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Biotopic Association of Earthworms in Intact Forests of Teberda Nature Reserve

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Abstract—Contribution of micromosaic structure of high mountain forests to ecological diversity of earthworms have been assessed. Intact forests of Arkhyz section of Teberda Nature Reserve were studied. The dominant types of forests have been recognized for the first time based on eco-coenotic classification. The ecological conditions of their functioning have been studied. Earthworm numbers have been studied in the recognized forest types. Diversity of earthworms was studied in soils under crowns, under fallen trees, and in mosses growing on rocks. 16 species of Lumbricidae have been found, with 4 of them being discovered for the first time. Full complexes of Lumbricidae were associated with biotopes of forest types of increased soil moisture content, low acidity, availability of nitrogen and pronounced litter. The largest abundance, diversity and biomass of Lumbricidae have been found in nitrophilous tallgrass gray alder forests. The lowest have been found in xeromesophytic pine forests with fir, spruce and birch. The most widespread dark coniferous forest with beech were inhabited by seven species of Lumbricidae, dominated by the epigeic species. There were few epi-endogeic and anecic species. The endogeic group of earthworms was represented by Crimea and Caucasus subendemic *Dendrobaena schmidti*. Diversity and biomass of earthworms in dark coniferous forests with beech were higher than in spruce-fir forests. During summer, dead fallen trees served as a microsite preferential for epigeic and endogeic species, while mosses growing on rocks were preferred by endogeic species.

Keywords: old growth forests, forest types, eco-coenotic structure, micromosaic structure, earthworms, Lumbricidae, microsites

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INTRODUCTION

The diversity of microhabitats provides the maintenance of biological diversity, reduces intra and interspecific competition, and ensures the sustainability of forest ecosystems (*Vostochnoevropeiskie lesa*..., 2004a; Pickett and White, 1985; Smirnova and Toropova, 2016). Therefore, studies of the micromosaic organization role of forests in plant and animal life are increasingly important. Many studies have been devoted to studying the role of microsites (microhabitats) in the life of the soil population (Scheu, 2005; Fischer et al., 2007; Dechene and Buddle, 2010; and others). It was established that the diversity of plant terrestrial litter, both deciduous and arboreal, provides sustainable maintenance of trophic networks by preserving the diversity of soil biota. The separation of trophic niches and increased resistance to abiotic factors were shown by the example of insects and oribatid mites inhabiting the soil and under the bark of fallen trees. The importance of microsites in maintaining the species and ecological diversity of the most important soil forming agents—earthworms in forest ecosystems—was understudied (Kooch, 2012; Goncharov et al., 2014; Geraskina, 2016; and others). In this regard, we selected intact forests in which the micromosaic organization, associated not only with the life and death of trees (Pickett and White, 1985; and others), but also with the relief elements of mountainous territories, which was well described. It is known that in mountain forests, the favorable microsite of Lumbricidae is the fallen trees and synusia of true mosses on stones (Rapoport and Tsepkova, 2015), composing a significant part of the mountain landscape.

Different-aged forests of the Arkhyz site of the Teberda Nature Reserve (North-West Caucasus) were selected as high-altitude, slightly disturbed forests. According to dendrochronological studies in the valley of the Kizgych River valley *Abies nordmanniana* and *Pinus sylvestris,* with ages over 450 years, were detected (Solomina et al., 2012). Forests of the Arkhyz site are close in composition and structure to natural forests and have a complex micromosaic organization, which in most communities is influenced by a free-living herd of bison. Therefore, the Arkhyz site of the Teberda Nature Reserve is of particular interest for studying the spatial and biotopic distribution of soil biota, i.e., distribution of soil animals on the main microsites in different types of forests.

Most of the studies related to the study of forest vegetation and the Lumbricidae fauna of the Teberda Reserve were carried out in the basin of Teberda River (Tumadjanov, 1947; Kononov, 1957; Perel, 1979; Geraskina, 2016; and others). The vegetation of the Arkhyz site was described by Kononov and Savel'eva (1977) based on a dominant approach. Information on the fauna of earthworms and biotopic confinement to some forest and meadow plant formations was presented in the publications of Rapoport (2014) and Rapoport and Tsepkova (2015). In our study of Lumbricidae, an attempt to conduct a comparative analysis with such microsites as fallen trees (decaying tree trunks) and mosses on stones and rocks (moss sods) was made, along with the examination of soil samples (hereinafter, the soil).

The aim of the study was the assessment of the biotopic distribution of earthworms in the main forest types of the Arkhyz site of the Teberda Biosphere Reserve.

The tasks of the study were: identification and description of the main types of forests of the Arkhyz site of the Teberda Biosphere Reserve; investigation of the ecological-cenotic structure and environmental analysis of the main types of forest; exploration of the earthworms fauna in the selected types of forests; analysis of the species, morpho-ecological and ontogenetic structure of the Lumbricidae population in three types of microsites—soil, fallen trees, and moss on stones; and identification of the relationship of the population of earthworms with forest types, considering the distribution of Lumbricidae on microsites.

MATERIALS AND METHODS

The Arkhyz site of the Teberda Reserve is located in the valley of the Kizgych River. In the south, the border runs along the Greater Caucasus Mountain Range, in the north—along the Abishir-Akhub Ridge. In the west and east, there are dividing ranges Chaget-Chat and Uzhum, respectively. The main type of relief is the morphostructures of the trough valleys and high mountain ranges, with a temperate continental climate. Precipitation mainly occurs during the warm period (65% of the annual value), with an annual amount of 800–850 mm. The strong ruggedness of the mountainous terrain and a significant difference in elevations (1500–2000 m) determine the vertical variability of all climatic indices (Shal'nev and Yurin, 2014).

Fieldwork was carried out from June 27 to July 17, 2015. Description, collection and processing of geobotanical material obtained during route surveys were carried out according to generally accepted methods (*Metodicheskie*.., 2010). The size of the test sites was 20 × 20 m; in total 124 descriptions were performed.

Ecological characteristics of communities (*Lc*—illumination *Rc*—acidity/alkalinity, *Hd*—soil moisture, *Nt*—availability of nitrogen, *Tr*—heat supply) were obtained as weighted average points for the corresponding characteristics of species according to the ecological scale of Landolt (1977). The descriptions were ordinated using the method of indirect gradient analysis for correspondence to a remote trend and determination of the level of correlation (r) and significance level (p) (Detrended Correspondence Analysis (DCA) in PC-ORD 5.0, SpeDiv, Past programs).

