Response of earthworms to changes in the aggregate structure of floodplain soils

G F Tutova¹, O V Zhukov¹, O M Kunakh² and Y O Zhukova²

¹ Bogdan Khmelnitsky Melitopol State Pedagogical University, 20 Hetmanska Str., Melitopol, 72300, Ukraine
² Oles Honchar Dnipro National University, 72 Gagarin Av., Dnipro, 49000, Ukraine

E-mail: annatutova37@gmail.com, zhukov_dnipro@ukr.net

Abstract. Earthworms are actively involved in the transformation of organic matter and in the formation of water-resistant soil aggregate structure. In the short time perspective earthworms are a factor that affects soil properties. However, other factors also influence soil properties and it is these factors that determine the total level of earthworm abundance and patterns of their spatial distribution. In urban park environments, the recreation load is an additional factor. The recreational load significantly affects the physical properties of the soil. An aggregate soil structure regulates the ratio of solid, liquid, and gaseous soil fractions and thus determines the living conditions of soil animals. Purpose/objective. The study tested the hypothesis about the influence of the aggregate structure of soil on the spatial distribution of earthworms under recreational load conditions. Methodology. Geostatistical methods and evaluation of animal response models to environmental factors. Results/findings. The aggregate structure of the soil is an important factor that affects the spatial patterns of earthworms under recreational load conditions. Earthworms prefer sites with a predominance of meso-aggregates. A recreational load leads to an increase in the proportion of macro- and micro-aggregates, which negatively affects the living conditions of earthworms. Conclusions. The processes of mutual influence of earthworms and soil aggregate structure have different temporal scales: earthworms influence soil structure in the time range of a few days or weeks, and aggregate structure influences in the time range of a few months or years.

1. Introduction

Soil is a specific environment for living organisms [1]. Soil is a polydisperse combination of three phases: liquid, solid and gaseous. The spatial and temporal organisation of these phases is the soil aggregate structure. The soil aggregate structure forms an ecological space in which a great diversity of forms of living organisms exist [2]. In turn, the living organisms influence the soil, which is reflected in the changes in its aggregate structure [3]. Earthworms play an important role in controlling soil structure dynamics [4]. The trophic and burrowing activities of earthworms greatly influence the physical environment in which they live and the dynamics of soil structure and the corresponding regulation of soil ecological functions and ecosystem services [5]. Soil aggregate structure controls water retention [6, 7], and infiltration [8]. The size distribution of the aggregate fractions significantly affects the gasses flux [9]. The importance of organic matter in the formation of soil aggregates is great [10,11]. An optimal aggregate structure is a condition for storage of organic matter in soil [12]. The aggregate structure regulates the dynamics of nutrients in the soil. The destruction of the aggregate structure leads to the opening of initially
inaccessible areas within the aggregates for the action of soil microorganisms and stimulates the turnover of nutrients, which is reflected in a significant decrease in their available forms [13]. The microbial trophic structure depends on soil texture and suitable habitable pore space, which determines the energy flow in terrestrial ecosystems [14]. Plant roots affect soil structure, and soil structure affects roots through regulation of root water uptake. The roots can decrease the average size of a soil aggregate as it grows among large soil peds, but can also increase the size of the aggregate if the aggregates are initially small [15]. Aggregate structure determines the sustainability of soil to water and wind erosion [16].

Aggregate structure forms the pore space of the soil. There is a significant correlation between average aggregate size and average pore size in the soil [17]. The size categories of soil animals are distinguished by their relation to the most typical conditions in the soil, which depend on the size of the soil pores [18]. The available soil pore volume determines the biomass of bacteria and their consumers among animals [19]. Small soil animals, such as Protozoa, are actually hydrobionts, since they live in the films of water that almost always cover soil particles. Mesofauna inhabit the soil crack system and are smaller than the soil pores. Soil macrofauna are larger than most soil pores and therefore have to either actively create soil tunnels to move, or use tunnels created by other soil animals or cavities that remain after the decomposition of plant roots [20]. The covers of most soil animals do not protect them from water evaporation, so the environment in which they live must have 100% humidity. Soil animals also need oxygen for active life. If the importance that the aggregate structure has for the formation of pore space, water regime and gas exchange is taken into account, the significance of the size ratio of aggregate fractions in shaping the living conditions of soil animals becomes clear [21].

