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Peculiarities of the biotic interactions in the soil system

Key words: soil communities, earthworms, burrows, locomotory activity, soil pores, soil aggregates, biotic interactions, soil fauna

Summary

The heterogeneity of soil environment is an important factor of the taxonomic and ecological diversity of the soil animal population. The contribution of invertebrates to the formation of aerial space in mineral soil horizons, in the form of a stable system of biopores, is considered on the basis of the author's original materials and literature data. Aerial space is the necessary condition for the life of aerobiotic forms in the mineral soil, which comprise the bulk of soil invertebrates belonging to meso- and macrofauna. Zoogenic mechanisms of the formation of soil pores and soil aggregates are analyzed. Pore walls and aggregate surfaces are populated by different groups of pedobionts. The partial isolation of these loci decreases predation, that creates conditions for the maintenance of a high diversity and abundance of animal populations in the restricted volume of populated soil profile.

1. Introduction

Soil animal communities are characterized by high levels of abundance and taxonomic diversity. In the soil, animal species richness per unit area exceeds the one in the aboveground stratum. The high

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diversity level of soil organisms can be compared with the "planktonic effect" in hydrobiotic communities outlined by Hutchinson (1961). The local diversity can be driven by high trophic mosaics (Pimm and Gittelman 1990), which produce competitive or mutualistic interactions (Melián *et al.* 2009). Investigation of factors supporting the high diversity and abundance of soil animal communities is of a profound interest.

This paper considers effects of the locomotory and trophic activity of soil invertebrates on their environmental conditions, which supports ecological and taxonomic diversity of soil communities.

2. Spatial heterogeneity of animal diversity and abundance in soil

Peculiarities of soil environment allow the coexististence of closely related species within the same habitat. For example, litter and soil macrofauna in primary forests of the southern Far East of Russia contains significant numbers of congeneric species, which can occur in the same habitat (Ganin and Striganova 2012). Table 1 illustrates this pattern, showing the numbers of the congeneric species of gastropods and diplopods in different forest stands.

The local fauna of gastropods includes 4 genera, each represented by 2-5 species. The affinity of the trophic dispersion of congeneric species averaged 70-80%. The local diplopod fauna includes 5 genera, each represented by 3-6 species, with one exception: *Diplomaragna* is represented by 16 species (of them, 8 and 5 species co-occurred in broad-leaved and pine forests, respectively).

At the same time, spatial distribution of soil animals is characterized by a high concentration of individuals, species, taxonomic and ecological groups in the relatively narrow soil layer enriched by organic matter. On the territory of East-European Plain the depth of populated horizons is, on average, 5-7 cm in gleyic glossisols, 10-12 cm in forest cambisols, and exceeds 60 cm only in chernozem soils.

Table 1. Numbers of congeneric species of litter and soil invertebrates in forest ecosystems of the Southern Far East (Ganin and Striganova 2012).

Taxonomic groups	Species number		
	Forest ecosystems in general	Separate forest types	
		Dark-coniferous forests	
Gastropoda			
Cochlicopa	3	2	
Bradybaena	4	3	
Vallonia	5	4	
Lindholmomneme	3	2	
		Broadleaved forests	Pine forests
Diplopoda			
Polyzonium	3	2	-
Diplomaragna	16	8	5
Uniramidesmus	6	3	4
Levizonus	4	2	4
Epanerchodus	3	2	2

A comparative investigation of the abundance and vertical distribution of invertebrates in the soil profile was carried out in the Polish Sudetes (Tab. 2; Striganova 1999). On the mountain macroslope along the altitude range of 500-1420 m a.s.l., animals populated a comparatively thin soil layer. Their abundance was not related to the volume of the populated soil horizon. Rather it was determined by abiotic factors, in particular, by soil temperature. Two peaks of abundance were recorded in the most warm habitats: in the submountain broadleaved forest and in the upper timberline belt (where the soil is substantially warmed in the absence of a closed canopy).

Table 2. Numbers and biomass of soil mesofauna and the depth of populated soil horizon in the altitude belts of Karkonosze mountains (Szrenica macroslope) (from Striganova 1999).

