

# Chapter 12

## Zoogenic Structure Aggregation in Steppe and Forest Soils



Volodymyr Yakovenko and Olexandr Zhukov

**Abstract** Soil macrofauna are ecosystem engineers. They create soil structure. In the steppe zone, differences in soil macrofauna, the intensity of their activity and particular effects of individual invertebrate communities may be observed within different facets of the landscape. In *Calcic chernozem*, under herbaceous vegetation and forest plantations, the casts of various animals that feed on decaying organic matter are an important component of the structure of A horizons, and the droppings of insect larvae are prominent. In *Luvic chernozem*, *Luvic chernic phaeozem* and *Pantofluvic fluvisol* under native forest, worm casts are the predominant component of the soil structure. The ecology of macrofaunal communities is correlated with soil morphology and can be applied to reconstruct possible mechanisms of soil genesis.

**Keywords** Organo-mineral horizons · Microstructure · Macrofaunal excrement · Porosity · Earthworms

### Introduction

The effects of soil macrofauna on soil properties and regimes are so comprehensive that the macrofauna may well be considered as ecosystem engineers (Bottinelli and others 2015; Jones and others 1994; Lavelle and others 1997). Macrofauna intensify soil aggregation and create pore space (Blanchart 1992; Capowiez and others 2015; Dawod and FitzPatrick 1993; Frazaoa and others 2019; Fujimaki and others 2010; Jongmans and others 2001; Jongmans and others 2003; Peres and others 2010; Piron and others 2012; Van Vliet and others 1993). In soils with substantial invertebrate communities, the macrofauna create the architecture of the topsoil (Castellanos-Navarrete and others 2012; Frouz and others 2007; Phillips and FitzPatrick 1999;

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V. Yakovenko (✉)

Oles Honchar Dnipro National University, 72 Gagarin Avenue, Dnipro 49010, Ukraine

e-mail: [yakovenko\\_v@i.ua](mailto:yakovenko_v@i.ua)

O. Zhukov

Bohdan Khmelnytsky Melitopol State Pedagogical University, 20 Hetmanska Street, Melitopol 72312, Ukraine

Sanborn and Pawluk 1989; Zanella and others 2018); Charles Darwin (1883) credited them with the creation of topsoil itself.

Macrofauna communities depend on the topography, water regime and plant communities. Correspondingly, the communities of soil invertebrates in native forest differ from those of steppe chernozem in species composition, population density, spatial distribution and the dynamics of animal activity during the growing season (Zhukov and others 2018, 2019). Here we investigate the role of soil macrofauna in the formation of soil aggregates under steppe and forest within the steppe zone of Ukraine.

## Materials and Methods

### *Study Area*

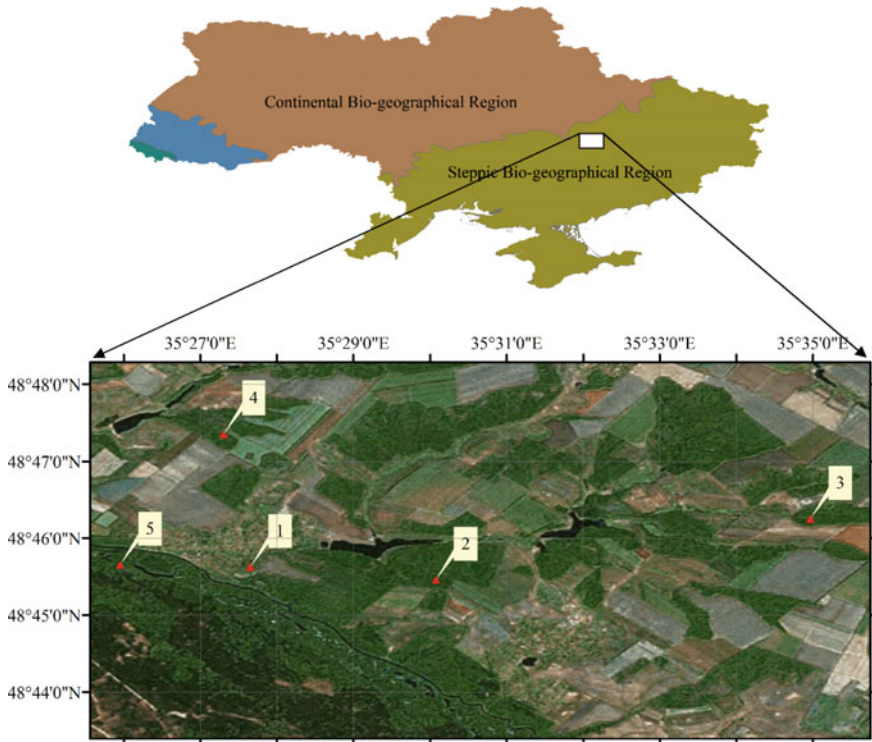
Studies were conducted in field sites within the Samara River valley (left-bank tributary of the Dnieper, Novomoskovsky Rayon, Dnipropetrovsk Oblast). The mean annual temperature is +8.3 °C, mean annual rainfall 508 mm, the period of maximum moisture begins in October and ends in March–April. Dry periods are common, most frequently in summer and autumn, rarely in spring (Gritsan 2000). Nowadays, steppe vegetation remains only on uncultivable land. Forest vegetation is represented by ravine and floodplain woodland with *Quercus robur* L., *Tilia cordata* Mill., *Fraxinus excelsior* L., *Acer campestre* L., *Ulmus minor* Mill., *Acer platanoides* L. and *Pinus sylvestris* L.