The area of influence or volume of soil affected by earthworms is called the drilosphere [22, 23]. Bioturbators affect the soil structure by forming a system of burrows and moving soil aggregates without changing their internal organization [3]. Galleries are formed by earthworms moving in the soil and create large networks that occupy a significant volume of soil [4, 24, 25]. These large macropores are crucial for regulating water infiltration, solvent diffusion [26, 27], gas exchange and aeration through the soil [28, 29]. Earthworm burrows affect the spatial distribution of roots and plants [30]. The interaction between plant roots is two-way: plant roots tend to determine the distribution of earthworm burrows and some plant roots tend to follow the burrows [31]. Soil aggregate reorganisers are capable of altering soil structure both by building galleries and by consuming soil aggregates called biogenic aggregates [32]. Most earthworm species belong to this group [33]. This group is characterised by the ability to alter the internal organisation of soil aggregates. The amount of soil aggregates created by soil engineers is difficult to estimate [34]. The earthworm casts may constitute a large part of the soil aggregates on the soil surface or even an entire soil horizon [35]. Earthworm activity is important for the long-term stabilisation of organic matter in soils [36]. The reorganisation of soil aggregates by earthworms is very important and leads to completely different physical, chemical and biological properties of the soil [37]. This occurs when the pre-existing microstructure of the soil aggregate is completely destroyed in the foregut [38]. Then, during transit through the gut, clay minerals and organic materials are closely mixed and coated with mucus, creating a new core to form microaggregates [39, 40]. Within excreted casts, drying and ageing promotes the strengthening of bonds between organic materials, mucus and minerals to stabilize newly formed micro-aggregates [36]. Earthworms can also select and enrich soil aggregates in terms of organic matter and clay content, which contributes to the stability of soil aggregates [41].

2. Research aim and objectives

There is thus a consensus in the current scientific literature on the great importance of aggregate structure in soil function. The aggregate structure is seen as a factor that shapes the habitat of the soil biota [42, 43]. The dependence of the aggregate structure on the influence of living...
organisms, primarily ecosystem engineers, is also recognized [44]. However, information on how aggregate structure directly affects soil animal populations is extremely scarce. There is also no information on the role of soil animals in the spatial variation of aggregate structure.

The aim of our work was therefore to solve two tasks:

(i) to find out how soil aggregate structure affects earthworm abundance at the ecosystem level;
(ii) to reveal how earthworms affect soil aggregate structure at the ecosystem level.

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). Soil properties were measured at 105 points, which were located on a regular grid. The points are located in the center of 3×3 meter squares, within which the relevés was made [45]. The squares are contiguous with each other, constituting a polygon. On the opposite corners of the polygon were placed locations where vertical soil transects were made.

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 [46]. Genetic type of soil profile was determined according to Rozanov [47]. The classification of soils was performed according to IUSS Working Group WRB [48]. The classification position according to WRB was Fluvic Gleysol (Arenic, Ochric).

3.3. 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. Plant taxonomic names follow the Euro+Med Plantbase resource (http://ww2.bgbm.org/EuroPlusMed). A phytoindication of environmental factors was performed based on the Didukh [50].

3.4. 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 [51, 52]. 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 fraction size distribution was carried out by dry sieving in a system of sieves [53].

3.5. Statistical analysis
The phytoindication estimates of environmental factors obtained on the basis of species composition and grass projective cover were used as predictors of the environment, as well as data on the crown cover of trees. The data on crown density and projective cover of herbaceous plants were transformed: \( \text{asin}(c_i)^{0.5} \), where \( c_i \) is the projective cover of the i-th species. Species that occurred in the relevés at least 10 times were selected for the ordination procedure. There were 18 such species. The ordination of the plant community was performed using the method...
of nonmetric scaling [54] using the Bray-Curtis distance [55, 56]. According to the criterion of decreasing stress, the ordinal solution with four dimensions was found to be optimal [57]. The environmental factors were fitted to the ordinal dimensions using the envfit function from the vegan package [58]. The soil penetration resistance data for each soil layer were standardised, after which their average value was set to zero, and the value itself was presented in units of root mean square deviation. A matrix consisting of standardised soil penetration resistance values was subjected to a Redundancy Analysis (RDA) [59, 60]. Based on the local coordinates of the sampling points, a distance matrix between points was generated. The distance-based Moran’s eigenvector maps [61, 62] were computed from the distance matrix using the function dbmem from the package adespatial [63]. The 48 dbMEM eigenfunctions were extracted. Each of the dbMEM eigenfunctions models a spatial pattern with a frequency that increases in proportion to the order number of the function. The dbMEM eigenfunctions were used as predictors in the Redundancy Analysis procedure of standardised soil penetration resistance data. The explanatory power of the predictors in the Redundancy Analysis was estimated using the function RsquareAdj2.rda [64]. A scalogram was constructed by estimating $R^2$ for each spatial predictor separately. The vegetation ordination dimensions were also considered as conditional predictors.