Habitats	Altitude m a.s.l.	Populated horizons cm (A_0/A_1)	Numbers ind. m^{-2}	Biomass g m^{-2}
Submontane beech stand	550	10/10	400	6.20
Mountain spruce forest	1100	4/3	522	1.57
Upper timberline	1300	10/4	1016	3.89
Crooked pine woodland	1400	3/6.5	292	3.52
Subalpine meadow	1420	3/4	190	0.83

A straight dependence of soil zoomass on abiotic factors suggests that these communities in Polish Sudetes are unsaturated. This means that ecological capacity of a soil environment can support higher numbers of animals under optimal conditions. Coexistence of closely related species demonstrates the presence of mechanisms lowering down the competition pressure. The environmental heterogeneity and temporal fluctuations of abiotic factors promote divergent trends in the use of resources by soil macrofauna.

3. Soil pores as living space of soil invertebrates

Ghilarov (1977) explained the high taxonomic diversity of soil fauna by mechanical peculiarities of soil environment, which represents a three-phase system containing large reserves of free water and air. The polydisperse structure of mineral soil provides the presence of water and aerial pores between the solid particles, which are used as topic niches by water and terrestrial organisms.

Soil invertebrates dwell on the surface of soil aggregates, on the walls of soil pores. The amount of pores, their diameters and the total surface of pore walls characterize the total space available for pedobionts. Representatives of separate size- and eco-physiological groups of animals occupy different kinds of pores and form specific zoo-microbial synusia in isolated porous spaces.

Table 3 demonstrates the classification of soil pores used by pedozoologists for the assessment of animal distribution. Firstly, the character of soil pores depends on soil granulometric content. In loamy-sandy soils, transmissive pores predominate between the aggregates with diameters up to 100 mm. In heavy loamy soils, small intra-aggregate pores are numerous. Abundance of accumulative pores is, on average, 22% in sandy soils, 40% in silt sandy clay soils and 72% in loamy soils (Heijnen *et al*. 1993). This determines the moisture retention capacity of soils and abundance of their animal populations. Transmissive pores filled by air in unsaturated soils are used by aerobiotic animals as ecotopes. Accumulative pores keep the capillary water and are populated by microflora and small hydrobiotic invertebrates.

Table 3. Size classification of soil pores (after Greenland (1977), with changes).

Pore diameter, mm	Pore types	Distribution of soil organisms
< 0.5	residual	microflora
0.50-50	accumulative	microflora + nanofauna
50-500	transmissive	microflora + microfauna

Representatives of animal groups of different size are distributed between the three phases of soil environment. Small water pores and water films around mineral particles are inhabited by the smallest (physiologically hydrobiotic) forms of the microfauna. Aerobiotic mesofauna group occupies aerial pores. For the largest size group, mesofauna, soil is a solid environment where they have to create the available space to realize the main functions of their life cycle: dispersion, feeding, growth and reproduction. This is performed by the burrowing activity, which is characteristic for many groups of large pedobionts. Soil animals construct a system of tunnels in the soil, which is accompanied by translocation of large masses of mineral and organic matter along the soil profile.

Requirements in oxygen concentration in the air hardly differ between the majority of soil- and surface-dwelling invertebrates. But, in comparison with the atmospheric air, in the soil air oxygen content decreases downward the profile, whereas carbon dioxide concentration increases by an order of magnitude (Fig. 1).