The Latin names of vascular plants are given according to Cherepanov (1995). Communities are typed based on the methods presented on the site "Coenofund of forests of European Russia" (Forest Fund of European Russia..., 2006).

Earthworms were collected in five types of forests, in which three types of microsites were examined: soil under the crown spaces, fallen trees, mosses on stones and rocks. Also examined were: the sizes of soil samples taken at a depth of 10–30 cm; 25 × 25 cm^2; moss sod—25 × 25 cm^2; and the number of samples from 10 to 20 in each type of forest. The fallen trees of the 2nd, 3rd, and 4th stages of decomposition were examined (Spirin, Shirokov, 2002). The length and diameter of the trunks were measured. In each type of forest, 8 to 12 sections of tree trunks 1 m long, from 30 to 60 cm in diameter, were examined. The results for all microsites were calculated per 1 m^2. For the calculation of the samples of worms in the fallen trees, we used a formula for calculating the area of the lateral surface of the cylinder.

The worms were fixed in 4% formalin, weighed and determined using an inventory and identification guide of earthworms of the Russian fauna (Vsevolodova-Perel', 1997). The biomass of worms was determined according to the method of Mazantseva (1975). Morpho-ecological groups are presented in accordance with the classification of Vsevolodova-Perel' (1997). The developmental stages were distinguished: cocoons, juvenile, submature and sexually mature worms (Fründ et al., 2010). In total, 1130 specimens were collected and identified. In all types of habitats (microsites), the temperature, humidity, and acidity of the substrate were measured using an electronic pH 300 indicator. For comparison of samples, the nonparametric Mann–Whitney criterion was used to identify significant differences.

RESULTS AND DISCUSSION

The Main Forest Types of the Kizgych River Valley

Riverbed nitrophilous tallgrass gray alder forests occupied floodplain areas annually flooded during spring and summer floods. In the tree layer, *Alnus incana* of overgrown origin was dominant. *Betula pendula*, *Padus avium*, *Sorbus aucuparia* were also detected. Cover density varies from 0.5 to 0.9; height 10–18 m. Natural seed regeneration due to developed grass cover and permanent floods was absent and replaced by overgrowth. The shrub layer included bushy trees (*P. avium*, *S. aucuparia*, *Salix caprea*) and shrubs (*Corylus avellana*, *Lonicera xylosteum*, *Ribes caucasica*, *Daphne mezereum* and others), the cover density was 0.2–0.5. The projective cover of the grass-shrub layer was 90–100%, height 1.0–2 (3.0) m. High mesophilic and meso-hygrophilous grasses determined the appearance of a multi-dominant grass layer. There are three sub-layers in the layer. The sub-layer of tallgrass included: *Filipendula ulmaria*, *Angelica sylvestris*, *Campanula latifolia* and others. In the second sub-layer *Bistorta major*, *Cardamine uliginosa*, *Carex sylvatica*, *Equisetum pratense* and others were typical. The third sub-layer was represented by herbs: *Chrysosplenium alternifolium*, *Galium odoratum*, *Myosotis sparsiflora,* and others.

The upland part of the floodplain, remote from the riverbed, was occupied by ***nitrophilous and meadow-edge-tallgrass birch-aspen forests***. These communities were flooded only in years with severe floods or after prolonged downpours in the mountains. *P. tremula* dominated in the tree layer, sometimes—*B. pendula,* in admixture—*Acer platanoides*, *Fagus orientalis*, *S. caprea*, *Malus orientalis,* and others. In the undergrowth layers, tree undergrowth occurred sporadically: *A. nordmanniana*, *A. platanoides* etc.) and shrubs (*C. avellana*, *L. xylosteum*, *R. caucasica*, *Rhododendron luteum*), the degree of sheltering was 0.1–0.3. In birch-aspen forests, as well as in gray alder forests, the projective cover of the grass-shrub layer was about 100%, grass height is 3.0 (4.0) m. In contrast to gray alder forests, meadow-fringed mesophilic grasses with an admixture of nitrophilous-tallgrass species predominated here. Typical species of the first sub-layer were: *Anthriscus sylvestris*, *Delphinium schmalhausenii*, *F. ulmaria, symphytum asperum,* and others; second—*Geranium sylvaticum*, *Poa nemoralis*, *Vicia cracca,* and others; third sub-layer—*Oxalis acetosella, Stellaria nemorum*, *Veronica filiformis,* and others.

Nemoral-boreal beech-spruce-fir green mosses communities occupied a much larger area than spruce-fir. The litter is well developed and is represented mainly by litter of *F. orientalis*. In the tree layer in different proportions, they are co-dominated by *A. nordmanniana*, *P. orientalis*, *F. orientalis*. In the old sites, single *A. platanoides*, *B. pendula*, *S. caprea* and *S. aucuparia* with decreased and low vitality were detected. The degree of sheltering of the layer was 0.8–0.9 and the height of individual trees was 40–45 m. The degree of sheltering of the layer of undergrowth and shrub layer varied from 0.3 to 0.6. The undergrowth of trees prevailed (immature and virgin specimens) with *A. nordmanniana* (abundance 1–3) *P. orientalis* (1–4), and *F. orientalis* (1–2). Singular shrubs were found—*C. avellana*, *L. caprifolium*, *Rh. luteum*, *Vaccinium arctostaphylos,* and others. The projective cover of the grass-shrub layer was 20–70%. The community was dominated by species of boreal short grasses, typical were *O. acetosella*, *Circaea alpina*, *Gymnocarpium dryopteris,* and others; nemoral species were represented *G. odoratum*, *Geranium robertianum*, *Mycelis muralis*, *S. nemorum,* and others.

Characteristic feature of ***nemoral-boreal spruce-fir green mosses communities*** was well-developed moss layer; projective cover was 40–100%. The litter mainly was formed by *A. nordmanniana* and *P. orientalis*. The dominant tree layer was *A. nordmanniana*, rarely *P. orientalis*. In the admixture in old sites, singular *A. platanoides*, *P. tremula*, *B. pendula* were present, while on the upper border of the dark coniferous belt, *Pinus sylvestris* were found. The degree of sheltering was 0.8–0.9; the height of individual trees reached 50 m. In the shrub layer, undergrowth of different age was developed (immature and virgin specimens) of *A. nordmanniana* (abundance 1–3) and *P. orientalis* (1–3). Single growth of trees (*A. platanoides*, *F. orientalis*) and shrubs (*C. avellana*, *D. mezereum*, *Rh. luteum* and others) was detected. The degree of sheltering was 0.2–0.6. The projective cover of the grass-shrub layer varied from 10 to 75%. Characteristic species were: *O. acetosella*, *G. dryopteris*, *Actaea spicata*, *Calamintha grandiflora*, *Solidago virgaurea,* and others. Single undergrowth *A. nordmanniana*, *A. platanoides*, *P. orientalis*, and *F. orientalis* were detected.

