variation in the soil macrofauna community \(F = 1.9, p < 0.001\). Different sources of community variation had a pure effect on soil macrofauna and also interacted with each other (figure 1).

The analysis of the scalogram allowed to extract the three scale components of the spatial community variation: broad-scale, medium-scale, and detailed-scale (figure 2). The broad-scale component was explained by the dbMEM 1–8 and was able to explain 8.3% of the community variation \(F = 2.7, p < 0.001\). The medium-scale component was explained by the dbMEM 13, 15–17, 19 and was able to explain 5.0% of community variation \(F = 1.6, p = 0.014\). The fine-scale component was explained by the dbMEM 29, 34, 35, 38, 39, 41, 42, 44, 48 and was able to explain 7.5% of the community variation \(F = 1.8, p = 0.002\).

The topsoil properties as a conditional variable reduced the variability of the soil macrofauna community that could be explained using the spatial variables to 34.3% \(F = 2.1, p < 0.001\).
The broad-scale component explained 7.8% of community variation \((F = 2.4, p < 0.001)\), the medium-scale component explained 4.9% of community variation \((F = 1.6, p = 0.007)\), and the fine-scale component explained 6.6% of community variation \((F = 1.5, p = 0.004)\). Thus, the topsoil properties mainly influenced the spatial patterns of the soil macrofauna community at the fine-scale level and had less influence on the broad- and medium-scale patterns. The *Otiorhynchus ligustici*, *Cepaea vindobonensis*, *Melolontha melolontha*, *Polyphylla fullo*, and *Dendrobaena octaedra* were most sensitive to the influence of soil properties (figure 3).

![Figure 1](image-url)  
*Figure 1.* Variance partitioning between spatial, topsoil, profile soil, and plant explanatory variables. [a] – variation captured by spatial (dbMEM) variables corresponds to pure spatial component; [b] – variation explained solely by topsoil variables (soil electric conductivity, forest litter depth, soil water content, soil bulk density, aggregate fractions 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 \((p < 0.001)\).

The profile values of soil penetration resistance as a conditional variable reduced the community variability that could be explained by spatial variables to 34.9\% \((F = 1.9, p < 0.001)\). The broad-scale component explained 6.7\% of community variation \((F = 2.1, p < 0.001)\), the medium-scale component explained 4.4\% of community variation \((F = 1.6, p = 0.007)\), and the fine-scale component explained 7.2\% of community variation \((F = 1.9, p < 0.001)\). Thus, the soil penetration resistance mainly influenced broad- and medium-scale patterns and had no effect on fine-scale patterns. The *Otiorhynchus ligustici*, *Lithobius curtipes*, *Cepaea vindobonensis*, *Megaphyllum sjaelandicum*, and *Polyphylla fullo* were most sensitive to the influence of soil properties (figure 3).

The phytindicative estimates of environmental factors as a conditional variable reduced community variability that could be explained by the spatial variables to 39.5\% \((F = 1.9, p = 0.002)\). The broad-scale component explained 6.7\% of the community variability \((F = 1.9, p = 0.002)\), the medium-scale component explained 2.7\% of the community variability \((F = 0.9, p = 0.47)\), and the fine-scale component explained 6.9\% of the community variability \((F = 1.5, p = 0.006)\). Thus, the vegetation mainly influenced broad- and medium-scale patterns and
had no effect on fine-scale patterns. The *Prosternon tessellatum*, *Pachymerium ferrugineum*, *Cepaea vindobonensis*, *Megaphyllum sjaelandicum*, *Geophilus proximus* were most sensitive to the influence of vegetation (figure 4).

The pure spatial component was able to explain 21.9% \( (F = 2.0, p < 0.001) \) of soil macrofauna community variation. The broad-scale component explained 6.1% of community variation \( (F = 1.7, p < 0.001) \), the medium-scale component explained 3.0% of community variation \( (F = 1.5, p = 0.007) \), and the fine-scale component explained 4.7% of community variation \( (F = 1.4, p = 0.002) \). The spatial component of community variability formed a pattern, the deviation from which can be interpreted as the result of the influence of individual soil and plant factors (figure 4).