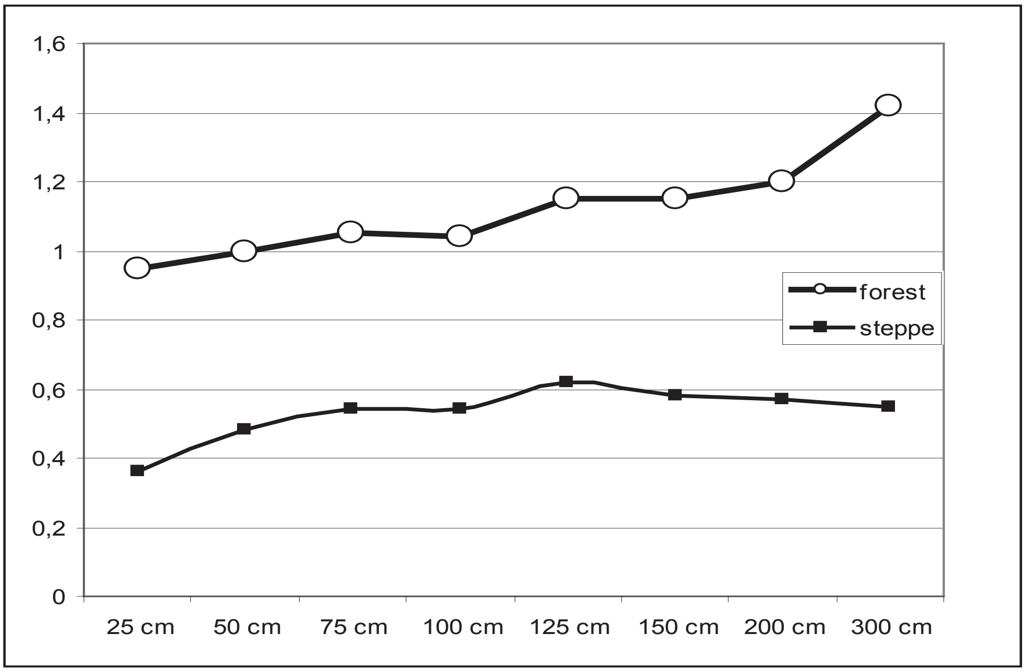

Fig. 1. Changes in CO_2 content in the air along the soil profile in two different habitats (Striganova 1996).

An especially high increase of carbon dioxide concentration with the soil depth has been recorded in the rhizospheres with high biomass of thin roots, due to intensive respiration of living roots and decomposition of dead root remains. However, many soil animals are attracted by rhizospheres, where living roots and root-associated microflora represent their feeding resources.

That is why the development of animal life in the mineral soil in the course of evolution was connected with the creation of intra-soil aerial space available for aerobionts. Many forms of pedobionts build burrow systems in soil and support these systems during their life cycle.

4. Burrowing activity and creation of aerial space in soil

The majority of investigations on animal burrowing activity have been carried out on earthworms. The results obtained allow to evaluate the volumes of zoogenic macropores.

In agrocenoses, the numbers of earthworm burrows correlate with the level of soil compaction: thus, in loose garden soils, crop fields and dense pasture soils 33, 360 and 800 burrows m^{-2} were recorded (Lee 1985). Rates of earthworm dispersion and burrow creation were studied in a pasture soil after inoculation of four earthworm species (Ligthart and Peak 1997). A 3-dimensional mapping of burrow systems during the subsequent 10 years allowed the tracing of earthworm dynamics. The rate of earthworm dispersion averaged 6.3 m y^{-1}, *Aporrectodea longa* being the most active colonizer. The maximum rate of burrowing reached 110 m m^{-2} y^{-1} during the first year, but later the rates of burrowing decreased, that correlated with the dynamics of earthworm population density. Young burrow systems were branched, later they shifted to a more vertical orientation. These temporal changes of the burrowing activity can be treated as a result of the restoration of aeration in mineral soil horizons populated by earthworms. Burrowing activity patterns can also be modified by competitive relations between the separate earthworm species.

Patterns of burrowing activity at different soil depths were compared in earthworm species representing endogeic (*Aporrectodea caliginosa*) and anecic (*Lumbricus terrestris*) ecological groups (Pitkänen and Nuutinen 1997). The burrow distribution was mapped at several horizontal levels along the profile of a gleyic glossisol. Some 1260 burrows m^{-2} were recorded at the depth of 30 cm, but only 180 burrows m^{-2} at the depth of 80 cm. The majority of the burrows belonged to *A. caliginosa.* Burrow diameters changed with soil depth: the smallest burrows (2-3 mm in diameter) predominated in the upper 40 cm, but deeper the proportion of larger burrows (3-5 mm) increased markedly.

Burrows of both species differed by the length and branching: the burrows of *L. terrestris* were not branched and extended deeper than 80 cm. *A. caliginosa* created a branched burrow system within a restricted part of the soil profile. Endogeic species preserved the patterns of their burrowing activity under different conditions. Burrows of A. *rosea* and *A. caliginosa* in the red-brown soils of Southern Australia occupied nearly the whole A-horizon (of 25 cm deep) (McKenzie and Dexter 1993). The burrows had 2-3 branches and were shifted to a more vertical orientation with soil depth.