### *Field and Laboratory Methods*

Typical soil profiles of natural ravine and floodplain forests, and Chernozem under herbaceous vegetation and forest plantations were studied (Fig. 12.1).

Field experimental polygon 201 (FEP 201, 48°45′37.9″N 35°27′40.1″E, 103 m above sea level) is flat, watered only by rainfall and snowmelt. The parent material is loess. The vegetation is steppe with *Festuca valesiaca* Gaud. s.l., *Thymus marschallianus* Willd., *Koeleria cristata* L. Pers., *Artemisia austriaca* Jacq., *Salvia nemorosa* L., *Linum hirsutum* L., *Achillea millefolium* L., *Euphorbia vigrata* Waldst. et Kit., *Medicago romanica* Prod., *Poa angustifolia* L. and *Elytrigia repens* L. Nevski.

Field experimental polygon 224 (FEP 224, 48°45′22.5″N 035°30′13.38″E, 156 m above sea level) is flat land under planted forest, watered by rain and snowmelt. The parent material is loess. The vegetation is *Quercus robur* L., *Acer tataricum* L., *Euonymus europaeus* L., *Elytrigia repens* L. Nevski, *Poa compressa* L., *Poa angustifolia* L., *Salvia verticillata* L., *Lathyrus tuberosus* L., *Daucus carota* L., *Anthriscus*



**Fig. 12.1** Study area and location of ecological experimental polygons: 1 FEP201; 2 FEP 224; 3 FEP 204; 4 FEP 109; 5 FEP 209

*sylvestris* (L.) Hoffm., *Viola hirta* L., *Brachypodium sylvaticum* Huds. Beauv., *Geum urbanum* L., *Convallaria majalis* L.

Field experimental polygon 204 (FEP 204, 48°46'14.8"N 35°35'19.5"E, 149 m above sea level) lies on the middle third of a north-facing ravine (slope angle 7°). The parent material is loess. Rainfall and surface runoff are the main water sources. Vegetation is native oak forest with *Quercus robur* L., *Acer platanoides* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Ulmus minor* Mill., *Euonymus europaeus* L., *Euonymus verrucosa* Scop., *Stellaria holostea* L., *Galium aparine* L., *Glechoma hederacea* L., *Asarum europaeum* L., *Viola odorata* L. and *Polygonatum multiflorum* L.

Field experimental polygon 109 (FEP 109, 48°47'17.5"N 35°27'16.5"E, 76 m above sea level) is flat bottomland (ravine floor). Parent material is colluvium. Rainfall, surface runoff and groundwater are all sources of water. Vegetation is native oak forest and meadow: *Quercus robur* L., *Fraxinus excelsior* L., *Acer campestre* L., *Ulmus minor* Mill., *Tilia cordata* Mil., *Acer platanoides* L., *Stellaria holostea* L., *Anthriscus sylvestris* L. Hoffm., *Geum urbanum* L., *Asarum europaeum* L., *Galium*

*aparine* L., *Viola odorata* L., *Glechoma hederacea* L., *Polygonatum multiflorum* L. All. and *Urtica dioica* L.