Xeromesophytic pine forests with fir, spruce, and birch were distributed along the upper border of the forest belt over dark coniferous nemoral-boreal green mosses communities. The distribution boundary of the pine belt corresponded to the distribution boundary of regular ground fires, which is confirmed by the presence of numerous traces of burns on tree trunks and coal in the soil. Pine forests were distributed on granitic soil brown forest and mountain meadow soils, the closeness of the forest stand was 0.3–0.7. *P. sylvestris* was dominant, sometimes *A. nordmanniana,* and *P. orientalis* were found as mixed species. Singular *P. tremula*, *B. pendula*, *F. orientalis*, and *S. aucuparia* were detected. The height of the layer reached 30–35 m. The undergrowth layer was uneven and depended on the degree of sheltering of tree layer; the degree of sheltering varied in the range 0.05–0.6. An *A. nordmanniana* undergrowth of different age (abundance 1–3) and *P. orientalis* (1–2) was well developed in the layer. The high abundance and age composition of the latter confirmed that the periodic lower fires, to which dark coniferous tree species are sensitive, play a regulatory role in maintaining pine forests in the Arkhyz section of the Teberda Reserve. Singular growth of trees (*A. platanoides*, *B. pendula*, *F. orientalis*, *P. sylvestris*) and shrubs (*C. avellana*, *L. xylosteum*) was detected, *Rh. luteum* (abundance 3–4) was often abundant. The projective cover of the grass-shrub layer was 10–40% (rarely 60%). Xeromesophytic herbs prevailed in the layer, typical species were *Festuca montana*, *F. pratensis, Hieracium murorum*, *Lathyrus roseus*, *Melampyrum pratense*, *P. nemoralis*, *Vicia sepium,* and others. The undergrowth (immature and juvenile specimens) of *A. nordmanniana* and *P. orientalis* was well developed.

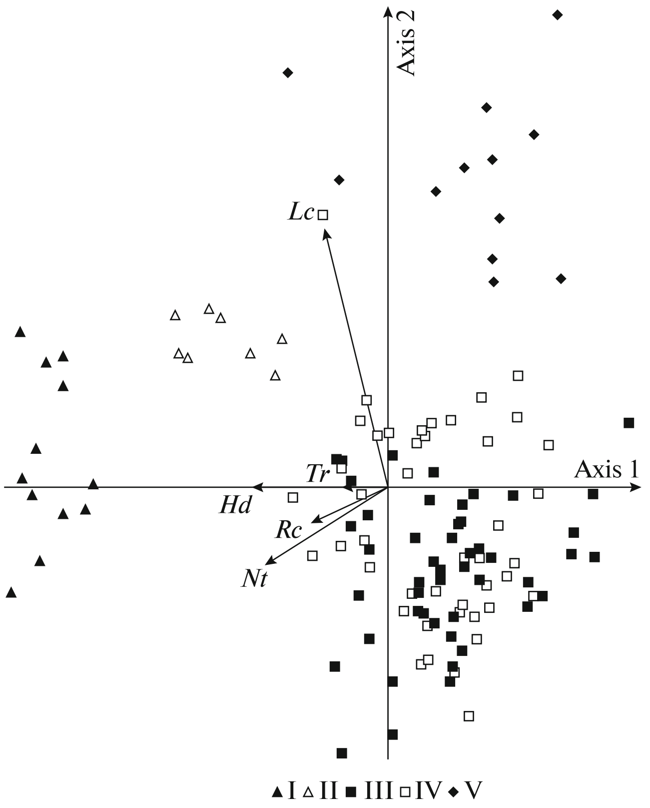

Fig. 1. The position of the geobotanical descriptions of the studied communities in the first two axes of DCA together with the vectors of environmental factors (ecological scale of Landolt). Note. In Figs. 1–3: I—riverbed nitrophilous tallgrass gray alder forests; II—nitrophilous and meadow-edge-tallgrass birch-aspen forests; III—nemoral-boreal beech-spruce-fir green mosses communities; IV—nemoral-boreal spruce-fir green mosses communities; V—xeromesophytic pine forest with spruce and fir; *Lc*—illumination; *Rc*—acidity/alkalinity; *Hd*—soil moisture; *Nt*—availability of nitrogen; *Tr*—heat supply.

The layer of mosses was located mainly on stones and near stem rises; the projective cover varied greatly from 15 to 70%.

Thus, the forests of the Arkhyz site of the Teberda Reserve was characterized by a well-defined successive shift along the catena: at the base of the slopes of the trough valley along the river channel, communities of nitrophilous tallgrass gray alder forests were distributed. In well-drained areas at the base of the slopes, nitrophilous and meadow-edge-tallgrass birch-aspen forests were detected. In the middle part of the slopes of the valley, there are ***nemoral-boreal spruce-fir green moss*** forests with and without *Fagus orientalis*. Xeromesophytic pine forests with fir, spruce and birch along the upper border of the forest belt were discovered.

The diagram (Fig. 1) shows vectors of environmental factors, the length and direction of which reflect the degree of correlation of factors with axes, but are not regression lines in the strict sense. With the first DCA axis, a close negative correlation ($p < 0.005$) is characteristic of indicators of availability of nitrogen in the soil ($r = -0.623$) and acidity/alkalinity ($r = -0.696$). With the second axis, the highest correlation coefficient was found for illumination ($r = 0.837$). There is no significant correlation with the third axis.

The results of multivariate analysis of geobotanical descriptions according to the ecological scale of Landolt (1977) confirmed that nitrophilous tallgrass gray alder forests and nitrophilous and meadow-edge-tallgrass birch-aspen forests were common under conditions of increased soil moisture, low acidity and availability of nitrogen compared to other types of forests. The diagram clearly demonstrates an intermediate position in terms of moisture, acidity/alkalinity, and availability of nitrogen in the soil of birch-aspen communities between gray alder forests and pine forests, since the latter occupied the non-floodable part of the floodplain and formed by nitrophilous and meadow-edged tallgrasses. Dark coniferous nemoral-boreal green mosses forests also occupied an intermediate position between gray alder forests and pine forests and were confined to well-drained slope areas with moderate moisture and soil richness. In turn, pine forests mixed with spruce and xeromesophyte fir were confined to well-lit, dry, and nitrogen-poor slope areas.