The burrow morphology seems to be species-specific. This was investigated in artificial soil cores by means of X-ray computer tomography (Capowiez *et al.* 2001). Burrows of the anecic earthworm species, *A. nocturna*, were longer, nearly vertical, less branched and with fewer connections than those of the endogeic species *A. chlorotica*. Burrows of the both species differed by diameter that allowed to assess interrelations between them. Thus, in the presence of *A. chlorotica*, burrows of *A. nocturna* were shorter and more vertically oriented. In multispecies earthworm communities, burrow systems of separate species tend to separate within the soil profile. For example, burrows of *Aporrectodea caliginosa* and *Lumbricus rubellus* are recorded in upper parts of the profile, while *A. longa* and *L. terrestris* occupy deeper horizons (Springett and Gray 1997). These results showed that burrows of different species do not overlap.

Patterns of the burrowing activity are related to the dispersion of plant roots and plant species. In the presence of roots, earthworms avoid to burrow into the root beds and roots rarely explore earthworm burrows, as it was shown in the field soils (Springett and Gray 1997).

An assessment of the total volume of biopores made by earthworms is an important measure of their activity. In the field experiments, earthworm burrowing activity was measured by Bastardie *et al.* (2005). Monoliths of a compact pasture soil were inoculated with earthworms at average density of 101 ind. m^{-2}; endogeic *Nicodrilus giardia* was the dominant species. After 3 years, biopores were recorded by means of X-ray computer tomography, which allowed to reconstruct 3D form of the burrow systems. Overall, these systems represented a dense net of interconnected burrows. A number of burrows was extended along the whole length of the monoliths (60 cm), but the majority of the burrows was shorter. A part of the burrows (9-43%) opened at the soil surface. The total burrow length in separate monoliths varied from 687 to 1212 m m^{-3}. The total area of burrow walls reached 12764 cm^2 m^{-3}, while the wall area of the burrows which were opened at soil surface, ranged between 1069 and 7237 cm^2 m^{-3}. These indices are important for the characteristic of the space inhabited by earthworms. Burrow walls covered by earthworm faeces and mucus are populated by microorganisms which represent food reserves. Earthworms graze on bacterial films and colonies of microfungi. Walls of the burrows opened at the soil surface, are populated by litter microflora and small invertebrates. Aerial conditions in these burrows enriched by organic matter allow the functioning of litter communities in mineral moist horizons, that promotes aerobic decomposition processes.

In separate years, burrow systems differed by the density of burrows and amount of outlets opened at the soil surface. Earthworms can regulate their burrowing activity depending on soil hydrothermal conditions: they create more burrows opening at the surface during moist seasons to optimize the aeration and reduce the numbers of surface burrows during dry periods.

Burrow walls (drilosphere) represent a compacted layer of 0.5-2 mm thick. At high earthworm densities, burrow total volume can reach 4-5% of the soil volume (Bastardie *et al*. 2005). The autoradiographic analysis of *L. terresiris* burrow walls showed that they are enriched by litter fragments incorporated into the compacted walls lined by excreta (Binet and Curmi 1992). Burrowing activity of earthworms modifies markedly the structure of soil porosity. Construction of stable burrow systems by earthworms results in a reduction of the native soil porosity due to the compaction of burrow walls and creation of biopore system.

The role of earthworms in the creation of the soil system porosity has been demonstrated in field experiments on artificially compacted soil plots (situated on the wheel tracks) (Capowiez *et al*. 2012). During the first three months, the earthworm biomass decreased in these plots by 70%, in parallel with the increase of soil bulk density (from 1.46 to 1.57 g cm^{-3}). The restoration of the soil functional properties – macroporosity and water infiltration capacity – took place due to the regeneration of earthworm activity, but this process required a long time.

We estimate that under a high population density and activity of earthworms, the total volume of their aerial macropores can reach 20-30% of the total soil volume.

Active burrowing is also known for some other groups of soil-dwelling arthropods. For the first time, quantitative assessments of the burrowing activity of invertebrates were carried out by Dimo (1945), who underlined a significant role of zoogenic processes in the soil formation.

The constructions of ants and termites are well known. Many species build composite subterranean and epigeic nests. They burrow chambers in soil, connected by extensive galleries.

In desert regions of Central Asia ants and termites construct primarily subterranean nests without epigeic structures. Table 4 shows the depth and volume of galleries in the nests of ant species typical for desert grey soils of the Middle Asia (Dlusskij *et al.* 1989). The depth of ant building activity is species-specific and also varies in separate nests of the same ant species. Especially wide differences were recorded in *Messor aralocaspius* and *Camponotus xerxes*, which burrow deep galleries down to 2-4 m under the soil surface. The total volume of galleries in subterranean nests can reach 40 l m^{-3}, that provides the sufficient aeration.

