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Biotopic Allocation of Morpho-Ecological Groups of Earthworms (Oligochaeta, Lumbricidae) to the Main Forest Types in the Bol'shaya Laba River Basin (Northwestern Caucasus)

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Abstract—This paper discusses earthworm communities inhabiting forests in the Bol'shaya Laba River basin. The biotopic allocation of morpho-ecological earthworm groups to various forest types, plant communities, and basic habitats (litter, soil, and deadwood) was examined. Fifteen Lumbricidae species have been identified, including two species registered in the study area for the first time. It has been established that, in all types of forests, the earthworm population is primarily represented by epigeic, endogeic, and anecic species. Epi-endogeic species occur rarely. The highest species diversity and biomass of earthworms were registered in broad-leaved forests with beech; the lowest values of these parameters were in dark coniferous forests; while the medium values were in mixed and beech forests. In all types of forests, small-grass, buckler-fern–small-grass, forb, and hazel–forb communities are most densely populated by earthworms, while in dead-cover, green-moss, and rhododendron plant communities, earthworms are less abundant. In all types of forests and in all plant communities, epigeic species inhabit mostly deadwood, and their biomass in deadwood significantly exceeds that in the litter horizon. Endogeic species, being the most abundant Lumbricidae group in the mountain–forest belt, inhabit soils under all types of forests and are less abundant in deadwood. Anecic species are rarely registered in collected samples, but traces of their vital activities (i.e., coprolites) and burrows are present in soils under almost all types of forests and plant communities.

Keywords: Lumbricidae, deadwood, litter, soil, community, tree stand, ground cover

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INTRODUCTION

The structural and functional organization of communities and their key species can be studied only in the most well-preserved natural ecosystems. Forests of the Northwestern Caucasus are of great interest both for floristic and faunistic studies and for studies addressing environmental and ecosystem issues because this region still accommodates nearly undisturbed old forests. One such unique large forest tract is located in the Bol'shaya Laba River basin. The diversity of forest types and plant communities, their uneven-aged structure, and the variety of microsites and microstations essential for soil invertebrates make it possible to solve a number of scientific issues related to the ecology of different pedobiont groups, including such widespread soil formers as earthworms. Even though the ecology of earthworms and other representatives of the forest macrofauna is addressed in many studies, the interrelationships between various environmental groups of pedobionts playing different functional roles in litter processing and soil formation on the one hand and plant communities on the other hand remain poorly researched (Hättenschwiler, 2005; Scheu, 2005; Cesarz et al., 2007; Jacob et al., 2009). As is well-known, the composition of lumbricofauna is significantly affected by the soil properties (Perel, 1979; Bouche, 1977; Lavelle, 1988) and the forest stand composition, which determines the litter quality (Hendriksen, 1990; Cortez, 1998; Schelfhout et al., 2017; Szlavecz, 2018). However, most studies do not take into consideration the ground cover, which determines the microconditions in the upper soil horizons, thus affecting the litter quality (Campana et al., 2002; Milcu et al., 2008). In addition, much attention has been paid in recent years to the role of other habitats (aside from soil) in the maintenance of a stable composition of morpho-ecological groups of earthworms in forests. It is shown that the results of earthworm censuses conducted only in soils underestimate not only the taxonomic, but also the functional diversity of earthworms (Geraskina, 2016; 2016a; Vorobeichik et al., 2018; Hendrix, 1996; Schmidt et al., 2015; Römbke et al., 2017). Under unfavorable conditions, many species use deadwood as a survival station (Geraskina and Shevchenko, 2018), while for some litter species, it serves as a permanent habitat (Römbke et al., 2017).

As is known, mountainous regions of the Caucasus are one of the speciation centers for earthworms (Kvavadze, 1985). Twenty-two species of the Lumbricidae family inhabit the Northwestern Caucasus, and endemic species often predominate in forest communities in terms of biomass and abundance (Rapoport and Tsepkova, 2015; Geraskina, 2016b). The landscape and biotopic allocation of earthworms in forests of the Northwestern Caucasus has been addressed in a number of studies (Rapoport, 2014; 2014a; 2014b; 2016; Rapoport and Tsepkova, 2015), including the analysis of the microsite structure of the forests studied (Geraskina, 2016b; 2018; Geraskina and Shevchenko, 2018). The studies of the lumbricofauna were carried in forests growing in the middle reaches of the Bol'shaya Laba River (Rapoport, 2017; Rapoport and Tsepkova, 2019). Our study presents data on the Lumbricidae population in the area stretching from the upper to the lower reaches of the Bol'shaya Laba River, including detailed information on the distribution of earthworms throughout the basic habitats in the summer period. Such information makes it possible to identify not only the taxonomic, but also the functional diversity of earthworms in the forests studied.

The purpose of this study was to assess the roles of the vegetation cover and degree of manifestation of the main forest mosaic elements in the maintenance of the taxonomic and functional diversity of earthworms and determine the quantitative parameters of the Lumbricidae population (abundance, biomass, and demographic state in the summer season) in the forest belt of the Bol'shaya Laba River basin.

The objectives of this study included the identification of distribution patterns for earthworm species and groups in dependence on the following:

(1) dominants of the tree story that determines the litter composition and quality in various forest types;

(2) dominants of the live ground cover that determines the microconditions in the litter and soil; and

(3) the presence of large-sized deadwood serving both as an essential permanent habitat and as a survival station under unfavorable conditions.

MATERIALS AND METHODS

The field data were collected in the period from May 22 to June 2, 2017, in the most well-preserved foothill and mountain forests in the Bol'shaya Laba River basin, Karachai-Cherkess Republic. The Bol'shaya Laba River flows through the Karachai-Cherkess Republic from south to north between the Arkasara, Zagedan, and Mnatatsara ridges. On the southwest and south, the river is bounded by the spurs of the Greater Caucasian Ridge and the Zakan Ridge dissected by deep wooded gorges and valleys with abundant mountain streams. The forests growing in the gorges and valleys are protected from cold northern and northeasterly winds by high mountain ridges and are open in the southwest to moist air masses penetrating from the Black Sea. The climate is temperate continental, humid, and mild; the average annual precipitation is some 1000 mm (Gvozdetsky, 1963).