Thus, it was shown that according to the ecological scale of Landolt in the communities of gray alder and birch-aspen tallgrass forests, compared to other types of forest, the percentage of photophilous, moisture-loving and nitrophilous species was higher, which was associated with the ecotope conditions. In post-fire pine forests, the proportion of xerophytic and oligotrophic species was higher; in dark coniferous nemoral-boreal green mosses forests the proportion of shade-tolerant, mesophytic and mesotrophic species was higher.

In all types of forests of the Kizgych River valley, boreal and nemoral species-which formed the main core of the forest flora of this territory-was dominant (Fig. 2). In the riverbed nitrophilous tallgrass alder forests, the proportion of costal and nitrophilous species was much higher, which is explained by the ecotope conditions. At the same time, more meadow-marginal tallgrass species were present in birch-aspen forests.

According to the ecological-cenotic structure, birch-aspen forests also occupied an intermediate position between nitrophilous tallgrass gray alder forests and other types of forests, as shown in the graph. The ratio of ecological-cenotic groups in the dark coniferous nemoral-boreal green mosses forest types with and without beech was almost identical. In these forests, more nemoral and boreal herb species were detected. In the xeromesophytic pine forests with fir, spruce and birch, the proportion of pine forest and meadow-edge species was significantly higher, the costal species were completely absent and the proportion of nitrophilous species was the lowest, which is explained by the low closeness of the forest stand, the dryness and thinness of soils in these communities.

The comparison of the obtained results of the ecological-cenotic structure of the high mountain forests of the Teberda Reserve, revealed their similarity with the results of similar studies for other territories. Dark coniferous nemoral-boreal green mosses forest types of the Teberda Reserve had a similar ecological and cenotic structure with spruce forests of the North-West of the European part of Russia (Vasilevich and Bibikova, 2004) and Moscow Region (Forest Fund of European Russia..., 2006). Nitrophilous and meadow-edge-tallgrass birch-aspen forests were similar to nitrophilous tallgrass aspen and birch forests of the Moscow Region and the Northern and Southern Urals (Forest Fund of European Russia..., 2006). The riverbed gray alder forests were similar by structure to the riverbed gray alder forests of the Novgorod Region (Liksako and 2004) and the North-West of the European part of Russia (Zaugolnova and Martynenko 2012). Xeromesophytic pine forests with an admixture of spruce and fir were similar with the xeromesophytic pine grass forests of the Southern Urals and the Urals (Zaugolnova and Martynenko, 2012).

Thus, the main forest types of the Arkhyz section of the Teberda Reserve were distinguished by a variety of ecological-cenotic groups of plants, combining the features of mountain and plain coniferous and coniferous-deciduous forests of the European part of Russia. This emphasizes the importance of the forests of the reserve and allows us to consider the studied forests as significant objects for assessing the potential for the implementation of the ecosystem functions of coniferous and coniferous-deciduous forests in the high mountains of the Northwest Caucasus.

Earthworm Population in Major Forest Types

In the selected forest types, 16 species of Lumbricidae family were found: *Aporrectodea caliginosa caliginosa* (Savigny, 1826), *A. jassyensis* (Michaelsen, 1891), *A. rosea* (Savigny, 1826), *Dendrobaena attemsi* (Michaelsen, 1902), *D. mariupoliensis* (Wyssotzky, 1898), *D. shmidti* (Michaelsen, 1907), *D. octaedra* (Savigny, 1826), *D. tellermanica* (Perel, 1966), *D. veneta* (Rosa, 1886), *Dendrodrilus rubidus tenuis* (Eisen, 1874), *Eiseniella tetraedra tetraedra* (Savigny, 1826), *Esenia fetida* (Savigny, 1826), *Lumbricus castaneus* (Savigny, 1826), *L. rubellus* (Hoffmeister, 1843), *L. terrestris* (Linnaeus, 1758), and *Octolasion lacteum* (Örley, 1885). Detected species belong to 4 morpho-ecological groups and 4 types of habitats (Table 1).

In ***riverbed nitrophilous tallgrass gray alder forests,*** maximum abundance, biomass, and species diversity of Lumbricidae were noted (Table 2). They were inhabited by 12 species of earthworms, out of which 11 were found in the soil, 9 in the fallen trees, and 4 in moss on stones. The found species belong to 4 morpho-ecological groups.

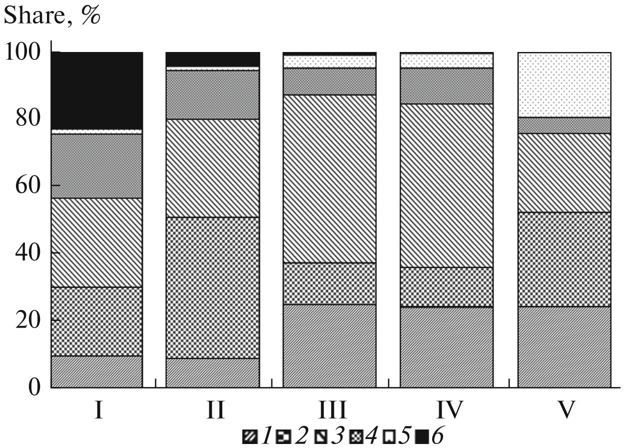

Fig. 2. Correlation of ecological-cenotic groups in the main forest types of the Arkhyz site of the Teberda Reserve Designation I—V see Fig. 1. Ecological-cenotic groups were unified: *1*—boreal species; *2*—meadow species; *3*—nemoral species; *4*—nitrophilous species, *5*—pine-forest species, *6*—coastal-aquatic species and species of mesotrophic bogs.

Epigeic species *D. rubidus tenuis* and *D. attemsi* out of all microsites more often inhabit in fallen trees. *Dendrobaena octaedra* almost evenly inhabits three types of microsites (Table 3). *Lumbricus castaneus,* a rare species in the Caucasus, was found only in the gray alder litter. For a long time, there was no data on the habitat of this species in the Caucasus before the finds of I. B. Rapoport (2005) in floodplain communities of the steppe zone of Kabardino-Balkaria. Due to the frequent flooding of soils, the epigeic amphibiotic species *E. tetraedra tetraedra* are present here.