Termites require oxygen concentration close to that in the open atmosphere. Measurements of air content in termite mounds showed that CO_2 concentrations fluctuated between 1.0 and 1.9%, while O_2 concentration averaged 19.1-19.9% (Day 1938). Termites survive at high CO_2 and low O_2 pressures. On an example of *Zootermopsis nevadensis* it has been shown that oxygen consumption of termites did not fall until O_2 concentration was decreased to 2% (Cook 1932). A high CO_2 concentration was related to the metabolic activity of termites and numerous representatives of microflora, which are cultivated in the nests as food reserve. Apart of this, decomposition of organic remains also creates a significant CO_2 input.

Table 4. Depth and volume of ant galleries in a desert grey soil (after Dlusskij *et al.* 1989).

Ant species	Depth of the nests cm	Total volume of burrows cm^3
Monomorium barbatulum	65-115	11-20
Tetramorium schneideri	30-37	83-279
Cataglyphis aenescens	78	787
Messor aralocaspius	170-330	7764-14075
Camponotus xerxes	240-390	7279-40560

The depth of termite nests (*Anacanthotermes ahngerianus*) in Central Asia varied from 1.5 to 10-15 m below the ground surface. Their galleries reach moist soil horizons (Valiakhmedov 1987). In the Western Africa termite galleries extend to 70 m deep and reach the water table (Yakushev 1968). A coincidence of depths of termite galleries and moist soil horizons has been discussed in the literature. Ghilarov (1962) considered this correlation as the way to supply the moist air into the nest. Valiakhmedov (1987) suggested that termites excavate moist loam from the deep soil layers to straighten the walls of their nests.

Termites excavate significant soil amounts to the soil surface in the process of construction of subterranean nests. They remove sand particles (0.2-2 mm) which form distinct heaps on the soil surface around the nest outlets. The height of these heaps can reach 20 cm in *Hodotermes mossambicus* and 15 cm in *Drepanotermes peringer* (Lee and Wood 1971). Termites were observed to create subterranean galleries by compressing soil sideways to form compact walls. This way of building requires moist fine mineral particles. Termites use their head capsule, mandibles and the whole body for the burrowing and compressing gallery walls. Many termite species cover the walls with excreta and saliva. External walls of epigeic mounds are also covered with mineral soil material. Some species compress loamy particles and fill cavities in mound walls with their compact faecal pellets. Soil-ingesting species construct mound walls from an amorphous mass consisting of sand grains, fine soil particles, undigested remains, metabolic products and saliva.

Termites and ants translocate large amounts of soil along the soil profile in the process of building. Excavation of clay from deep soil horizons results in significant changes of soil granulometric content in the nest area (Tab. 5). Thus, clay content in the nests of Central-Asiatic species was by 2-5 times higher in comparison with the control soil (Valiakhmedov 1987, Sojunov 1991). The content of clay and sand in the mounds of *Cubitermes umbratus* averaged 67.2% and 26.5%, respectively, as compared with 30.8% and 63.0% in the surrounding soil (Kemp 1955). In the subterranean part of the nests of *Drepanotermes rubriceps*, the ratio between the coarse and fine soil fractions averaged 75 to 25%, as compared with 84% to 13% in the soil. In the above-ground galleries this ratio was 73% to 23%, as compared with 80% to 8% in the soil (Lee and Wood 1971). Together with clay, termites elevate many microelements and shift the salt maximum upwards by their nest construction.

Table 5. Effects of burrowing activity of ants and termites on the granulometric content of soil (Valiakhmedov 1987).

Species	Content of physical clay, %	
	Control	Nest
Ants		
Cataglyphis setipes	36-54	48-61
Messor variabilis	8-22	18-40
Termites		
Anacanthotermes turkestanicus	9.4	20.8
A. ahngerianus	15.3-32.3	36.8-37.1

Termite show selectivity to the size of soil particles used for their constructions. They avoid particles of 100-500 μm (Stoops 1964). Large-sized particles are transported by mandibles, fine particles are swallowed, carried in crops and excreted in the nests, but the particles of 100-500 mm are too small to take them by mandibles and too big to swallow.