Field experimental polygon 209 (FEP 209, 48°45′46.1″N 35°26′03.9″E, 62 m above sea level) is the flat central floodplain of the Samara River. Parent material is alluvium. Periodically, rainfall, surface runoff, floodwater and groundwater are all sources of water. The vegetation is native oak forest and meadow: *Quercus robur* L., *Fraxinus exelsior* L., *Ulmus minor* Mill., *Tilia cordata* Mill., *Acer campestre* L., *Acer platanoides* L., *Acer tataricum* L., *Euonymus verrucosa* Scop., *Galium aparine* L., *Stellaria holostea* L., *Anthriscus sylvestris* L. Hoffm., *Asarum europaeum* L., *Urtica dioica* L., *Viola odorata* L. and *Glechoma hederacea* L.

Soil profile description followed FAO (2006) and classification according to IUSS Working Group WRB (2015). Undisturbed soil samples were collected from genetic horizons. Thin sections were prepared following Gagarina (2004). Micro-morphological examination employed a polarizing microscope; soil microstructure was described following Stoops (2003); photographs were obtained using a UCMOS14000KPA digital camera.

## Results and Discussion

The morphology of the studied soil profiles is summarized in Table 12.1.

*Calcic chernozem* developed in loess under steppe vegetation; groundwater is encountered at a depth of 40 m (Belova and Travleev 1999). In some places, oak plantations were established 60 years ago. *Luvic chernozem* developed in loess under native vegetation on ravine slopes; in addition to precipitation, they receive surface runoff; groundwater may be encountered within 23 m. *Luvic chernic phaeozem* developed under native forest and meadow in colluvium in bottomlands (Yakovenko 2017) watered by precipitation and surface runoff; groundwater occurs at a depth of about 1 m in some years. *Pantofluvic fluvisol* developed under native floodplain forest in loamy over sandy alluvium; the main sources of soil water are precipitation and groundwater that occurs at a depth of about 3 m (Kotovich 2010), as well as periodic spring floods.

### *Macrostructure*

#### **Calcic Chernozem**

The A1 horizon of *Calcic chernozem* exhibits very fine subangular blocky and fine and very fine granular aggregates (Fig. 12.2a). The A2 horizon is distinguished by fine and very fine subangular, fine and medium granular and prismatic structure. Overall, porosity is high but markedly less in the A2 horizon. The voids include interstitial,

Table 12.1 Soil profile descriptions

Horizon	Depth (cm)	Munsell colour	Consistency	Field texture	Carbonate content	Secondary carbonates	Roots
FEP 201 <i>Calcic chernozem</i> (siltic, tongueic)							
O	Litter	n.a. <sup>a</sup>	n.a.	n. a	n.a.	n.a.	n.a.
A1	0-7	2.5 YR 4/1	Slightly hard	Silt loam	Non-calcareous	-	Many
A2	7-26	2.5 YR 4/4	Slightly hard	Silt loam	Non-calcareous	-	Many
Bk1	26-42	2.5 YR 5/3	Hard	Silt loam	Moderately calcareous (medium effervescence from 32 cm)	-	Common
Bk2	42-57	2.5 YR 7/3	Very hard	Silt loam	Strongly calcareous	Dispersed powdery lime	Few
Ck	57-130+	2.5 YR 7/2	Very hard	Silt loam	Extremely calcareous	Soft concretions, dispersed powdery lime	Very few
FEP 224 <i>Calcic chernozem</i> (siltic, tongueic)							
O	Litter	n.a.	n.a.	n.a.	n.a	n.a.	n.a.
A1	0-8	2.5 YR 2/1	Slightly hard	Silt loam	Non-calcareous	-	Many
A2	8-42	2.5 YR 2/1	Slightly hard	Silt loam	Non-calcareous	-	Many
B	42-58	2.5 YR 4/2	Hard	Silt loam	Moderately calcareous (Slight reaction at 48 cm)	-	Common
Bk	58-74	2.5 YR 5/2	Very hard	Silt loam	Strongly calcareous	Dispersed powdery lime	Common
Ck	74-120+	2.5 YR 7/4	Very hard	Silt loam	Extremely calcareous	Soft concretions, dispersed powdery lime	Very few
FEP 204 <i>Luvic chernozem</i> (siltic, hyperhumic, pachic)							
O	Litter	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
A1	0-9	2.5 YR 3/1	Slightly hard	Silt loam	Non-calcareous	-	Many

(continued)

Table 12.1 (continued)