Out of epi-endogeic species *L. rubellus, D. veneta, D. shmidti* and *E. fetida* were found. All four species inhabited places where traces of bison life were noted: tree gnaws, push cars for bison, and bison excrement, which can serve as a source of nutrition for *D. veneta* and *E. fetida*—species used in vermicomposting and processing of various organic substrates, including animal manure (Wang et al., 2007; and others). In a number of studies, confinement of *L. rubellus* to manure of cattle and other large mammals (Antoshchenkov, 1985; Seeber et al., 2005) was also noted. Findings of *E. fetida* were described earlier on the Arkhyz site of the reserve in alder-mixed grass communities (Rapoport, 2014). In our findings, *E. fetida* was detected only in the fallen trees beneath the *Alnus incana* bark. Information about the distribution of *D. veneta,* common in the Caucasus, in the valley of the Kizgych River was not provided before. *Dendrobana veneta* inhabits forest litter, river sediments, and rotting fallen trees (Vsevolodova-Perel', 1997); in our records, worms of this species were found in waterlogged soil and in fallen trees. Sexually mature epi-

Table 1. The species composition, habitat types, and morpho-ecological groups of earthworms in forest communities of the Arkhyz site of the Teberda Nature Reserve

No.	Species Lumbricidae	Area	Morpho-ecological group
1.	*D. shmidti*	Caucasian	Polymorphic species*
2.	*D. mariupoliensis*		Anecic
3.	*D. attemsi*	Mediterranean	Epigeic
4.	*D. veneta***		Epi-endogeic
5.	*A. jassyensis*		Endogeic
6.	*D. tellermanica*	East Asian	
7.	*L. castaneus***	Cosmopolitan	Epigeic
8.	*D. rubidus tenuis*		
9.	*D. octaedra*		
10	*E. tetraedra tetraedra****		
11.	*E. fetida*		Epi-endogeic
12.	*L. rubellus*		
13.	*A. caliginosa caliginosa***		Endogeic
14.	*A. rosea*		
15.	*O. lacteum*		
16.	*L. terrestris***		Anecic

* The species has three morpho-ecological forms (epigeic, epi-endogeic and endogeic).

** Species detected on the Arkhyz site of the Teberda Reserve for the first time.

*** The species belongs to a subgroup of amphibiotic species (Perel’, 1997).

endogeic worms *D. shmidti* were found at a height of 2 m under the bark of a broken *Alnus incana* trunk.

In terms of abundance and biomass, the main species out of the group of endogeic species was *D. shmidti*, which was often found in three examined microsites of all types of forests. This species dominates in many communities of the mountain regions of the Caucasus (Rapoport and Tsepkova, 2015; etc.). Only in the riverbed nitrophilous tallgrass gray alder forests *A. rosea* and *O. lacteum* were found. Rapoport (2014) noted the exceptional biotopic confinement of these species to alder forests in the studied area. From the group of anecic species, *L. terrestris* was found in soil at shallow depths due to severe waterlogging of the soil, as well as several sexually mature worms were found in the fallen trees.

In all microsites of riverbed gray alder forests, earthworms of 4 ontogenetic states were found (Fig. 3). Juvenile worms predominate in the soil and fallen trees, and mature in mosses on stones.

In ***nitrophilous and meadow-edge-tallgrass birch-aspen forests,*** the diversity, abundance, and biomass of earthworms were lower than in the riverbed gray alder forests. Seven species of earthworms were detected, which all inhabited the soil. In fallen trees and in mosses on stones, 4 species were noted. The highest abundance and biomass of worms were identified in the fallen trees (Table 2), since in these communities the most optimal humidity was noted in the fallen trees (fallen trees 25–30%, soil 15–20%, mosses on stones 10–15%). The detected species belong to 3 morpho-ecological groups. Epigeic species *D. octaedra, D. attemsi,* and *D. rubidus tenuis* were found more often in fallen trees, and the highest number of specimens was found in rotting *Betula pendula* trunks under poorly decomposed bark in raw decaying wood. Out of the group of epi-endogeic species, *D. shmidti* (inhabits all types of microsites) and *L. rubellus* (singular specimens found in aspen) were detected. Out of the group of endogeic species, the most numerous was *D. shmidti* (Table 2), the endogeic form of which inhabits the soil where juvenile worms were mainly found. Large, mature specimens were more often found in mosses on stones, in a well-moistened litter and moss cover on the fallen trees *Populus tremula* and *Acer sp.* of 2–3 stages of decomposition. In soil singular *D. tellermanica* and *A. caliginosa caliginosa* specimens were detected. *Dendrobaena tellermanica* was recently isolated as a separate species (Vsevolodova-Perel’, 2003), characteristic of the Arkhyz site of the Teberda Reserve (Rapoport and Tsepkova, 2015). *Aporrectodea caliginosa caliginosa* was recorded in the Arkhyz site for the first time;

Table 2. Species composition and biomass ($X \pm SE$) of earthworms in the main types of forest, taking into account microsites: soil, fallen trees, mosses on stones in the Arkhyz site of the Teberda Reserve