The surveyed forests are located in the vicinity of the following settlements: Kurdzhinovo (left bank of the Bol'shaya Laba River), Rozhkao (Rozhkao River), Zagedan (right bank of the Bol'shaya Laba River), Pkhiya (right bank of the Bol'shaya Laba River), Solenoe (Ugol'naya River), and Damkhurts. In addition, forests of Damkhurtskii Nature Reserve (Shantatsara River) were surveyed (Fig. 1).

One hundred twenty-six geobotanical descriptions were produced in the study area on sampling sites 20 × 20 m in size (Zaugolnova and Braslavskaya, 2010); quantitative censuses of earthworms were conducted; the soil types were identified (World Reference Base..., 2015); and the following soil parameters were determined: acidity, current temperature, current humidity (a PH 300 electronic soil indicator), and density (a Wile Soil penetrometer, the ASAE S313.3 standard). The soil parameters studied characterize the living conditions of earthworms during the sample collection period and largely determine (primarily moisture) the quantitative parameters (i.e., abundance and biomass) of earthworms.

Based on the dominants in the tree story, four main forest types were identified; plant communities were distinguished within these types based on the ground cover. Dark coniferous forests (dominants *Picea orientalis* and *Abies nordmanniana*) are represented by buckler-fern–small-grass, dead-cover, and *Festuca drymeja* plant communities. The brown forest soils under them are medium and heavy loamy by granulometric composition. The litter is often poorly manifested (0–3 cm) and consists of fir and spruce fall. The soil acidity is 5.0–6.0; moisture, 20–25%; temperature, 8–10°C; and density, 900–1900 kg/m^3.

Mixed forests (dominants *Fagus orientalis*, *Picea orientalis*, and *Abies nordmanniana*) are represented by buckler-fern–small-grass, *Festuca drymeja*, and green-moss plant communities. The brown forest soils under them are medium loamy by granulometric composition, sometimes with signs of gleyzation (World Reference Base..., 2015). Litter is manifested moderately (2–4 cm) and consists of beech, fir, and spruce fall. The soil acidity is 5.5–6.0; moisture, 30–35%; temperature, 7–10°C; and density, 900–1500 kg/m^3.

Beech forests (dominant *Fagus orientalis*) are represented by small-grass, dead-cover, and rhododendron plant communities. The brown forest soils under them are medium loamy by granulometric composition. The litter is manifested clearly (4–10 cm) and consists of beech fall. The soil acidity is 6.0–6.5; mois-

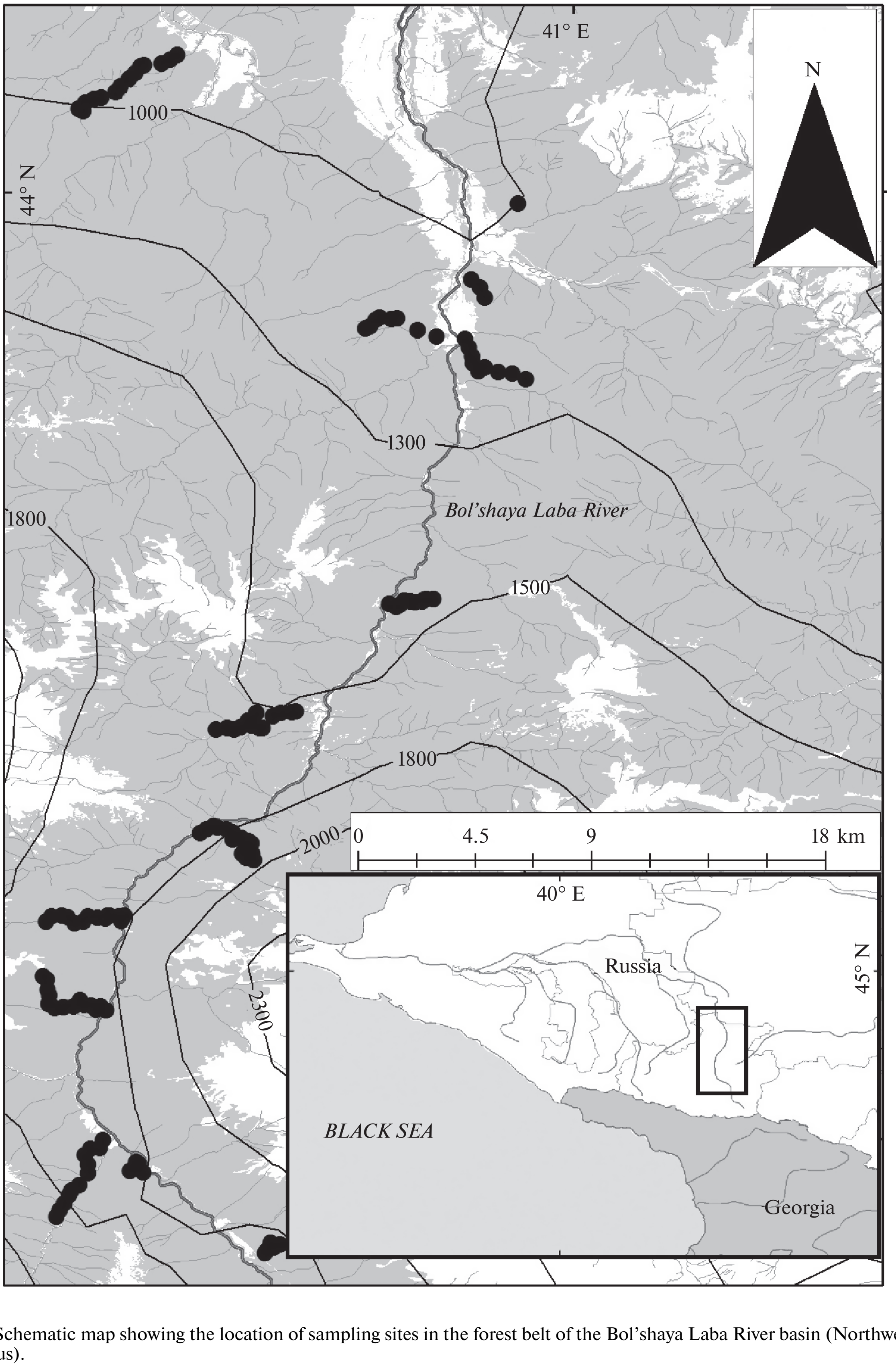

Fig. 1. Schematic map showing the location of sampling sites in the forest belt of the Bol'shaya Laba River basin (Northwestern Caucasus).

ture, 30–40%; temperature, 7–10°C; and density, 700–1300 kg/m^3.