In spite of the increase in the content of fine soil fraction, the bulk density of the material in termite nests is lower than that in the surrounding soil. For example, in the nests of *Anacanthotermes ahngerianus* the bulk density of the nest material was 1.112 g cm^{-3}, as compared with 1.226 g cm^{-3} in the control soil (Dimo 1945). The decrease of the bulk density is related to the increased soil porosity. It is the result of construction of subterranean galleries accompanied with the excavation of soil material to the surface.

In arid soils, zoogenic activity is shifted into deep mineral horizons, in search of water. That is why the aeration of deep horizons in such soils is of a special importance. Numerous populations of soil dwelling woodlice occur in desert regions of different continents. In the Near East, Central Asia and Northern Africa they are represented by species of *Hemilepistus*, in America – by *Venecillio arizonicus*, in Australia – by *Buddelungia* (Ghilarov 1970). Their burrowing activity and behavior have been studied on an example of *H. cristatus* populating desert grey soils in Central Asia (Striganova 2000). Their colonies occur in loamy soils, where woodlice burrow vertical galleries of 0.5-0.7 cm in diameter, down to 1 m deep.

They burrow soil by sclerotized combs on their backs and lift it to the soil surface. The woodlice do not strengthen the walls of their galleries. This is the reason why their distribution is restricted by soils with a heavy granulometric structure. A quantitative assessment of the density of woodlice burrows in their colonies was carried out in southern Turkmenia (Striganova 2000). Numbers of woodlice burrows averaged 70 per m^2. Each burrow was populated by a woodlice family consisting of a parental pair with their brood (20-30 specimens). The total volume of aerial space in a soil core of $100 \times 100 \times 80$ cm averaged more than 1500 cm^3 (*i.e. ca* 2% of the soil volume). Woodlice regulate air content and hydrothermic regime in the burrows. They close the outlets during the hot period of the day and eliminate faeces which emit carbon dioxide.

In the course of evolution, the transition of desert woodlice to subterranean mode of life was accompanied by complex adaptations related to their behavior, activity rhythms, parental care and special morphological structures for the burrowing. However, the woodlice retained some ancestral connections with the surface soil stratum, such as feeding (on above-ground plant remains) and respiration (using air with oxygen pressure close to the atmospheric air).

Quantitative investigations of the burrowing activity of beetles and beetle larvae have hardly been performed. But it is well known that many species of Scarabaeidae, Elateridae, Tenebrionidae, Alleculidae and Phylloceridae construct soil burrows and chambers for their offspring. Such chambers, with walls built of mineral particles and faeces and fastened by saliva, were found at different depths of mineral soil horizons in arid soils (Valiakhmedov 1987). In some habitats the total volume of numerous chambers reached 40% of the soil volume. Some species of scarabaeids and phyllocerids build chambers for their brood with double walls, with air layer between the walls.

Female beetles burrow deep tunnels which reach the moist soil horizons, build chambers at the end of the tunnels, supply them with food for the larvae and leave the soil after oviposition.

After hatching from the eggs, the larvae complete the larval and pupal stages in the chambers, and the new generation of adult beetles emerges on the soil surface. Chamber walls, impenetrable for water evaporation, are usually considered as the protection from a water deficiency in the soil. But the chambers are placed in deep, respectively moist horizons. That is why we suggest that these chambers represent aerial cavities necessary for the existing of large-sized aerobionts deep in the soil.

Chamber diameters, as measured for some beetle groups (Valiakhmedov 1977), allow to calculate air volume in their chambers: Phylloceridae – up to 140 cm^3, *Lethrus* – 4-8 cm^3, *Copris hispanus* – 25 cm^3, *Synaptus tmolus* – 100 cm^3. In habitats with high population densities of these beetles, the chamber construction significantly affects the structure and aeration regime of the soil.

The constructive activity of large-sized soil invertebrates results in the increase of diversity of their ecotopes and modifies structural and functional characteristics of soil environment and soil communities. During the latest decades, this kind of animal activity was determined as "engineering activity" and burrowing animals – as "ecosystem engineers" (Jones *et al*. 1994). Another term, "environmental conditioning" (proposed by Swift *et al*. 1979), has been used in the previous decades in respect to animals inhabiting soil and plans remains.

The engineering activity and conditioning of environment by the animals are of a primary significance for the soil system. The aeration of mineral soil horizons allows the penetration and settling of small invertebrates and aerobic microflora and promotes aerobic processes of organic matter decomposition.