Horizon	Depth (cm)	Munsell colour	Consistency	Field texture	Carbonate content	Secondary carbonates	Roots
A2	9–38	2.5 YR 4/2	Slightly hard	Silt loam	Non-calcareous	–	Many
A3	38–62	2.5 YR 5/2	Hard	Silty clay loam	Non-calcareous	–	Common
Bt	62–86	2.5 YR 6/6	Very hard	Silty clay loam	Non-calcareous	–	Common
Ck	86–140+	2.5 YR 7/6	Very hard	Silty clay loam	Moderately calcareous (Reaction with HCl detected at 92 cm)	not found	Few
FEP 109 <i>Lovic chermic phaeozem</i> (siltic, pantocolluvic, hyperhumic, pachic)							
O	Litter	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
A1	0–8	2.5 YR 4/1	Slightly hard	Silt loam	Non-calcareous	–	Many
A2	8–34	2.5 YR 5/2	Slightly hard	Silt loam	Non-calcareous	–	Many
A3	34–60	2.5 YR 5/4	Hard	Silt loam	Non-calcareous	–	Many
At	60–118	2.5 YR 6/4	Very hard	Silty clay loam	Non-calcareous	–	Common
ABt	118–132	2.5 YR 6/4	Very hard	Silty clay loam	Non-calcareous	–	Few
FEP 209 <i>Pantofluvic fluvisol</i> (loamic, humic)							
O	Litter	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
A1	0–9	2.5 YR 4/1	Slightly hard	Loam	Non-calcareous	–	Many
A2	9–36	2.5 YR 5/2	Slightly hard	Loam	Non-calcareous	–	Many
A3	36–60	2.5 YR 6/3	Hard	Loam	Non-calcareous	–	Many
A4	60–120	2.5 YR 6/3	Very hard	Loam	Non-calcareous	–	Common

<sup>a</sup>Not analysed



**Fig. 12.2** Subangular and granular structure of the A1 horizon of *Calcic chernozem* under herbaceous vegetation (a) and the vermicular granular and subangular structure of the A1 horizon of *Pantofluvic fluvisol* (b)

vughs, planes and channels, mainly interstitial and vughs in the A1 horizon, predominantly planes and vughs in the A2. The B horizons initially break into large blocks and prisms (several cm across) which in turn separate into smaller subangular and prismatic peds with clearly expressed vertical separation in the lower B horizon. Porosity varies from medium (5–15%) to low (2–5%). Planes, large cracks, vughs, burrows and root canals all feature in the architecture of the pore space. The structure of the parent material is mainly angular and subangular blocky and prismatic; porosity is low to medium, comprising planes, vughs, burrows and root channels.

### **Luvic Chernozem, Luvic Chernic Phaeozem, Pantofluvic Fluvisol**

Compared with *Calcic chernozem* under herbaceous vegetation and planted woodland, the soils of native forests are characterized by greater macrofaunal activity. Their A1 horizons separate into vermicular fine and medium granular and very fine and fine subangular aggregates (Fig. 12.2b); the faces of neighbouring aggregates do not match and the subangular peds appear themselves to be granular aggregates. The material of the A2 and A3 horizons initially separate into coarse peds (3–10 cm) that, in turn, separate into fine and medium subangular blocky peds that also look like granular aggregates; however, the peds fit with the adjacent peds and the initial aggregates are bigger than those of the surface horizon.

Pore space in the surface horizon comprises mostly interstitial pores and vughs corresponding to the complete aggregation of the soil fabric. In contrast, the pore space of the second and third horizons includes interstitial, vughs, planes and channels, the latter increasing into the third horizon where the planes are mostly spaces between the fitting surfaces of subangular and prismatic peds. In *Luvic chernozem* and *Luvic chernic phaeozem*, the structure of the lower horizons is prismatic, subangular and angular blocky, and angular blocky wedge-shaped. Porosity varies from medium (5–15%) to low (2–5%), mostly planes, vughs and root channels.