In broad-leaved forests with beech (dominants *Carpinus betulus*, *Acer platanoides*, *Fagus orientalis*, and *Quercus* sp.), hazel–forb, small-grass, and rhododendron communities were distinguished. The brown forest soils under them are medium and light loamy by the granulometric composition. The litter is manifested moderately (2–4 cm) and consists of beech, oak, hornbeam, and maple fall. The soil acidity is 6.0–6.5; moisture, 35–40%; temperature, 8–11°C; and density, 600–1300 kg/m^3.

In addition to the above-listed main types of forests, faunistic censuses of earthworms were carried out in tall-grass and large-fern black-alder forests. The brown forest soils under them are heavy loamy. The soil acidity is 5.0–6.0; moisture, 45–55%; temperature, 6–10°C; and density, 1500–2800 kg/m^3.

Quantitative censuses of earthworms were carried out in all plant communities of each forest type and involved two types of habitats: soil and deadwood at the 2nd–3rd decomposition stages. In each forest type, 28 to 36 soil samples (25 × 25 cm in size and 30–40 cm in depth) were collected (8–16 samples per plant community), and deadwood at the 2nd–3rd decomposition stages was surveyed (Spirin and Shirokov, 2002). The length and diameter of tree trunks were measured. In each type of forest, 6 to 12 sections of tree trunks 1 m long and 20–60 cm in diameter were surveyed. Earthworms inhabiting deadwood at the 2nd–3rd decomposition stages do not penetrate into the rotting trunks and live mostly under the bark; accordingly, the census data were recalculated per 1 m^2 both for soil and deadwood (Ashwood et al., 2019). The formula for the lateral surface of a cylinder was used in quantitative computations of the earthworm abundance in deadwood (Geraskina and Shevchenko, 2018).

The collected earthworms were fixed in 95% ethanol. Their biomass was determined by weighing the fixed worms with full intestines on an electronic balance. The species composition was determined in accordance with *Earthworms of the Fauna of Russia: Cadastre and Key* (Vsevolodova-Perel, 1997). In total, 650 individuals were collected and identified. The nonparametric Kruskal–Wallis test was used to identify statistically significant differences between samples.

The ordination of the habitats studied with the vectors of soil parameters (temperature, moisture content, acidity, and density) was performed using detrended correspondence analysis (DCA) with determination of the correlation level (r) and significance level (p) in the PC-ORD 5.0, SpeDiv, and Past programs. The positions of the vectors were determined based on the total biomass of all earthworm species in the soil samples.

RESULTS

In the course of the soil–zoological study, 15 earthworm species belonging to four morpho-ecological groups (Perel, 1979; Vsevolodova-Perel, 1997) and confined to four types of distribution ranges (Rapoport, 2011, 2013) were registered (Table 1).

Dark coniferous (fir–spruce) forests are inhabited by six Lumbricidae species that can be conditionally divided into three morpho-ecological groups: epigeic (*D. attemsi*, *Dendrodrilus rubidus tenuis*, and *D. octaedra*), endogeic (*D. schmidti* and *A. jassensis*), and anecic (*D. mariupolienis*). The abundance and biomass of earthworms in buckler-fern–small-grass fir–spruce forests are significantly higher in comparison with dead-cover and *Festuca drymeja* fir–spruce forests (Table 2).

The epigeic species *D. attemsi* and *Dendrodrilus rubidus tenuis* occur mostly in fir deadwood at the 3rd decomposition stage (abundance 12.0 ± 3.7 ind./m^2; biomass 4.3 ± 0.5 g/m^2) and sporadically in spruce deadwood at the 3rd decomposition stage (abundance 2.0 ± 0.7 ind./m^2; biomass 1.3 ± 0.8 g/m^2). *D. attemsi* and *Dendrodrilus rubidus tenuis* were not found in the litter horizon under dark coniferous forests. *D. octaedra* inhabits both litter and deadwood. The total biomass of epigeic species in deadwood is higher in comparison with the litter (Fig. 2).

The endogeic species occur only in soil (were not found in deadwood); the share of juvenile individuals is higher than the share of sexually mature animals (60 and 40%, respectively).

The anecic species *D. mariupolienis* occurs both in soil and in deadwood (under the bark of fir at the 3rd decomposition stage) in a dark coniferous *Festuca drymeja* community. Sparse burrows of this species and coprolites on the soil surface were also noted in dark coniferous buckler-fern–small-grass plant communities.

Mixed (beech–fir and beech–spruce) forests are inhabited by eight Lumbricidae species that can be conditionally divided into three morpho-ecological groups: epigeic (*D. attemsi*, *Dendrodrilus rubidus tenuis*, *D. octaedra*, *D. hortensis*, and *D. schmidti*), endogeic (*D. schmidti*, *A. jassensis*, and *O. lacteum*), and epi-endogeic (*E. fetida*). The highest abundance, biomass, and diversity of earthworms were noted in mixed buckler-fern–small-grass plant communities; in mixed green-moss and *Festuca drymeja* communities, the values of these quantitative parameters are statistically significantly lower (Table 2).