5. Discussion

Soil and plant environmental factors influence variation in the soil macrofauna community \([42, 53]\). These factors interact with each other and are spatially structured \([51]\). The study was conducted within a relatively small area, but within which there is a significant variability in gradients due to which the response of most animal species is not monotonic, but is more bell-shaped. For this reason, we chose canonical correspondence analysis for the ecological ordination procedure. A considerable heterogeneity of ecological conditions is typical of floodplain ecosystems \([2, 54]\). The dynamics and variability of floods leads to the different intensity of redeposition of alluvium, as a consequence of which there is a significant variability in the granulometric composition of the soil-forming sediments of floodplain soils \([55]\). The granulometric composition is a factor that determines other physical properties of soil, as well as water, air regime and salt accumulation regime \([52, 56]\).

The influence of soil properties in the upper soil layer on soil macrofauna is completely spatially structured and correlated with the variability of soil properties in the soil profile as a whole, as well as correlated with the variability of vegetation cover. The microorganisms in the litter layer are limited mainly to nitrogen, while the soil microorganisms are limited mainly to phosphorus. The earthworms are limited by carbon availability. Earthworms and microorganisms compete for carbon resources, with microorganisms being more competitive when carbon and nutrients are available \([32]\). An important aspect of the influence on the soil macrofauna is the spatially structured relationship between all three sources of influence considered: the top soil layer, the soil profile, and the vegetation cover \([43, 57]\). The upper soil layer has a certain spatial independence in comparison with the soil profile as a whole \([44, 58]\). The reason for this phenomenon may be twofold. First of all, the independence of variation of the upper soil layer may be due to the fact that alluvial processes primarily affect the upper soil layer. The redeposition of suspended matter and organic matter occurs primarily on the soil surface. The deeper soil layers of floodplain soils are involved in the processes of redeposition of matter during periods of significant floods, which occur relatively rarely \([59]\). Another reason for the isolated variability of topsoil properties may be the backward influence of soil animals \([60]\). The soil animals are important factors of soil formation and influence soil properties \([61]\). This influence is proportional to their abundance, so in microsites, which are favorable for the development of populations of soil animals, especially ecosystem engineers, there is a significant transformation of soil properties \([41]\). The basis of the structure of the studied soil macrofauna community is composed of earthworms, which can significantly change the aggregate structure of soil, create a system of soil galleries, and promote the movement of dead plant residues from the soil surface deep into the soil \([62]\). The community of earthworms is represented by the epigeic *D. octaedra* and the top-layer endogeic *A. c. trapezoides*. The soil-forming activity of these animals is focused on the litter or upper soil layer. The mid-layer endogeic earthworm *A. rosea* was observed sporadically. The endogeic species of soil animals are represented mainly by phytophages, whose spatial distribution depends on the spatial organization of the vegetation.


Figure 2. Scalograms illustrating the scaling of spatial structured variation in soil macrofauna community data (No variables as covariates, blue bars) and 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 spatial structured variation and pure spatial models, and the differences between variations explained by the spatial models and explained variations for topsoil, profile soil and plant models. The dbMEMs are ordered decreasingly according to the scale of spatial patterns they represent $x$-axis is the number of dbMEM.
Figure 3. Procrustean analysis of the effect of soil properties in the topsoil as a conditional variable on ordinal solutions with spatial variables as predictors: 1 – Agriotes lineatus, 2 – Agrotis segetum, 3 – Amara familiaris, 4 – Amara similata, 5 – Amphimallon solstitiale, 6 – Aporrectodea trapezoides, 7 – Athous haemorrhoidalis, 8 – Calathus fuscipes, 9 – Cardiophorus rufipes, 10 – Cepaea vindobonensis, 11 – Chrysolina fastuosa, 12 – Dendrobaena octaedra, 13 – Forficula auricularia, 14 – Geophilus proximus, 15 – Isomira murina, 16 – Lithobius curtipes, 17 – Lumbricidae sp, 18 – Megaphyllum sjælandicum, 19 – Melolontha melolontha, 20 – Otiorhynchus ligustici, 21 – Pachymerium ferrugineum, 22 – Polyphylia fullo, 23 – Prosternon tessellatum, 24 – Serica brunnea, 25 – Tabanus sp 1, 26 – Trachelipus rathkii, 27 – Xerolycosa miniata.

Therefore, the specificity of the spatial variability of soil properties indicated by the zoogenic factor covers the upper soil layer to the greatest extent.