4. Results

Three species of earthworms were found in the ecosystem studied: *Dendrobaena octaedra* (Savigny, 1826), *Aporrectodea trapezoides* (Dugès, 1828), and *Aporrectodea rosea* (Savigny, 1826). The abundance of the epigeic earthworm *D. octaedra* was $0.26 \pm 0.043$ ind./m$^2$. The abundance of the endogeic earthworm *A. trapezoides* was $3.84 \pm 0.25$ ind./m$^2$. The endogeic earthworm *A. rosea* occurred sporadically.

The aggregates with sizes 2–3 and 3–5 mm were the most abundant in the aggregate structure (23.77$\pm$0.198 and 21.57$\pm$0.061%, respectively) (figure 1).

![Figure 1. Proportions of aggregate fractions of soil. Abscissa axis is fraction size (in mm), ordinate axis is fraction proportion by weight (in %).](image)

The aggregates of size <0.25, 0.25–0.5, and 0.5–1 mm had the lowest proportion (2.81$\pm$0.067, 3.71$\pm$0.041, and 3.92$\pm$0.040%, respectively). Other fractions had intermediate proportions in the aggregate structure. The electrical conductivity of the soil was $0.22 \pm 0.009$ dSm/m. The
height of litter was 2.42±0.04 cm, soil moisture content was 17.34±0.13%, bulk density was 1.12±0.0037 g/cm³. The soil penetration resistance increased with depth (figure 2). In the upper soil layer, the penetration resistance was 1.28±0.023 MPa. Up to the depth, the penetration resistance changed insignificantly. From a depth of 25–30 cm to a depth of 65–70 cm a rapid increase in the penetration resistance with depth was found. With further increase in depth, the soil penetration resistance changed slightly. At the depth of 95–100 cm the soil penetration resistance was the highest and was 9.96±0.0078 MPa. There were 52 plant species identified in the vegetation cover of the studied polygon. The phytoindication assessment indicated that the moisture regime was suitable for mesophytes, and the estimate of the range of available moisture was 127 mm (figure 3).

![Figure 2. Variation of soil penetration resistance. Abscissa axis is penetration resistance, MPa, ordinate axis is soil layers: 0–5, ..., 95–100 cm.](image)

The regime of the contrasting conditions of soil moisture favored plants adapted to forest-meadow habitats with moderately irregular moistening of the soil layer, fully saturated by precipitation or groundwater. The phytoindication assessment indicated soil acidity, which was pH = 6.6. Trophic conditions were favorable for mesotrophs, which inhabit soils not very rich in salts (95–150 mg/l). The plants avoid carbonate substrates (CaO, MgO = 0.5%). The phytoindication of the cryoregime indicates the average temperature of the coldest month was
The coarse aggregates (greater than 10 mm and up to 5 mm in size) and fine aggregates (less than 1 mm in size) were positively correlated with each other and were negatively correlated with aggregate fractions of 1 to 5 mm in size (Figure 4). The aggregate structure was correlated with other soil properties. A decrease in soil electrical conductivity and moisture content and an increase in soil density were related to an increase in the proportion of aggregates larger than 5 mm or smaller than 1 mm (table 1).

Figure 3. Phytoindication assessment of environmental factors: Hd is the soil water regime, fH is the variability of damping, Rc is the soil acidity, Sl is the total salt regime, Ca is the carbonate content in soil, Nt is the nitrogen content in soil, Ae is the soil aeration, Tm is the thermal climate, Om is the ombroregime, Kn is the continentality, Cr is the cryo-climate, Lc is the light regime.