Epigeic species *D. attemsi* and *Dendrodrilus rubidus tenuis* occur only in deadwood (were not found in the litter horizon). Their abundance and biomass in fir deadwood (8.5±0.7 ind./m^2 and 2.5±0.6 g/m^2) are higher than in beech deadwood (3.0±0.5 ind./m^2 and 1.5 ± 0.6 g/m^2). *D. octaedra* inhabits both the litter horizon and deadwood (mostly fir deadwood). A rare epigeic form of *D. schmidti* was found in the litter hori-

Table 1. Species composition, types of distribution ranges, and morpho-ecological groups of earthworms inhabiting the main forest types in the Bol'shaya Laba River basin (Northwestern Caucasus)

Lumbricidae species	Distribution range	Morpho-ecological group
Allolobophora chlorotica (Savigny 1826)	Palearctic	Endogeic
Dendrobaena schmidti (Michaelsen 1907)	Crimean–Caucasian	Epigeic and endogeic
Dendrobaena mariupolienis Wyssotzky 1898		Anecic
Dendrobaena attemsi Michaelsen 1902	Mediterranean	Epigeic
Dendrobaena hortensis (Michaelsen 1890)		
Dendrobaena veneta (Rosa 1886)		Epi-endogeic
Aporrectodea jassyensis (Michaelsen 1891)		Endogeic
Dendrobaena tellermanica Perel 1966	East Eurasian	
Dendrodrilus rubidus tenuis (Eisen 1874)	Cosmopolitan species	Epigeic
Eiseniella tetraedra tetraedra (Savigny 1826)		
Dendrobaena octaedra (Savigny 1826)		
Eisenia fetida (Savigny 1826)		Epi-endogeic
Lumbricus rubellus Hoffmeister 1843		
Octolasion lacteum (Örley 1885)		Endogeic
Aporrectodea rosea (Savigny 1826)		

zon only under the *Festuca drymeja* beech–fir forest. *D. hortensis* was found in litter under a beech–spruce buckler-fern–small-grass community. In mixed forests, the total biomass of epigeic species in litter is higher than that in deadwood (Fig. 2).

The epi-endogeic species *E. fetida* (sexually mature individuals) was found in spruce deadwood at the 3rd decomposition stage in a buckler-fern–small-grass beech–fir forest. No other discoveries of this species were made in forests of the Bol'shaya Laba River basin.

The endogeic species inhabit both soil and deadwood, and their biomass in soil is statistically significantly higher in comparison with deadwood (Fig. 3).

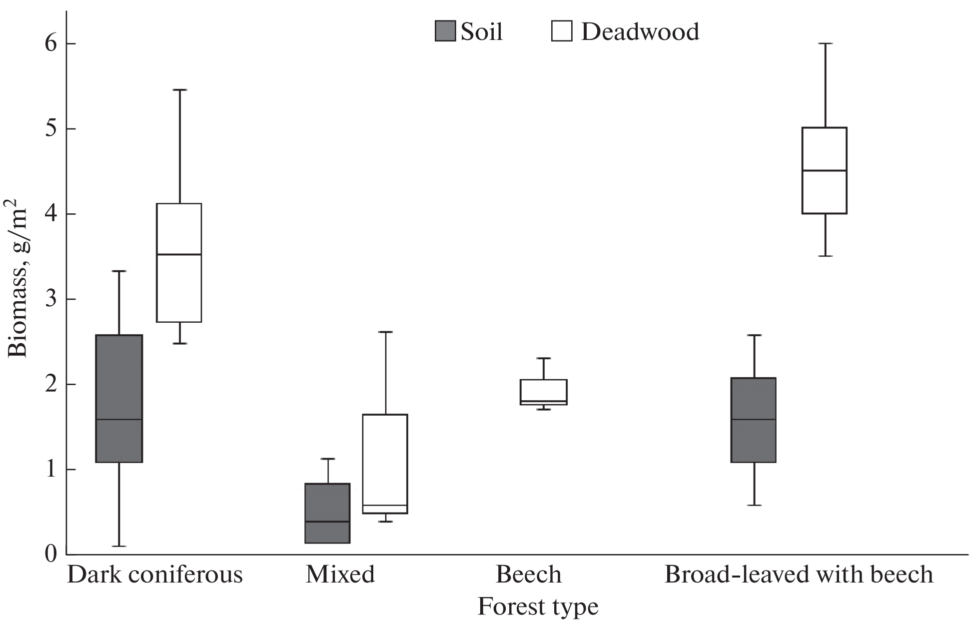

Fig. 2. Biomass of epigeic earthworm species in the main forest types of the Bol'shaya Laba River basin (Northwestern Caucasus).

Table 2. Abundance (ind./m^2, $X \pm SE$) and total biomass (g/m^2, $X \pm SE$) of earthworms in the main forest types of the Bol'shaya Laba River basin