5. Effects of animal feeding activity on soil porosity

The majority of soil invertebrates belong to saprotrophic forms, feeding on litter, root debris and saprotrophic microflora. They form initial trophic levels of detrite food chains. Primary decomposers are known to realize comminution, partial digestion of plant remains and mixing them with mineral particles. In soils with a high abundance of saprovores, the organic horizon nearly completely consists of coprogenic organic-mineral aggregates, that has been demonstrated on examples of primary soils on mountain rocks and of alluvial-organic horizons in flood-plain soils (Dobrovolsky and Titkova 1960, Striganova 2012).

The yearly production of coprogenic aggregates by primary decomposers (litter feeders) averages *ca* 150% of their zoomass. The production of aggregates by soil-feeding detritovores exceeds their zoomass by 3 orders of magnitude (Striganova 2000). That is why the feeding activity of saprovores plays an important role in the formation of aggregate structures in soil.

The aggregative soil structure forms a complex system of the porous space between and inside the coprogenic aggregates. Biopores in soil are represented by "active" air and water pores supporting the aeration and moisture regime in the animal-populated horizons. The porous volume between zoogenic aggregates averages 60.7% of the total volume of structured soil (Striganova 2000). Aerial and water biopores increase the diversity of ecotopes populated by different groups of pedobionts, particularly for small secondary decomposers of organic remains and for microbivores (representing micro- and mesofauna).

Rates of the formation of aggregative soil structure by animals are important for theoretical studies on soil-forming processes, and for the practical use of invertebrates to restore soil structure disturbed by anthropogenic impacts.

The role of earthworms in the formation of the aggregative soil structure was studied on example of a tropical ferrasol in African savanna (Blanchart 1997). The material of extracted soil cores was homogenized, sieved and returned to the natural habitats. After 14 and 30 months, in the control treatment (without earthworms) macroaggregates (> 2.0 mm) averaged 12 and *ca* 50% of the soil volume respecively. In the presence of megascolecid earthworms *Millsonia anomala*, macroaggregation progressed more rapidly (31.7% after 6 months and >60% after 30 months).

Rates of macroaggregate formation were compared in an experiment with two common European earthworm species (B.R. Striganova, unpubl.). *Aporrectodea caliginosa* and *Lumbricus rubellus* were kept in 5 l containers with a forest glossysol (homogenized by wet sifting) and a leaf litter layer (1 earthworm per 1 l of soil). After three months the aggregate content was compared in the control (without earthworms) and in experimental containers with *A. caliginosa* and *L. rubellus* (Tab. 6).

Table 6. Effects of earthworms on production of soil aggregates (Striganova, unpubl.)

Aggregate size, mm	% of aggregates of different sizes		
	Control (without earthworms)	*Aporrectodea caliginosa*	*Lumbricus rubellus*
< 0.25	42.3	31.5	33.4
0.25-0.5	43.4	17.0	36.0
0.5-1.0	3.7	3.4	4.0
1.0-2.0	2.6	4.8	2.4
2.0-3.0	2.0	3.5	2.4
3.0-5.0	2.0	9.5	5.5
5.0-7.0	0.8	7.6	4.0
7.0-10.0	1.6	11.8	4.3
> 10.0	1.6	11.0	8.0

Aggregates larger than 2 mm consisted only 8% in the control but 24% in the presence of the litter species *L. rubellus* and >43% in the presence of the endogeic species *A.caliginosa*. These results show the importance of the feeding activity of earthworms for the creation and supporting of the soil structure and providing the system of microhabitats for different groups of pedobionts.

7. Conclusion

In the course of evolution, the development of animal life in mineral soil was related to the creation of intra-soil aerial space in the form of macropore system enriched by organic matter. The locomotor (burrowing) and trophic activity of invertebrates increases the diversity of trophic niches. The system of soil pores allows a partial isolation of separate animal groups that reduces the press of predation and competition.

Trophic relations among saprovores (dominants in soil communities), are based on the temporal discrepancy in the consumption of organic remains at different decomposition stages. Saprotrophic microflora, which populates the organic remains, plays a great role in the feeding of soil invertebrates (microbivores). Some invertebrate species, including soil-consuming endogeic earthworms, demonstrate a selectivity in relation to different groups of microflora. The selectivity to organic remains and microflora leads to a decrease in competition between soil saprovores. Differentiation of trophic niches, as an adaptive strategy developing in the course of evolution, determines the possibility of sustainable existence of multispecies invertebrate communities in the restricted populated soil volume.

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