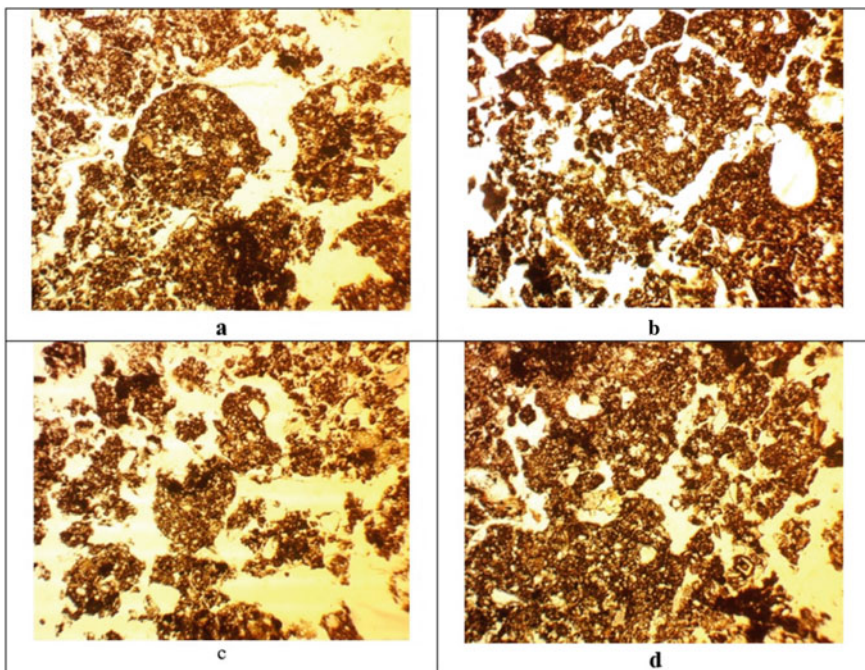


## *Microstructure*

Microstructure corresponds to the macrostructure. Surface layers under native forest exhibit granular and crumb microstructure; its shape, size, composition and behaviour denote its zoogenic origin.

### **Calcic Chernozem Under Herbaceous Vegetation**

Horizon A1 is characterized by crumb and subangular blocky microstructure in equal proportion. In the second horizon, the relative proportion of subangular blocky microstructure and the variety of voids increases against the background of a decrease in overall porosity, while there is greater accommodation of the aggregates and an increase in the planar pore space. Among the soil saprophages, the structure-forming activity of insect larvae is conspicuous; their excrement is prominent in the pore space and forms separate sections with granular microstructure (Fig. 12.3). Earthworm burrows and casts are prominent.



**Fig. 12.3** Microstructure of *Calcic chernozem*: earthworm casts and insect larva excrement in addition to crumb microstructure. **a** A1 and **b** A2 horizons under herbaceous vegetation. **c** A1 and **d** A2 horizons in oak plantation. PPL, width of photo: 1.54 mm



### **Calcic Chernozem in Oak Plantation**

In the A1 horizon, the microstructure consists mainly of crumb aggregates with compound packing voids, vughs and channels. Within these pores and, also, within the peds themselves, many fine granular droppings of insect larvae are deposited (Fig. 12.3). In the A2 horizon, crumb microstructure is accompanied by vermicular and less spongy microstructure. The pore space comprises the compound packing voids of the aggregates, channels and vughs.

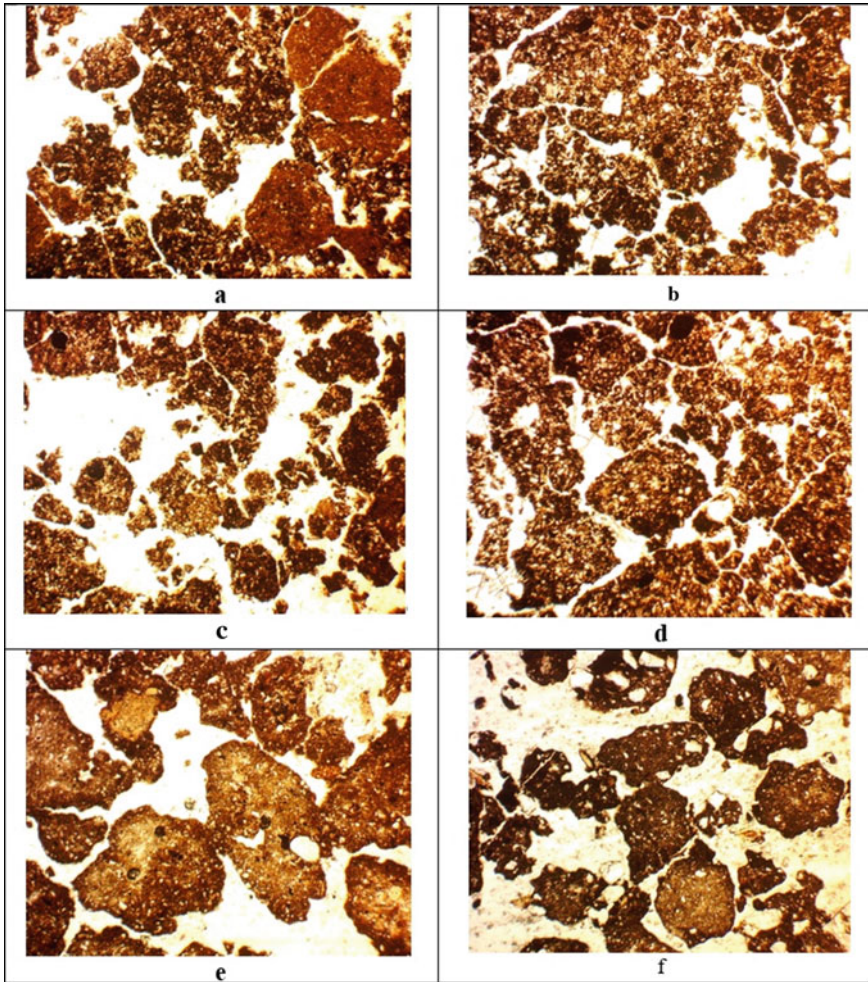
### **Luvic Chernozem, Luvic Chernic Phaeozem**