Species	Forest type											
	dark coniferous ($N = 28$)			mixed ($N = 28$)			beech ($N = 34$)			broad-leaved with beech ($N = 36$)		
	buckler-fern–small-grass ($N = 12$)	dead-cover ($N = 8$)	Festuca drymeja ($N = 8$)	buckler-fern–small-grass ($N = 10$)	Festuca drymeja ($N = 9$)	green-moss ($N = 9$)	small-grass ($N = 16$)	dead-cover ($N = 10$)	rhododendron ($N = 8$)	hazel–forb ($N = 16$)	small-grass ($N = 12$)	rhododendron ($N = 8$)
D. attemsi	+	+	+	+	+	+	+	+	+	+	+	+
Dendrodrilus rubidus tenuis	+	+	+	+	+	+	+	+	+	+	+	+
D. octaedra	**15.0 ± 4.1^{a,b}**	**6.0 ± 0.1^{a,b}**	**8.0 ± 1.1^{a,b}**	3.0 ± 2.1	2.0 ± 0.9	+	+	+	+	+	+	+
D. hortensis	0	0	0	1.5 ± 1.5	0	0	0	0	0	0	0	0
D. schmidti (epigeic form)	0	0	0	0	2.5 ± 1.7	0	0	0	0	4.5 ± 1.1	0	0
E. fetida	0	0	0	+	0	0	0	0	0	0	0	0
D. tellermanica	0	0	0	0	0	0	0	0	0	8.0 ± 4.4	0	0
Al. chlorotica	0	0	0	0	0	0	0	0	0	1.0 ± 0.5	0	0
D. schmidti (endogeic form)	11.0 ± 4.5	8.5 ± 0.1	12.9 ± 2.3	16.9 ± 2.8^{a}	8.9 ± 1.1	8.9 ± 0.3	**28.0 ± 4.5^{b}**	**25.0 ± 6.5^{b}**	**20.5 ± 0.8^{b}**	**35.0 ± 5.8^{b}**	**34.0 ± 9.9^{b}**	**35.0 ± 8.5^{b}**
A. jassensis	9.0 ± 2.0	4.5 ± 3.1	6.9 ± 1.0	9.4 ± 3.3	11.5 ± 0.3	6.1 ± 0.5^{a}	16.2 ± 4.9	12.2 ± 4.3	8.5 ± 0.9^{a}	**43.5 ± 11.0^{a}**	**33.5 ± 12.9**	**21.5 ± 8.5**
D. mariupolienis	++	++	2.0 ± 1.0	0	0	0	2.0 ± 0.7	++	++	4.0 ± 3.7	++	0
O. lacteum	0	0	0	0	2.0 ± 1.0^{b}	0	0	0	0	**10.0 ± 3.4^{b}**	0	0
Total abundance	35.0 ± 4.5	19.0 ± 2.2^{a}	29.8 ± 3.3	30.8 ± 5.5	26.9 ± 3.8	15.0 ± 0.3^{a}	46.2 ± 5.6^{a}	37.8 ± 4.1	29.0 ± 4.3	**106.0 ± 14.3^{a,b}**	**69.5 ± 10.2^{b}**	**56.5 ± 10.9^{b}**
Total biomass	18.0 ± 4.8	8.9 ± 0.5^{a}	15.4 ± 1.5	**22.4 ± 3.5^{a}**	14.1 ± 3.1	14.0 ± 0.6	**25.2 ± 6.4^{a}**	19.2 ± 1.6	19.8 ± 0.8	**41.0 ± 8.6^{a}**	**33.0 ± 6.5^{b}**	**25.0 ± 2.5^{b}**

(+)species found only in deadwood, (++) burrows of the species noted in soil.
[a] Values differ statistically significantly in communities within the same forest type (Kruskal–Wallis test, $p < 0.05$).
[b] Values differ statistically significantly in comparison with other forest types (Kruskal–Wallis test, $p < 0.05$).

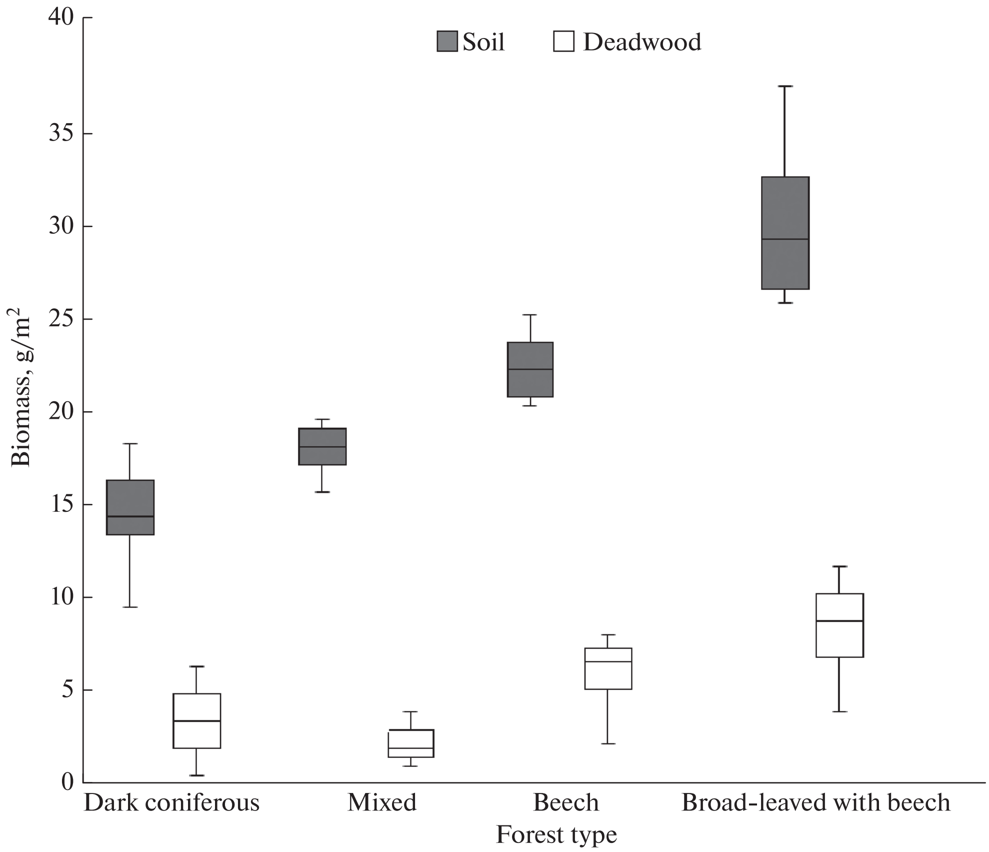

Fig. 3. Biomass of endogeic earthworm species in the main forest types of the Bol'shaya Laba River basin (Northwestern Caucasus).

In mixed forests, *D. schmidti* and *A. jassensis* occur in all types of plant communities; while *O. lacteum* occurs only in a beech–spruce dead-cover community (Table 2).

In mixed forests, the share of sexually mature individuals is higher than the share of juvenile earthworms both in soil and in deadwood (Fig. 4).