The spatial component described 34.32% of the variation in soil aggregate structure ($F = 2.13, p < 0.001$). The profile variation in soil penetration resistance explained 26.05% of the variation in soil aggregate structure ($F = 2.83, p < 0.001$). The phytoindication estimates of ecological properties explained 21.83% of the variation in soil aggregate structure ($F = 3.42, p < 0.001$). Three sets of predictors together explain 47.05% of the variation in soil aggregate structure ($F = 2.15, p < 0.001$). 3.9% of the variation in soil penetration resistance is spatially structured, as is 9.3% of the variation in phytoindication estimates (figure 5).

Aggregate fractions formed gradients of environmental conditions in which the abundance of earthworms varied in a pattern (figure 6, 7). The earthworms *A. trapezoides* and *D. octaedra* responded with a decrease in abundance when the proportions of aggregate fractions larger than 5 mm increased. With increasing aggregate fractions of 2–3 mm the abundance of earthworms increased. For the other aggregate fractions, the response of the earthworm *A. trapezoides* was bell-shaped symmetrical or asymmetrical.

An increase in aggregates smaller than 0.25 mm had a negative effect on the abundance of the earthworm *D. octaedra*. The response of the earthworm *D. octaedra* to an aggregate proportion of 0.25–0.5 mm was bell-shaped symmetrical, while the response to an aggregate proportion of 0.5–5 mm was monotonic with the presence of a plateau. The earthworms responded negatively to a high proportion of aggregates of 0.5–1 mm or a low proportion of

−0.64°C.
1–2 and 3–5 mm in size. The residuals of the CCA model with spatial variables, soil penetration rates and phytoindication scales as constrained variables correlated with earthworm abundance (table 2). As the abundance of *A. trapezoides* increased, the proportions of fractions larger than 5 mm decreased and those of 2–5 mm increased compared to the prediction of the CCA model. The abundance of this earthworm species had no effect on the predicted proportions of the other fractions. The abundance of *D. octaedra* negatively correlated with model residuals for the 7–10 mm fraction.

### Table 1. Correlation matrix of aggregate fraction content and the physical properties of soil in the 0–10 cm layer (correlation coefficients are shown significant for $p < 0.05$).

| Fraction size, mm | Electrical conductivity | Litter depth | Wetness | Bulk density |
|-------------------|-------------------------|--------------|---------|--------------|
| > 10              | 0.36                    | –0.26        | –0.49   | 0.56         |
| 7–10              | –0.34                   | –            | –0.55   | 0.52         |
| 5–7               | –0.47                   | –0.25        | –0.44   | 0.49         |
| 3–5               | –                       | 0.36         | –       | –0.24        |
| 2–3               | 0.46                    | 0.23         | 0.35    | –0.53        |
| 1–2               | 0.46                    | 0.20         | –       | –            |
| 0.5–1             | –0.54                   | –0.26        | –       | 0.31         |
| 0.25–0.5          | –0.63                   | –0.34        | –       | 0.30         |
| <0.25             | –0.74                   | –0.33        | –       | 0.30         |

### 5. Discussion

A soil texture is inherited from the parent material [65]. The soil texture is the ratio of primary soil particles of different sizes [66]. However, these primary particles are not separate, but are combined into aggregates [67]. The primary soil particles are bounded into the aggregates and are retained in this state by adhesives of organic and inorganic origin [68]. The adhesives of organic origin provide the aggregates with water resistance, i.e. the ability to persist in both dry and wet conditions [69]. Non-water-resistant aggregates, which exist in the dry state due to inorganic adhesives, disintegrate when wet. The arrangement of soil aggregates is called soil structure which is an important soil physical property [70]. Soil aggregation is a key ecosystem process leading to the formation and stabilization of soil structure, consisting of soil aggregates and the resulting matrix of pore spaces.