The microstructure of the A1 horizon is vermicular with alternating zones of compact fabric and large cavities with scattered (in 2D space) aggregates (Fig. 12.4). In the compact zones, there is a high degree of ped-surface accommodation, but not in the very porous zones although the aggregates have well-defined faces. All the pore space may be considered as compound packing voids of granular aggregates that are all, essentially, earthworm casts, characterized by almost complete aggregation, very high overall porosity within the horizon but low porosity within the peds themselves. The microstructure in horizon A2 is similar to the surface layer but with greater accommodation of the surfaces of the aggregates, less space between them, and various linear cavities. The third horizon is marked by a change from vermicular to blocky, non-aggregated microstructure.

### **Pantofluvic Fluvisol**

Granular vermicular microstructure is prevalent in the A1 horizon. The aggregates are earthworm casts of different sizes and highly porous crumbs (Fig. 12.4); the casts show no accommodation of ped surfaces while partial accommodation is observed in the crumb microstructure. The pore space is comprised by inter-aggregate compound packing voids and burrows filled with excrement. The A2 horizon also exhibits granular vermicular microstructure, mainly low-porous casts of various sizes, with some very porous crumb aggregates that may be aged, disintegrating casts. The A3 horizon exhibits subangular blocky microstructure with fitting surfaces and lesser porosity; the main cavities are planes between the peds but large vughs and channels are also present. Thus, the structure-forming activity of soil macrofauna is manifest mainly within organic-mineral A horizons but, below these, animal activity is responsible for burrows and chambers.

The contribution of earthworms to the structure of the studied soils is ambiguous. In *Calcic chernozem* under herbaceous vegetation and plantations, earthworm casts are less common than the droppings of insect larvae, whereas earthworm casts are an important component of the microstructure of organic-mineral A1 and A2 horizons of *Luvic chernozem*, *Luvic chernic phaeozem* and Pantofluvic fluvisol under native forest.



**Fig. 12.4** Vermicular microstructure of organic-mineral horizons under native forests: **a, b** *Luvic chernozem*, subangular and granular microstructure of horizons A1 and A2. **c, d** *Luvic chernic phaeozem*, crumbly and granular microstructure of horizons A1 and A2. **e, f** *Pantofluvic fluvisol*, granular and crumb microstructure of horizons A1 and A2. PPL, width of photo: 1.54 mm

### *Ecology of Macrofauna*

Steppe communities of soil macrofauna are represented by 81 species of invertebrates numbering more than 400 individuals per square metre. The most common are earthworms *Aporrectodea rosea rosea* (Savigny 1826); and insect larvae *Dorcadion carinatum* (Pallas 1771), *Byrrhus pilula* (Linnaeus 1758), *Agriotes gurgistanus* (Faldermann 1835), *Tentyria nomas* (Pallas 1781) and *Serica brunnea* (Linnaeus 1758). The macrofauna community is based on steppe species (89%) (Table 12.2).