Beech forests are inhabited by six Lumbricidae species that can be conditionally divided into three morpho-ecological groups: epigeic (*D. attemsi*, *Dendrodrilus rubidus tenuis*, and *D. octaedra*), endogeic (*D. schmidti* and *A. jassensis*), and anecic (*D. mariupolienis*). The abundance and biomass of earthworms in beech small-grass communities is statistically significantly higher in comparison with beech dead-cover and beech rhododendron communities (Table 2).

The epigeic group of species was found only in deadwood (Table 1). Epigeic species occur under the bark of beech at the 2nd–3rd stage of decomposition; their abundance and biomass are low (5.0 ± 1.7 ind./m^2 and 2.3 ± 0.5 g/m^2); and the share of sexually mature individuals is almost 80%.

In soil, species of the endogeic group constitute 98% of the total abundance and 70% of the total biomass of earthworms. Endogeic species are more abundant in beech small-grass communities (Table 2). They were found in beech deadwood at the 3rd decomposition stage (Fig. 3). In both soil and deadwood, the majority of individuals (80%) are sexually mature.

The anecic species *D. mariupolienis* was found only in soil of a beech small-grass community; in addition, burrows of this species were noted in dead-cover and rhododendron beech forests.

In beech forests, the majority of individuals inhabiting soils and deadwood are sexually mature (Fig. 4).

Broad-leaved forests with beech are inhabited by ten Lumbricidae species that can be conditionally divided into three morpho-ecological groups: epigeic (*D. attemsi*, *Dendrodrilus rubidus tenuis*, *D. octaedra*, and *D. schmidti*), endogeic (*D. schmidti*, *A. jassensis*, *D. tellermanica*, *O. lacteum*, and *Al. chlorotica*), and anecic (*D. mariupolienis*). In hazel–forb plant communities of broad-leaved forests with beech, the abundance, biomass, and diversity of earthworms are statistically significantly higher in comparison with small-grass and rhododendron communities (Table 2).

The epigeic species *D. attemsi*, *Dendrodrilus rubidus tenuis*, and *D. octaedra* were found only in deadwood. Their highest abundance (15–20 ind./m^2) was regis-

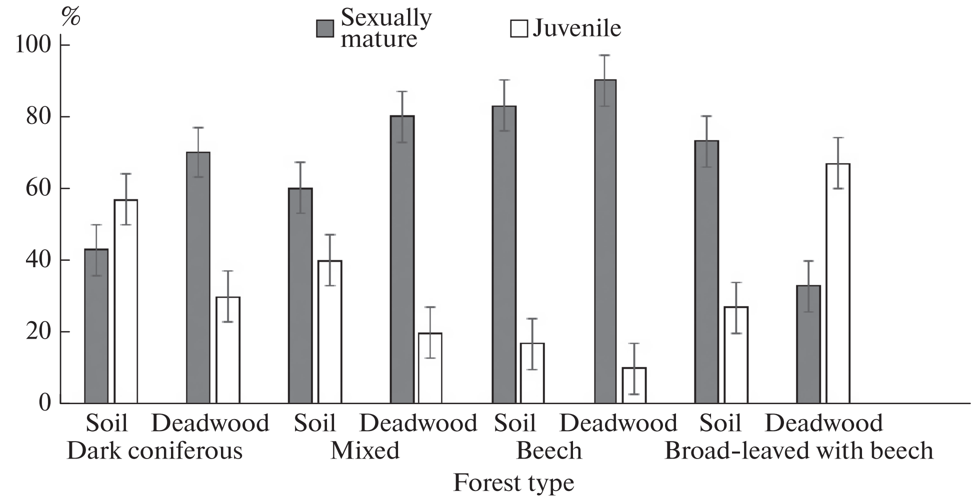

Fig. 4. Shares of sexually mature and juvenile earthworms (%) in soils and deadwood under main forest types in the Bol'shaya Laba River basin (Northwestern Caucasus).

tered in maple and oak deadwood at the 2nd–3rd stages of decomposition. An epigeic form of *D. schmidti* was found in litter under a beech–hornbeam–maple hazel–forb community. More than 50% of individuals in this group are juvenile.

In the endogeic group, more than 60% of individuals belong to the species *D. schmidti* and *A. jassensis*. They inhabit soil and, to some extent, deadwood under various types of broad-leaved forests with beech. *D. tellermanica* and *Al. chlorotica* were found only in soils of hazel and hazel–forb communities. No representatives of these species were found in deadwood. *O. lacteum* inhabits soils of hazel–forb plant communities. The majority of individuals in the endogeic group of species are sexually mature.

The anecic species *D. mariupolienis* inhabits soils of hornbeam–beech hazel–forb communities. Both sexually mature and juvenile individuals were found. Burrows were noted in soils of small-grass and rhododendron broad-leaved forests with beech.

Overall, the majority of earthworms inhabiting soils under the forest types studied are sexually mature; while in deadwood, the majority of individuals are juvenile (Fig. 4).

Several species not found in beech, dark coniferous, mixed, and broad-leaved forests were discovered in black alder forests: the epigeic *Eiseniella tetraedra tetraedra*, endogeic *D. veneta* and *L. rubellus*, and anecic *A. rosea*. In addition, the endogeic form of *D. schmidti* occurs in black alder forests. No other Lumbricidae species were found in black alder forests.

DISCUSSION

The earthworm communities inhabiting the identified forest types differ in species composition, composition of morpho-ecological groups, and quantitative parameters (abundance and biomass). Out of the 15 earthworm species identified, 13 were registered earlier in forests of the Bol'shaya Laba River basin (Rapoport, 2017; Rapoport and Tsepkova, 2019). *A. c. trapezoides* (Duges 1828) was not found in the course of our study because it is more confined to meadow biotopes (Rapoport, 2017). Two species were identified in the study area for the first time: *Al. chlorotica* and *D. mariupolienis*. Even though *Al. chlorotica* is widespread in the Palearctic realm and common in the South Caucasus, it rarely occurs in the Northwestern Caucasus (Kvavadze, 1985), but the high expansion capability of this species was noted earlier (Vsevolodova-Perel, 1997). By contrast, the Crimean–Caucasian endemic species *D. mariupolienis* is widespread in the Northwestern Caucasus but was never found outside its distribution range. Apparently, the species *D. mariupolienis* was not noted earlier in this area due to the difficulties associated with censuses of anecic species living at significant depths.