The aggregate structure is the proportion of aggregates of different sizes. The size and shape of aggregates is the result of the influence of two opposing complexes of processes: the formation and destruction of aggregates. These processes are biotic and abiotic in origin [71]. The ability to form soil aggregates depends on the size of the soil particles [72]. Large particles (sand) are less tend to form aggregates than fine particles (silt and clay) [73]. Thus, the spatial variability of soil texture determines the level of soil aggregate formation. In floodplain soils, the soil texture strongly depends on the processes of redeposition of turbid substances during flooding, which strongly influences the mosaic texture of floodplain soils and causes spatial patterns in the aggregate structure [74,75]. Distance from the river and channel networks are the most important environmental variables for predicting the soil textural fractions in floodplain soils [76]. Freezing and thawing of soils leads to the formation or destruction of soil aggregates [77]. The role of the temperature regime is superimposed on the moisture regime, since dry soils are less affected by freezing/thawing processes than wet soils [78, 79]. The constant variability of the water regime
as a result of floods, which is superimposed on the variability of the temperature regime in winter, is important for the area we studied. The average temperature of the coldest month has a value slightly less than zero, which confirms the presence of constant weather variability and the alternation of freezing and thawing of the soil. The spatial variability of soil moisture can strongly influence aggregation under the influence of temperature differences near the zero level.

**Figure 4.** Correlation matrix of aggregate fractions (after arcsine transformation).

Swelling and shrinkage also affect the formation of aggregates [80]. An increase in silt and clay contribute to the intensification of these processes [81]. Also the phenomena of soil salinisation, which are typical for the floodplains of steppe rivers [82,83], affect the soil aggregate formation and the resistance to destruction. The average size of aggregates decreases as the sodium content of the soil increases. The decrease in aggregate stability under the influence of sodium is caused by a weakening of the binding capacity of the cementitious substances that connect the domains that form the aggregates [17]. Thus, the presence of spatial patterns in the variability of soil aggregate structure can be explained by the spatial organization of the soil formation process in the floodplain. This assumption is confirmed by the fact that the variability of soil penetration
resistance in the soil profile allows us to explain the variability of the aggregate structure in the upper soil layer. Also, the profile distribution of soil properties is spatially structured. Obviously, the structuring factors are soil-forming processes in the soil.

Plants are important in the formation of soil aggregates [84]. The root system of plants contributes to the formation of soil aggregates, mainly mesoaggregates [85]. Plants also enrich the soil with organic matter, which contributes to the formation of water-resistant aggregates [86]. Obviously, the spatial organization of the plant community determines the spatial patterns of aggregate structure [87]. The results obtained indicate that the influence of the plant community on the aggregate structure is fully spatially structured. The generation and redistribution of organic matter should be noted to affect soil animals as well [42]. The plant organic matter is the basis of the trophic chains of pedobionts [88]. Also organic matter in the form of forest litter forms microclimatic conditions, which affect the spatial distribution of soil animals [45,81].

![Figure 5](image)

**Figure 5.** Variance partitioning between spatial and soil explanatory variables: [a] – variation explained solely by the values of penetration resistance within the soil profile; [b] – variation captured by the spatial (dbMEM) variables corresponds to pure space (residual spatial component); [c] – variation explained solely by the phytoindication assessments of environmental factors; [a]+[b] – variation explained both by the spatial and soil penetration resistance variables; [a]+[c] – variation explained both by the soil penetration resistance variables and phytoindication values; [b]+[c] – variation explained both by the spatial (dbMEM) variables and phytoindication values; [a]+[b]+[c] – variation explained by spatial, soil penetration resistance variables and phytoindication values. All the variance fractions shown are significant (p < 0.001).

The combination of factors and processes that influence the formation of soil structure creates the ecological environment for the existence of soil animals. The soil aggregates structurise the internal space of the soil, dividing it into intra-aggregate and inter-aggregate pore space [89]. The inter-aggregate space provides the soil biota with air [90–92], while the intra-aggregate space is a reserve of soil moisture [93]. Thus, due to the aggregate structure, the soil combines anaerobic and aerobic conditions [94]. The final outcome of aerobic processes is mineralization of organic matter, which makes nutrients available to plants [95]. The final outcome of anaerobic processes is humification, which provides stability of the soil environment both through immobilization of nutrients in the organic matter of the soil and through the formation of a water-resistant soil structure [96].

A high proportion of mesoaggregates provides the optimal ecological regimes in the soil. Coarse or fine aggregates create unfavorable living conditions for the majority of pedobionts. Our
results indicate that the abundance of earthworms decreases under conditions of predominance of large aggregates (size greater than 5 mm).