Table 12.2 Ecological structure of the soil macrofauna communities

Traits	FEP 201		FEP 224		FEP 204		FEP 109		FEP 209	
	S	A	S	A	S	A	S	A	S	A
<i>Ceonomorphs</i>										
Pal	5.1	0.3	14.3	4.6	8.5	2.1	10.5	18	26	19.7
Pr	15.4	6.9	28.6	34	23.4	35.2	31.6	40	32.5	54
Sil	21.8	3.8	38.1	36.7	51.1	49.2	42.1	30.9	32.5	19.4
St	57.7	89	19	24.7	17	13.5	15.8	11.1	9.1	7
<i>Hygomorphs</i>										
Hg	10.3	3.7	34.9	28.6	21.3	32.8	28.9	31	26	33.7
Xr	46.2	35.3	14.3	21.6	17	9	7.9	2.5	7.8	2.9
Ms	43.6	60.9	50.8	49.8	48.9	52	57.9	60.1	51.9	55.5
UHg	–	–	–	–	12.8	6.2	5.3	6.4	14.3	7.9
<i>Trophocoeonomorphs</i>										
MgTr	35.9	54.2	41.3	40.7	40.4	45.7	39.5	43.5	36.4	58.9
MsTr	30.8	31.9	39.7	48.8	34	35.8	36.8	35.3	44.2	29
OlgTr	–	–	6.3	1.2	6.4	8.8	7.9	7.4	6.5	6.5
UMgTr	33.3	13.8	12.7	9.2	19.1	9.7	15.8	13.8	13	5.6
<i>Aeromorphs</i>										
APhil	71.8	76.6	58.7	54.8	55.3	52	55.3	37.5	46.8	34.2
HAPhob	2.6	3.3	3.2	1.5	2.1	2.6	10.5	19.9	18.2	31.7
SAPhil	25.6	20.1	38.1	43.7	42.6	45.5	34.2	42.6	35.1	34.1

(continued)

Table 12.2 (continued)

Traits	FEP 201		FEP 224		FEP 204		FEP 109		FEP 209	
	S	A	S	A	S	A	S	A	S	A
<i>Carbonatomorphs</i>										
ACarPhil	28.2	20.1	31.7	24.8	57.4	49.1	26.3	24.5	39	25.5
CarPhil	43.6	49.5	23.8	31.5	17	20.2	34.2	34.1	24.7	37.9
CarPhob	–	–	4.8	0.9	2.1	0.2	5.3	7.8	10.4	5.5
HemCarPhil	9	24	33.3	30.7	17	18.6	21.1	24.7	20.8	25.8
HiperCarPhil	19.2	6.4	6.3	12.1	6.4	11.9	13.2	8.8	5.2	5.3
<i>Topomorphs</i>										
Anec	2.6	1.6	3.2	1.2	4.3	3.7	5.3	10.6	2.6	2.7
End	60.3	80	39.7	45.3	38.3	31	26.3	29.1	26	28.6
Ep	37.2	18.4	57.1	53.4	57.4	65.2	68.4	60.3	71.4	68.7
<i>Trophomorphs</i>										
FF	46.2	22.7	19	17.6	23.4	11.2	15.8	7.8	28.6	14.1
SF	19.2	22.9	33.3	30.6	48.9	60.3	52.6	80.6	28.6	49.8
ZF	34.6	54.5	47.6	51.8	27.7	28.4	31.6	11.6	42.9	36.1
<i>Phoromorphs</i>										

(continued)

Table 12.2 (continued)

Traits	FEP 201		FEP 224		FEP 204		FEP 109		FEP 209	
	S	A	S	A	S	A	S	A	S	A
A1	16.7	6	9.5	13.9	8.5	14.5	7.9	8.4	19.5	29.1
A2	7.7	3.1	15.9	13.7	10.6	9.9	13.2	6.2	13	9.5
A3	20.5	13.3	33.3	28.8	31.9	40.2	36.8	31	33.8	31.6
B4	10.3	13.4	20.6	24.3	34	30.2	28.9	49	18.2	22.2
B5	14.1	16.9	14.3	11.9	4.3	0.9	5.3	3.4	9.1	6.1
B6	12.8	4.7	1.6	2.2	2.1	0.6	-	-	2.6	0.6
B7	17.9	42.6	4.8	5.1	8.5	3.6	7.9	2.1	3.9	1

Legend S—% of total number of species number total, A—% of species abundance total. *Coenomorpha*: St—Stepants, Pr—Pratams, Pal—Palludants, Sil—Silvants, *Hygomorpha*: Xr—Xerophilous, Ms—Mesophilous, Hg—Hygrophilous, Uhg—Ultrahygrophilous. *Trophocoenomorpha*: MsTr—Mesotrophocoenomorpha; MgTr—Megatrophocoenomorpha; UmgTr—Ultramegatrophocoenomorpha. *Aeromorpha*: APhil—Aerophilous; SAPhil—Subaerophilous; HAPhob—Hemiaerophobes. *Carbonatomorpha*: CarPhob—Carbonatophobes; ACaPhil—Acarbonatophilous; HemiCarPhil—Hemicarbonatophilous; CarPhil—Carbonatophilous, HiperCarPhil—Hipercarbonatophilous. *Topomorpha*: End—Endogeic; Ep—Epigeic, Anec—Anitic. *Trophomorpha*: SF—saprophagous; F—phytophagous; ZF—zoophagous. *Phoromorpha*: A—Movement using existing soil porosity; B—Active soil tunnels construction; 1—soil animal body size smaller than soil pores or cracks; 2—soil animal body size commensurate with soil pores or cracks; 3—soil animal body sizes larger cavities in the litter or commensurate with large gaps or cracks in the soil; 4—movement with changes of the body thickness; 5—movement with unchanged thickness of the body; 6—movement due to digging holes using limbs; 7—C-shaped body form profile the burrowing activity of invertebrates and transport of organic matter sets the stage for deep ramification of the plant root system, infiltration of rainfall and transmission of water to streams and groundwater