The soil properties are believed to be of prime importance for the life of earthworms. In addition to the climate, relief, and parent rock features, the properties of forest soils are significantly determined by the composition of terrestrial vegetation (Wedin and Tilman, 1990; Muys et al., 1992; Pastor et al., 1993; Binkley and Giardina, 1998). The ordination diagram produced based on the data collected (Fig. 5) indicates that the differences in moisture content and acidity primarily affect the distribution of earthworms (the vector length reflects the degrees of correlation between the soil parameters and the axes). The ordination of sampling sites based on the biomass of earthworms in the four forest types and on the soil properties indicates the confinement of earthworms to moderately moist soils of broad-leaved forests with beech and beech forests. The soil acidity index affects the

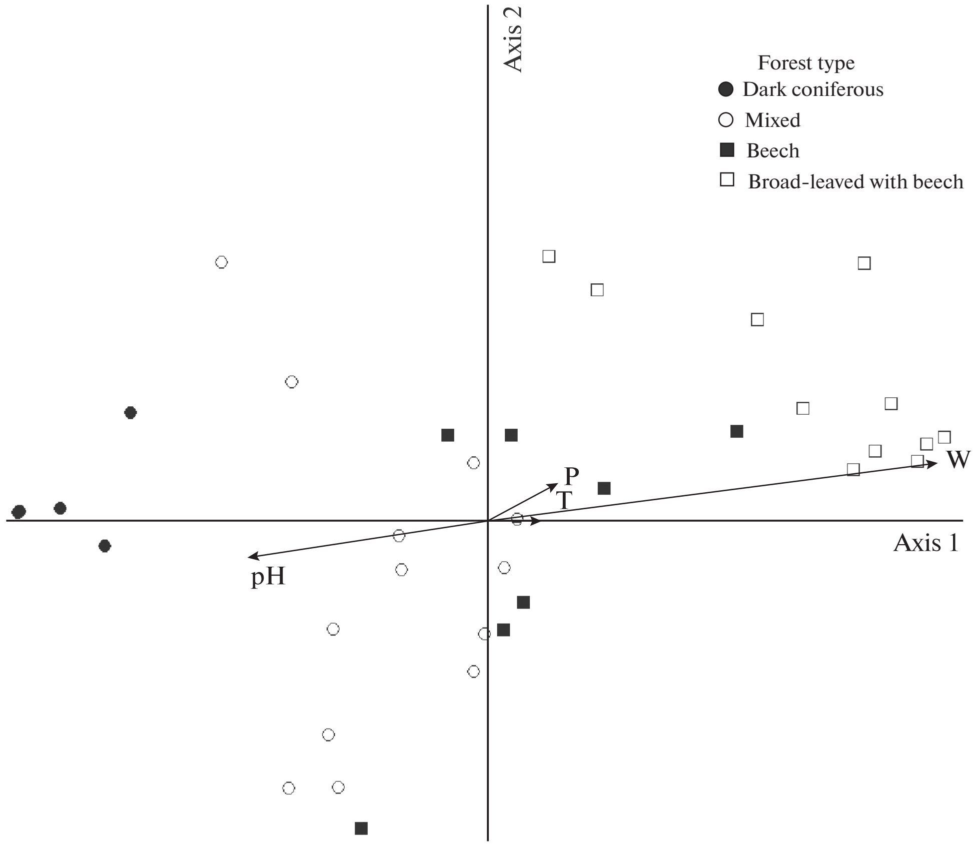

Fig. 5. Ordination of sampling sites based on the biomass of earthworms in the main forest types in the first two DCA axes with the vectors of soil parameters: (T) temperature, (W) moisture content, (pH) acidity, and (P) density.

biomass of earthworms in mixed and dark coniferous forests where the acidity is higher (pH 5.0–6.0) than in other forest types: the biomass of earthworms in such forests is statistically significantly lower (Table 2). The soil density and temperature turned out to be less significant than the acidity and moisture content for the distribution of earthworms; more favorable values of these parameters are observed in mixed forests with beech and beech forests (Fig. 5).

The soil moisture is a more significant factor in beech forests and broad-leaved forests with beech forests (Fig. 5). The presence of Oriental beech significantly reduces the evapotranspiration in such forests (Qulehle et al., 2006; Gebauer, 2010), both due to the lower evaporation of moisture from the leaf surface (Backes and Leuschner, 2000; Kecher et al., 2009) and due to the greater litter thickness preventing evaporation of moisture from the soil surface.

The acidity of litter and soil is higher in dark coniferous forests (Shleynis, 1965; Noirfalise and Vanesse, 1975) because needles falling from mostly young fir and spruce trees cause the acidification of organogenic horizons (Orlova et al., 2011). Combined with low soil moisture levels, this factor significantly contributes to the reduction of the biomass of earthworms.

The impacts of woody vegetation on the soil properties that provide trophic and topical conditions for the soil macrofauna are also exercised through leaf litter and deadwood. In our study, the highest species diversity and biomass of earthworms were registered in broad-leaved forests with beech; the lowest values of these parameters occurred in dark coniferous forests; while medium values were found in mixed and beech forests.

The role of leaf litter falling from woody plants in the formation of trophic and topical conditions for the soil macrofauna is well researched. Needles falling from trees in dark coniferous forests contain large amounts of secondary metabolites (polyphenols, tannins, and lignin); these metabolites suppress the development of soil invertebrates by inhibiting their intestinal enzymes (Schultz et al., 1992; Lavelle et al., 1993). However, it was shown recently that surface-active metabolites (drilodefensins) are synthesized in the intestines of earthworms and neutralize the inhibitory effect of polyphenols (Liebeke et al., 2015). Apparently, these mechanisms enable earthworms to consume slowly decomposing litter and live in coniferous forests. The majority of earthworms registered in dark coniferous forests in the middle reaches of the

Bol'shaya Laba River belong to epigeic species (Rapoport, 2017). Our data also indicate that the group of epigeic species is confined mostly to dark coniferous forests (Table 2, Fig. 2); in addition, the abundance of endogeic and anecic species in such forests is lower in comparison with other forest types.