Figure 6. Response of *A. trapezoides* abundance in a gradient of aggregate fraction proportions. The ordinate axis is the number of worm individuals in a 25×25 cm soil sample; the abscissa axis is the proportion of aggregate fractions; 1 – fractions > 10 mm; 2 – fractions 7-10 mm; 3 – fractions 5-7 mm; 4 – fractions 3-5 mm; 5 – fractions 2-3 mm; 6 – fractions 1-2 mm; 7 – fractions 0.5-1 mm; 8 – fraction of size 0.25-0.5 mm; 9 – fraction of size <0.25 mm; model II – monotonic response; IV – symmetrical bell-shaped response; V – asymmetrical bell-shaped response (response models from the HOF list of functions [97,98]).

This result is true for both endogeic *A. trapezoides* and epigeic *D. octaedra*. The large
aggregates provide conditions for hyperaeration of the soil and its rapid desiccation. Obviously, this very reason explains the negative response of earthworms to the high proportion of large aggregates. This assumption is confirmed by the fact that an increase in the proportion of large aggregates is accompanied by changes in other soil properties, including a decrease in soil moisture [83].

The role of aggregate structure is more important for the endogeic earthworm *A. trapezoides*. For the epigeic earthworm *D. octaedra*, aggregate structure is also important, but it is most probable that the influence of aggregate structure is mediated by the coordinated variability with other soil properties. Thus, an increase in the proportion of large aggregates is associated with a decrease in the depth of the forest litter, which is the habitat of *D. octaedra*. The response of *D. octaedra* to some aggregate fractions also has a plateau, indicating the presence of some zone of indifference of the epigeic earthworm to the aggregate structure.

Table 2. Correlation of earthworm abundance with CCA model residuals with spatial variables, soil penetration indices and phytoindication scales as constrained variables (correlation coefficients are shown significant for $p < 0.05$).

| Fraction, mm | *A. trapezoides* | *D. octaedra* |
|--------------|------------------|---------------|
| > 10         | −0.44            | −             |
| 7–10         | −0.34            | −0.32         |
| 5–7          | −0.28            | −             |
| 3–5          | 0.24             | −             |
| 2–3          | 0.26             | −             |
| 1–2          | −                | −             |
| 0.5–1        | −                | −             |
| 0.25–0.5     | −                | −             |
| <0.25        | −                | −             |

Thus, the aggregate structure of soil, the variability of which is coordinated with the variability of other soil properties and processes, affects earthworms. However, earthworms are also active aggregate formers, and they also affect the aggregate structure. To distinguish in this case the cause from the effect is extremely difficult, because suitable for earthworms are conditions with the predominance of meso-aggregates. The earthworms form zoogenic aggregates (coprolites), which are also mesoaggregates in size [99]. We hypothesized that earthworms, in the case of their influence, should explain that part of the variability of soil aggregate structure that factors of other origin do not explain. The soil penetration resistance is a reliable marker of variability of a whole complex of properties. A measurement of this index in the soil profile indirectly indicates variation in other soil properties. The phytoindication estimates show not only the variability of the vegetation structure, but also on the environmental factors that caused this variability. The spatial variables reflect the fact of the spatial structure of both soil properties and vegetation properties. They are also proxies for other environmental factors that have not been explicitly measured, but are spatially structured. The model residuals with these factors as constrained variables were found to be correlated with earthworm abundance. In this case, the hypothesis that earthworms are the cause of such deviations rather than the consequence should be considered the most probable. However, one cannot exclude the mechanism of an inverse positive relationship, when the production of mesoaggregates by earthworms contributes to the optimization of living conditions for earthworms and thus
Figure 7. Response of *D. octaedra* abundance in a gradient of aggregate fraction proportions. The ordinate axis is the number of worm individuals in a 25×25 cm soil sample; the abscissa axis is the proportion of aggregate fractions; 1 – fractions > 10 mm; 2 – fractions 7-10 mm; 3 – fractions 5-7 mm; 4 – fractions 3-5 mm; 5 – fractions 2-3 mm; 6 – fractions 1-2 mm; 7 – fractions 0.5-1 mm; 8 – fractions 0.25-0.5 mm; 9 – fractions <0.25 mm; model II – monotonic response; II – monotonic response with plateauing; IV – symmetrical bell-shaped response; IV – asymmetrical bell-shaped response (response models from the HOF list of functions [97,98]).