Lumbricidae Species	Forest type														
	River-bed nitrophilous tallgrass gray alder forests			Nitrophilous and meadow-edge-tallgrass birch-aspen forests			Nemoral-boreal beech-spruce-fir green mosses forests			Nemoral-boreal spruce-fir green mosses forests			Xeromesophytic pine forests with fir, spruce and birch		
	soil	fallen trees	mosses	soil	fallen trees	mosses	soil	fallen trees	mosses	soil	fallen trees	mosses	soil	fallen trees	mosses
D. attemsi	3.6 ± 1.1	9.1 ± 2.5	0	2.45 ± 0.4	9.1 ± 1.7	12.8 ± 2.3	0	17.7 ± 5.4	12.8 ± 3.6	0	10.1 ± 2.7	2.0 ± 0.4	0	8.0 ± 1.4	0
D. octaedra	5.4 ± 1.1	15.6 ± 3.5	8.6 ± 2.7	5.4 ± 1.4	7.5 ± 0.7	12.6 ± 3.5	8.3 ± 3.7	29.1 ± 6.7	6.2 ± 1.2	3.5 ± 0.7	9.5 ± 1.4	1.2 ± 0.4	1.1 ± 0.2	9.0 ± 2.1	0.5 ± 0.1
D. shmidti (epigeic form)	0	0	0	0	0	0	0	0	0	0	2.5 ± 0.7	0	0	2.0 ± 0.5	0
D. rubidus tenuis	0.4	2.0 ± 0.6	4.6 ± 1.1	2.2 ± 0.7	15.1 ± 4.5	4.1 ± 1.2	3.1 ± 0.7	0	0	0	18.7 ± 4.5	0	0	6.0 ± 1.4	0
E. tetraedra tetraedra	0.8 ± 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. castaneus	1.3 ± 0.4	0	0	0	0	0	0	t0	0	0	0	0	0	0	0
D. veneta	1.0 ± 0.1	5.7 ± 0.7	0	0	0	0	0	0	0	0	0	0	0	0	0
D. shmidti (epi-endogeic form)	0	7.25 ± 2.1	0	1.1 ± 0.3	12.3 ± 2.5	2.1 ± 0.4	0	0	0	0	0	2.0 ± 0.2	0	0	0
E. fetida	0	13.7 ± 4.5	0	0	0	0	0	0	0	0	0	0	0	0	0
L. rubellus	8.3 ± 3.5	5.5 ± 1.4	0	5.7 ± 1.8	0	0	2.3 ± 0.5	0	0	0	0	0	0	0	0
A. caliginosa caliginosa	0	0	0	3.27 ± 1.4	0	0	0	0	0	0	0	0	0	0	0
Aporrectodea rosea	5.5 ± 1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. jassyensis	0	0	0	0	0	0	0	0	0	0	0	0	3.2 ± 0.8	1.2 ± 0.7	0
D. shmidti (endogeic form)	34.6 ± 7.9	42.7 ± 8.7	65.3 ± 10.1	30.6 ± 3.8	65.0 ± 6.6	27.1 ± 3.4	20.5 ± 5.5	49.0 ± 6.8	50.3 ± 7.3	41.0 ± 6.6	47.6 ± 3.9	30.0 ± 9.7	13.5 ± 7.8	18.0 ± 6.7	2.5 ± 0.8
D. tellermanica	0	0	0	4.9 ± 2.2	0	0	3.5 ± 0.7	0	0	0	0	0	0	0	0
O. lacteum	16.0 ± 3.8	15.8 ± 5.5	15.5 ± 4.9	0	0	0	0	0	0	0	0	0	0	0	0
D. mariupoliensis	0	0	0	0	0	0	0	0	0	10.1 ± 3.7	0	0	0	0	0
L. terrestris	12.5 ± 4.9	6.1 ± 3.2	0	0	0	0	4	0	0	0	0	0	0	0	0
Total biomass	89.4 ± 10.9*	123.0 ± 27.0	94.8 ± 12.7	55.6 ± 6.14	**109 ± 10.5**^{ac}	58.7 ± 8.6	**41.7 ± 5.3**^{c}	**95.8 ± 51.0**^{ac}	**69.3 ± 8.1**^{a}	**54.6 ± 8.76**^{c}	**85.9 ± 41.0**^{c}	**35.2 ± 7.2**^{a}	**17.8 ± 6.1**^{c}*****	44.2 ± 2.0^{ac}	3.0 ± 0.3^{a}
Total abundance	146.0 ± 18.2*	**285.0 ± 9.1**^{a,c}	166 ± 16.2	85 ±9.12	**175 ± 11.0**^{ac}	65 ± 10.7	78 ± 4.1	**173.5 ± 37.5**^{ac}	92 ± 8.8	**72 ± 12.0**	**161 ± 17.5**^{ac}	**68 ± 7.8**	**30 ± 2.5**^{c}*****	67 ± 28.0^{ac}	4 ± 1.6^{a}

* Statistically significant differences between samples in the soil for forest types (Mann–Whitney test, $p < 0.05$).

Statistically significant differences between samples within the forest type in different microsites are marked in bold: ^{a}, the soil; ^{b}, fallen trees; ^{c}, mosses on stones (Mann–Whitney test, $p < 0.05$).

Table 3. The occurrence of earthworms in samples (%) in three types of habitats in the main forest types of the Arkhyz site of the Teberda Nature Reserve

Lumbricidae species	Riverbed nitrophilous tallgrass gray alder forests	Nitrophilous and meadow-edge-tallgrass birch-aspen forests	Nitrophilous and meadow-edge-tallgrass birch-aspen forests	Nemoral-boreal spruce-fir green mosses forests	Xeromesophytic pine forests with fir, spruce and birch
D. attemsi	S, 20 F, 65 M, 10	S, 10 F, 40 M, 15	F, 42 M, 15	F, 70 M– 14	F, 25
D. octaedra	S, 80 F, 95 M, 75	S, 50 F, 35 M, 60	S, 40 F, 75 M, 35	S, 70 F, 95 M, 60	S, 25 F, 50 M, 15
D. schmidti (epigeic form)	0	0	0	F, 5	F, 20
D. rubidus tenuis	S, 15 F, 80 M, 50	S, 10 F, 35 M, 25	F, 50	F, 35	F, 30
E. tetraedra tetraedra	S, 12	0	0	0	0
L. castaneus	S, 13	0	0	0	0
D. veneta	S, 12 F, 20	0	0	0	0
D. shmidti (epi-endogeic form)	F, 10	S, 10 F, 20 M, 20	0	M, 20	0
E. fetida	F, 15	0	0	0	0
L. rubellus	S, 20 F, 10	S, 10	S, 10	0	0
A. caliginosa caliginosa	0	S, 10	0	0	0
A. rosea	S –12	0	0	0	0
A. jassyensis	0	0	0	0	S, 15 F, 10
D. schmidti (endogeic form)	S, 82 F, 90 M, 95	S, 80 F, 50 M, 40	S, 50 F, 85 M, 85	S, 35 F, 75 M, 95	S, 20 F, 65 M, 80
D. tellermanica	0	S, 10	S, 10	0	0
O. lacteum	S, 25 F, 13 M, 13	0	0	0	0
D. mariupoliensis	0	0	0	S, 10	0
L. terrestris	S, 25 F, 13	0	S, 10	0	0

Habitat types: S—soil, F—fallen trees, M—moss cover on stones.