In terms of their preferred humidity regimes, some 60% are *mesophiles* and 35% *xerophiles*. This reflects the dynamism of a community that relies on one fairly short period of activity in spring when *mesophiles*, or even *hygrophiles* like enchytraeids, multiply. But the soil dries out quickly and, later, only soil phytophages prevail, adapting to the water shortage by feeding on plant roots.

The structure of the macrofauna community reflects the trophic structure of the plant community. *Calcic chernozem* creates favourable conditions for providing soil invertebrates with oxygen, which is reflected by the predominance of *aerophiles* (77%); favourable conditions for providing soil with calcium are indicated by the predominance of *carbonatophiles* (50%) and groups close to them in the community. Among the trophic groups, zoophages prevail (55%), and the number of *saprophages* is matched by the number of phytophages (23%). The abundance of zoophages that feed on animals smaller than macrofauna emphasizes the dynamism of the community. By way of soil engineering, many of the animals form burrows, especially C-shaped insect larvae.

Forest vegetation changes the ecological conditions on watersheds and this is reflected in the structure of soil animal communities. In forest plantations, the macrofauna is represented by 63 invertebrate species numbering almost 250 individuals per square metre, including a forest component (37%) but, also, meadow (34%) and steppe (25%) species. *Mesophiles* predominate but, compared with steppe habitats, there is an increase of *hygrophiles* (29%) and, although aeration remains favourable, the proportion of *aerophiles* is somewhat reduced (55%). *Carbonatophiles* remain common (32%). The trophic structure of soil macrofauna in the forest plantation is similar to that of *Calcic chernozem* under herbaceous vegetation but there is an increased proportion of saprophages at the cost of phytophages.

The community of invertebrates on the ravine slope is represented by 47 species numbering 250 individuals per square metre. These are forest species, (49%) and meadow species (35%) but, also, steppe species (14%). The change reflects the greater water supply, reflected in the increased proportions of *mesophiles* and *hygrophiles*, and leaching is indicated by a greater share of *carbonatophiles* (49%). The native forest community is characterized by a predominance of epigeous (surface dwelling) forms (65%) and saprophages (60%). Animals are actively moving within the litter and many are able to enlarge cracks and pores in the soil and litter.

The bottomland community includes 38 species of invertebrates numbering 288 individuals per square metre, predominantly meadow species (40%). At times, the ground is wet and this is reflected by a relatively high proportion of *hygrophiles* (31%) and *ultrahygrophiles* (6%). Accordingly, proportion of *hyperaerophobes* (20%) is also increased. The community is dominated by epigeous forms (60%) and saprophages (81%). On the floodplain, the community is represented by 77 species of invertebrates numbering 480 individuals per square metre. Compared to ravine bottom community, proportion of meadow species increased to 54% and the share of saprophages is reduced.

## Conclusions

1. Within different elements of the steppe landscape, there are differences in the composition of the soil macrofauna, the intensity of zoogenic formation of soil structure, and the contribution of individual invertebrate groups in this process.
2. In *Calcic chernozem* under herbaceous vegetation and oak plantations, the droppings of soil saprophages, in particular insect larvae, are an important component of the structure of organo-mineral A horizons.
3. Under native forest, *Luvic chernozem*, *Phaeozems* and *Fluvisols* on various parent materials in different facets of the landscape, the organo-mineral A horizons share a common, zoogenic vermicular soil structure and similar soil macrofaunal communities.
4. The most intense zoogenic structure formation is observed in the A1 and A2 horizons of *Luvic chernozem*, *Luvic chernic phaeozem* and *Pantofluvic fluvisol*. Soil saprophage excrement is the main component of the soil structure, earthworm casts in particular.
5. The ecological structure of macrofaunal communities correlates with the morphological features of the corresponding soil structure, which means that we can use this information to reconstruct possible mechanisms of soil genesis.

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