The spatial component of the variability of topsoil soil properties is most represented by the broad- and medium-scale components, which also confirms our assumptions about the sources of influence that generate the corresponding patterns. The broad-scale component may be generated by microrelief features, which are formed as a result of flooding [64]. The micro-relief features are places of concentration of forest litter and moisture [65, 66]. These conditions are...
Figure 4. The spatial component of soil macrofauna community variation (I) and the direction and intensity of deviation from it as influenced by topsoil properties (II), soil profile properties (III), vegetation, and the difference between total spatial variation and net spatial component (IV) measured in procrustean residuals.
favorable for epigean soil animals and become foci of their development. As a consequence, a broad-scale spatial pattern is formed. The effect of variation of soil properties in the top horizon is closely correlated with the vegetation cover, which suggests the presence of a phytogenic component as a factor in the variability of soil properties. The phytogenic factor can explain the presence of a medium-scale component in the spatial pattern [67]. The vegetation cover modifies the microclimatic regime of the ecosystem, is a source of dead plant residues that fall to the surface or directly into the soil profile [68]. The soil animals respond to these processes, resulting in the formation of individual patterns of organization of the soil macrofauna community.

The variation of soil properties in the soil profile causes a separate spatial pattern of soil macrofauna, as well as a pattern that is induced by the joint influence of soil properties and vegetation. The peculiarities of the spatial pattern of soil-forming parent materials can be the cause of variation in soil properties throughout the profile [69]. The endodynamic soil-forming processes that encompass the soil profile as a whole also shape the living conditions of soil animals, which causes the structuring of their community. The plants are also important in the variability of soil properties [70]. The hierarchical organization of variation of soil properties in the profile is represented by broad-, medium-, and fine-scale components. The broad-scale component can be explained by the topography and mosaic nature of the soil-forming material. The medium-scale component can be explained by the vegetation factor. The fine-scale component can be induced by endogenetic processes of soil formation.

The medium-scale component is the most important for explaining the influence of vegetation on soil macrofauna. The presence of a "negative" explained variance of vegetation should also be noted. An additional explained variance of the soil macrofauna community, which is the cause of the "negative explained variation," occurs when the influence of vegetation is extracted. The estimation without vegetation extraction provides misinformation, or false information about the absence of plant influence at some spatial levels, as a consequence of which the explained variance is smaller than after extraction of vegetation influence. We can assume that a competing source of information is superimposed on the overall spatial pattern, which is significantly inferior in power to the dominant pattern, but can be established after filtering. The mechanism of the competing influence is the endogenetic dynamics of the vegetation cover, which superimposes its own pattern on the processes caused by soil heterogeneity. Remarkable is that the "negative" dispersion is also observed in the detailed-scale processes in the soil profile, which we also interpreted as endogenetic.

The pure spatial component of macrofauna community variation can be a consequence of the influence of unmeasured environmental factors, or be of a neutral nature [13]. The hypothesis that the purely spatial component is a neutral factor is valid only when all important environmental variables are taken into account. Otherwise, the unknown fraction of the purely spatial component may be represented by unmeasured environmental variables [18, 71]. The pure spatial pattern has three scale components. The broad-scale component may be a consequence of topographic heterogeneity of the studied polygon, which was not directly measured. In the floodplain, the topography has a wave-like character with frequency characteristics that are quite consistent with the large-scale component of the pure spatial pattern [72]. The medium-scale component can be induced by unmeasured vegetation indices. The phytoindicative assessments of environmental factors reflect changes in vegetation structure, but do not fully characterize them [31, 73]. The fraction of vegetation variability that also affects soil animals may be independent of environmental gradients or environmental scales may not always be sensitive to such gradients. The medium-scale component of pure spatial variability may be due to the vegetation variability that cannot be fully characterized by phytoindicator scales [73]. The fine-scale component represents the variability of the soil macrofauna community, which is related to factors of a neutral nature. An important component of the soil macrofauna community is represented by insect larvae. At the place of egg laying, larvae aggregation can
be observed, which is caused by factors of a neutral nature rather than particularly favorable habitat conditions. The soil larvae, especially C-shaped larvae, have low migratory capacity, so such aggregations may persist in the soil for a long period of time. The small dispersal radii of larvae in soil are the reason why the corresponding spatial patterns are fine-scale.

6. Conclusion
The community of soil macrofauna of floodplain forest is spatially structured. The factors of spatial organization are soil properties, influence of vegetation cover and pure spatial component of variability. The influence of factors of different nature manifests itself at different scale levels. The soil factors form large-scale patterns, the vegetation factors form medium-scale patterns, the factors of neutral nature form fine-scale patterns. The soil animals are important factors in the formation of the spatial structure of the soil cover and, by a positive feedback mechanism, can form conditions that contribute to the growth of populations and the functional activity of macrofauna.

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