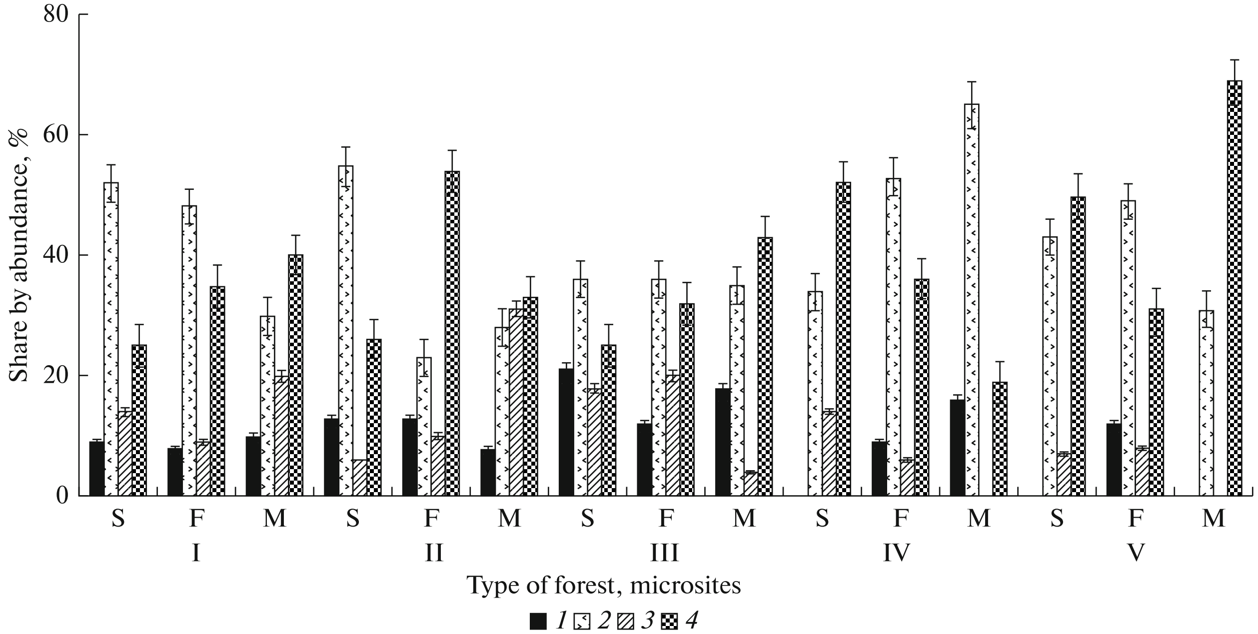

Fig. 3. Ontogenetic spectra of local populations of earthworms in three types of microsites: soil, fallen trees, mosses on stones in the main forest types of the Arkhyz site of the Teberda Reserve. Designation I –V see Fig. 1. S—soil, F—fallen trees, M—mosses on stones; *1*—cocoons, *2*—juvenile worms, *3*—sub-mature worms, *4*—sexually mature worms.

this species is widely distributed in broad-leaved and mixed forests of the Russian Plain (Vsevolodova-Perel', 1997). In the Caucasus, it is more common under forest vegetation in the forest-steppe belt and the broad-leaved forest belt (Rapoport, 2010, 2013; Rapoport et al., 2017).

The ontogenetic spectra of earthworms in these forests were complete. At the same time, the proportion of juvenile worms in the soil is higher than in the fallen trees and moss cover on stones. Mature worms prevail in the fallen trees. In mosses on stones, the share of juvenile, submature, and sexually mature specimens was approximately the same (Fig. 3).

In boreal beech-spruce-fir-small grass-green mosses communities, 7 species of Lumbricidae were found, of which 5 were found in the soil, 4 in the fallen trees, and 3 in mosses on stones. The highest number and biomass of worms were detected in the fallen trees, lower values were detected in mosses on stones and the smallest values were characteristic for the soil (Table 2). The obtained results of the abundance of worms in the soil correspond to data for beech-dark coniferous forests (Perel', 1979; Scheu and Falka, 2000; Rapoport et al., 2017). The found species belong to 4 morpho-ecological groups. From the group of epigeic species *D. octaedra* was detected in three microsites, *D. attemsi* was found more often in fallen trees, less often in mosses on stones, not found in the soil, and *D. rubidus tenuis* was detected only in fallen trees. The only representative of the epi-endogeic group *L. rubellus* was found in the soil of the forest part where traces of bison activity were noted; in the same part of the forest, at a greater depth, anecic species *L. terrestris* was found. Out of the group of endogeic species, *D. shmidti* dominated in three microsites. In the soil, *D. tellermanica* was found singularly. The ontogenetic spectra of Lumbricidae were complete, more cocoons in the soil than in other microsites were detected, and the proportion of juvenile worms was higher in the soil and fallen trees than in mosses (Fig. 3).

In nemoral-boreal spruce-fir green mosses forests, 5 species of earthworms were found in the forests, out of which 4 were found in the fallen trees, 3 in the soil and mosses on stones. The highest abundance and biomass of worms were revealed in the fallen trees, in which these values were somewhat lower in the soil and the lowest in moss on stones (Table 2). In comparison with the previous forest type, in moss cover on stones and rocks, the biomass of worms was 2 times lower, which was associated with a decreased humidity in this habitat (12.5% in spruce-fir forests and 17.5% in beech-spruce-fir). The detected species belong to 4 morpho-ecological groups. Only in this forest type, three *D. shmidti* forms were found. Epigeic species *D. octaedra, D. attemsi, D. rubidus tenuis,* and *D. shmidti* inhabited mainly fallen trees. *D. octaedra* was also common in litter, upper soil, and moss on stones. *D. attemsi* in addition to fallen trees was found in mosses on stones. From the epi-endogeic group, only *D. shmidti* was detected in a moss cover on stones. The endogeic group itself was represented by one species *D. shmidti*. Its highest occurrence in samples was found in mosses on stones (95%), in the fallen trees it was lower (75%), and least in the soil (35%). Only in this type of forest a large anecic worm the Crimean-

Caucasian subendemic *D. mariupoliensis* was found in the soil. In the ontogenetic spectrum, the largest proportion of juvenile worms was found in fallen trees and in mosses on rocks, which was most likely associated with the release of juveniles from cocoons, which were laid during the wetter period. In the soil, on the contrary, sexually mature worms predominated and cocoons were not found. Cocoons were probably located much lower than the low-power soil horizon, which we analyzed under stones, in deep passages and their branches (Perel', 1979)