stimulates the development of their populations. The water stability of coprolite aggregates of Aporrectodea caliginosa is 2–2.5 times higher than that of soil aggregates of the same size [99]. The coprolite aggregates contain more clay particles and organic matter and less sand
than the surrounding soil, because earthworms selectively absorb smaller particles and organic residues. The average size of mineral particles found in the digestive tract of earthworms is 100–500 m [100]. The shape and increased stability of coprolites positively affect aeration, water infiltration, water-holding capacity of soils, and increase their specific surface area. The coprolites and coprogenic aggregates have high water stability. The coprolites can persist for several months or even years, depending on soil moisture and temperature [101,102]. The water stability of coprolites depends on their enrichment with polymeric compounds and calcium (excreted by earthworms), poorly decomposed organic matter, clay and silt particles, humates, and microbial polysaccharides [103]. An important role in increasing the water stability of coprolite aggregates belongs to fungi, which form a branched mycelial network on the surface and inside coprolites [100]. There is notable that the abundance of earthworms explains the variability of the model residuals, which by definition are without the spatial component of variability within the chosen sampling strategy. The influence of earthworms can be assumed to be spatially structured at the spatial level, to account for which studies with a more detailed spatial resolution are necessary.

6. Conclusion

The aggregate structure of the soil is influenced by the pedogenic, phytogenic and zoogenic factors. The action of these factors is spatially structured. The endogeneous earthworm *A. trapezoides* is more sensitive to the effects of soil aggregate structure than the epigeneous *D. octaedra*. An increase in the proportion of large aggregates (greater than 5 mm in size) negatively affects earthworm abundance. The response of earthworms to the proportion of meso-aggregates is predominantly bell-shaped. Earthworms at the ecosystem level stimulate an increase in the proportion of meso-aggregates.

**ORCID iDs**

O. Zhukov https://orcid.org/0000-0003-3661-3012
A. Tutova https://orcid.org/0000-0003-0961-7608
O. Kunakh https://orcid.org/0000-0002-3631-8884
Y. Zhukova https://orcid.org/0000-0001-6208-7218

**References**

[1] Gilarov M S 1949 *Features of soil as an environment and its significance in the evolution of insects* (USSR Academy of Sciences Press)
[2] Elliott E T and Coleman D C 1988 *Ecological Bulletins* - Swedish Natural Science Research Council 39 23–32
[3] Bottinelli N, Jouquet P, Capowiez Y, Podwojewski P, Grimaldi M and Peng X 2015 *Soil and Tillage Research* 146 118–124
[4] Blouin M, Hodson M E, Delgado E A, Baker G, Brussaard L, Butt K R, Dai J, Dendooven L, Peres G, Tondoh J E, Cluzeau D and Brun J J 2013 *European Journal of Soil Science* 64 161–182
[5] Birkhofer K, Bezemer T M, Bloem J, Bonkowski M, Christensen S, Dubois D, Ekelund F, Fließbach A, Gunst L, Hedlund K, Mäder P, Mikola J, Robin C, Setälä H, Tatin-Froux F, Van der Putten W H and Scheu S 2008 *Soil Biology and Biochemistry* 40 2297–2308
[6] Guber A, Pachepsky Y, Shein E and Rawls W 2004 *Soil aggregates and water retention* p 143–151
[7] Lipiec J, Waleczak R, Witkowska-Waleczak B, Nosalewicz A, Słowińska-Jurkiewicz A and Sławiński C 2007 *Soil and Tillage Research* 97 239–246
[8] Franzluebbers A 2002 *Soil and Tillage Research* 66 197–205
[9] Mangalassery S, Stügersten S, Sparkes D, Sturrock C and Mooney S 2013 *Soil and Tillage Research* 132 39–46
[10] Devine S, Markewitz D, Hendrix P and Coleman D 2014 *PLoS ONE* 9 e84988
[11] Six J, Paustian K, Elliott E T and Combrink C 2000 *Soil Science Society of America Journal* 64 681–689
[12] Zhou M, Liu C, Wang J, Meng Q, Yuan Y, Ma X, Liu X, Zhu Y, Ding G, Zhang J, Zeng X and Du W 2020 *Scientific Reports* 10
[102] Tiunov A 2000 *Soil Biology and Biochemistry* **32** 265–275
[103] Smagin A V and Prusak A V 2008 *Eurasian Soil Science* **41** 618–622