In xeromesophytic pine forests with fir, spruce and birch, the lowest values of the abundance and biomass of Lumbricidae were noted (Table 2). Five species were found in fallen trees, 3 endogeic species, and 2 species characteristic for mosses on the rocks were found. The highest total abundance and biomass of worms were found in the fallen trees of the 2nd–3rd stage of decomposition, since in these habitats that higher humidity in comparison with the soil and moss cover on stones was preserved. Moss cover on stones in the pine forests on the upper border of the forest was often very dry and therefore became an unfavorable habitat for earthworms. Discovered species belong to two morpho-ecological groups: epigeic and endogeic groups. From the group of epigeic species, *D. octaedra* dominated, which is more common in fallen trees, less often detected in litter, and even less often in moss cover on rocky surfaces (tab. 3). *Dendrobaena attemsi, D. rubidus tenuis* and the epigeic form *D. schmidti* were found only in fallen trees. From the endogeic group, two species were found: *D. schmidti* and *A. jassyensis.* The actual endogeic form *D. schmidti* was found mainly in mosses on rocks and in wet fallen trees *Picea orientalis* of the 2nd and 3rd stages of decomposition; in minor soil it was quite rare and, as a rule, only appeared in the upper part of the humus horizon under the litter horizon. *Aporrectodea jassyensis* was found in a small number of soil samples at a depth of 10–15 cm, and singular *Abies nordmanniana* specimens were found in the fallen trees of the 3rd stage of decomposition.

A complete ontogenetic spectrum with a predominance of juvenile worms was detected only in the fallen trees, which indicates the topical advantage of fallen tree microsites in this type of forest compared to other examined microsites. Cocoons were not found in soil and moss on stones, mature worms prevailed, and the ontogenetic spectrum was incomplete (Fig. 3).

The analysis of the relationship between the population of earthworms and the ecological conditions of the selected forest types showed that earthworms were confined to habitats with increased soil moisture, low acidity, and availability of nitrogen in the soil: the highest abundance, diversity, and biomass of earthworms were identified in the riverbed nitrophilous tallgrass gray alder forests. This forest type according to results of multivariate analysis of geobotanical descriptions of E. Landolt scale prevail under the specified environmental conditions.

In forest types with an intermediate position in terms of moisture, acidity/alkalinity, and availability of nitrogen in the soil of birch-aspen, beech-spruce-fir, and spruce-fir forests, a decrease in species diversity and a statistically significant decrease in the number and biomass of earthworms were revealed in comparison with the riverbed gray alder forests. Moreover, in birch-aspen forests and dark coniferous forests with beech, the diversity of earthworms was higher than in spruce-fir forests. It is known that the litter of deciduous trees is more favorable for earthworms in comparison with the litter of deciduous conifers (Perel', 1979; etc.). The high content of secondary metabolites (polyphenols, tannins, lignin) in the falling needles of spruce, stem and crown waters (Orlova et al., 2011) inhibits the development of soil mesofauna, especially earthworms (Ibragimov et al., 2006). In beech forests, despite the difficult accessibility of beech litter, the presence of a powerful horizon of long-decomposable litter, along with other factors, causes a variety of morpho-ecological groups of earthworms (Rapoport et al., 2017).

In xeromesophytic pine forests with fir, spruce and birch, confined to arid and poor nitrogen soils, the lowest diversity and a statistically significant decrease in the number and biomass of earthworms were found in comparison with other types of forests. I. B. Rapoport (2014) also presented similar data for the pine forests of the Arkhyz Gorge. It is widely known that the low humidity of the substrate is the main limiting factor in the habitat of earthworms (Perel', 1979; etc.). In addition, numerous traces of bottom fires were noted in these forests, which always leads to a significant reduction in the soil mesofauna as a result of the disappearance of the litter and the upper organic soil horizon during the fire (Gongalsky, 2011).

An analysis of the microsite distribution of Lumbricidae within forest types in summer showed that earthworms, along with soils, were confined to microsites such as fallen trees and mosses on stones. Moreover, in the flooded gray alder forests, fallen trees and mosses on stones allowed earthworms to avoid flooding of the soil, and in drier environmental conditions in other types of forests, on the contrary, drainage of soils, and in this case, the fallen trees served as stations for experiencing adverse conditions. Comparison of the composition of earthworms in three microsites of different types of forests showed that fallen trees were mainly inhabited by epigeic and endogeic species, mosses on stones were inhabited by endogeic species, and in the soil, subjected to sufficient moisture, all morpho-ecological groups detected for the forest were present.

CONCLUSIONS

(1) It was established that the forests of the Arkhyz site of the Teberda Reserve are characterized by a well-defined successive shift along the catena: at the base of

the slopes of the trough valley along the riverbed, communities of nitrophilous tallgrass gray alder forests were distributed; in well-drained areas birch-aspen, nitrophilous and meadow-edged-tall forests were present; in the middle part of the slopes of the valley, dark coniferous nemoral-boreal green mosses forests with and without *Fagus orientalis* were detected; and xeromesophytic pine forests with fir, spruce and birch were revealed along the upper border of the forest belt.

(2) The described forest types of different ages of the Teberda Reserve were characterized by high ecological and ecological-cenotic diversity. The ecological-cenotic structure of these types of forests corresponds to the ecological-cenotic structure of the plain and mountain conifers, as well as coniferous-deciduous forests of the European part of Russia.

(3) Sixteen species of earthworms were revealed, out of which four species were noted for the first time in the Arkhyz site of the Teberda Reserve. The biotopic confinement of epigeic, epi-endogeic, endogeic and anecic morpho-ecological groups of Lumbricidae to forest types with increased soil moisture, low acidity, availability of nitrogen in the soil and a well-defined litter horizon has been established. The highest abundance, diversity, and biomass of Lumbricidae were found in nitrophilous tallgrass gray alder forests; the lowest abundance, diversity, and biomass of Lumbricidae were detected in xeromesophytic pine forests with fir, spruce, and birch.

(4) In all forest types, ontogenetic spectra of local populations of Lumbricidae were complete with a high proportion of juvenile specimens, which indicated a stable state of the earthworm population.

(5) Earthworms were characteristic for three types of microsites (habitats): under-crown sections of soil, fallen trees, and mosses on stones. Epigeic and endogeic species mainly inhabited fallen trees, and mosses on stones were inhabited by endogeic species and in the soil at unlimited moisture. All the morpho-ecological groups noted for the forest were detected.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

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