The most favorable trophic conditions for earthworms are formed in broad-leaved forests; it is known that the biomass of earthworms in maple and ash plantings is several times higher than in coniferous, oak, or beech communities (Perel, 1979; Reich et al., 2005; Suarez et al., 2006). A number of researchers have already demonstrated the benefits of mixed litter (from deciduous and coniferous tree species) for the soil macrofauna (Hättenschwiler and Gasser, 2005; Sariyildiz and Küçük, 2008): coniferous litter (as well as oak and beech litter) decomposes slowly, thus serving as a favorable habitat for the epigeic macrofaunal group, while quickly decomposing deciduous litter serves as a source of nutrients and energy (Sayad et al., 2012). It was shown that the biomass and functional diversity of earthworms in the mountain forests of Hainich National Park (Thuringia, Germany) directly correlate with the forest stand diversity; by contrast, only one group of epigeic earthworms inhabits monodominant beech forests (Cesarz et al., 2007). According to our data, species found in beech forests are mostly endogeic; this is consistent with the earlier data on the earthworm population in the middle reaches of the Bol'shaya Laba River (Rapoport, 2017). Epigeic and anecic species were found as well, but their abundance was low.

The role of deadwood in the maintenance of the earthworm population in a stable state in forest communities is researched poorly in comparison with the role of soils. At the end of the 20th century, "tree" earthworm species living primarily under the bark and in trunks of rotting trees had been distinguished (Bouche, 1972; Lee, 1985), and the "lumbricidal" timber decomposition stage was introduced (Mamaev, 1960). Recent studies indicate that a number of earthworm species and even groups of species often remain undetected during forest surveys if the researchers do not examine habitats such as deadwood (Geraskina, 2016; 2016a; Vorobeichik et al. 2018; Hendrix, 1996; Schmidt et al., 2015) and even live wood (Römbke et al., 2017). For instance, the species *D. attemsi* was excluded from the "rare" category in Ireland based on the results of detailed studies of invertebrates living in deadwood (Schmidt et al., 2015). The species *Allolobophoridella eiseni* was discovered in beech forests of Germany using funnel traps set on live tree trunks in the course of autumn and winter censuses (Römbke et al., 2017). Epigeic species (*Dendrodrilus rubidus tenuis*, *D. attemsi*, and *D. octaedra*) are most closely interrelated with timber; as a result, this group may be incorrectly represented in censuses. Our data indicate that, in spring and summer, *Dendrodrilus rubidus tenuis* and *D. attemsi* can be found only in deadwood and are not detected in standard soil samples. *D. octaedra* occurs in both soil and deadwood (Table 2). Concurrently, the biomass of epigeic species in deadwood is often statistically significantly higher than that in the litter horizon (Fig. 2). Both mature and juvenile individuals occur in deadwood. In addition to the epigeic species, endogeic earthworms are frequently found in deadwood as well (anecic species are discovered there less often). Normally, all these earthworms are mature individuals that colonize deadwood under favorable moisture conditions (Geraskina and Shevchenko, 2018). In all forest types, the biomass of endogeic species in deadwood is several times lower than that in soil (Fig. 3).

The role of the ground cover in the formation of the earthworm population is addressed in just a few studies (Babel et al., 1992; Curry and Schmidt, 2007; Campana et al., 2002; Milcu et al., 2008). Our data indicate that plant communities with rich species composition, good representation of all morpho-ecological groups, and high abundance and biomass of earthworms can be distinguished in all forest types (e.g., small-grass, buckler-fern–small-grass, forb, and hazel–forb communities). By contrast, in dead-cover, green-moss, and rhododendron communities, the abundance, biomass, and diversity of earthworms are low (Table 2). Communities belonging to the first group are inhabited by representatives of all morpho-ecological earthworm groups. Communities belonging to the second group are usually inhabited only by endogeic species: anecic earthworms rarely occur there, while epigeic species inhabit only deadwood. The correlation between the spatial heterogeneity of the earthworm population and the type of ground cover was earlier demonstrated for beech forests of France: only endogeic earthworms live in dead-cover forests (where forest litter is formed exclusively by beech fall); while forests with ferns and small grasses (mostly gramineous species) are inhabited by several morpho-ecological earthworm groups (Campana et al., 2002). The chemical properties of herbaceous vegetation affect soil saprophages both directly and indirectly. It is known that anecic earthworms can consume not only dead but also live aboveground parts of plants (Needham, 1957; van Rhee, 1963; Schönholzer, 1999). The composition of the herbaceous story indirectly affects epigeic, endogeic, and epi-endogeic groups of earthworms: the high content of readily soluble carbohydrates in dying aboveground parts provides good trophic conditions for all groups of earthworms, feeding both in the soil and on the surface (Satchell, 1967). Analysis of the entire range of plant communities studied shows that the most favorable trophic conditions are formed in hazel–forb broad-leaved forests with beech where the highest Lumbricidae diversity and biomass are registered.

CONCLUSIONS

In forests of the Bol'shaya Laba River basin, the earthworm population is represented by epigeic, endogeic, and anecic species. Epi-endogeic species occur rarely. In all forest types, the biomass of epigeic species in deadwood is higher than that in the litter horizon. Endogeic earthworms, being the most abundant group of Lumbricidae species in the mountain–forest belt, inhabit soils under all forest types and colonize, subject to favorable conditions, fragments of rotting deadwood. Anecic species are rarely registered during censuses, but traces of their vital activities (i.e., coprolites) and burrows are present in soils under almost all types of forests and plant communities.

The highest species diversity and biomass of earthworms are registered in broad-leaved forests with beech; the lowest values of these parameters are in dark coniferous forests; while medium values occur in mixed and beech forests. Broad-leaved forests with beech provide the optimal soil moisture and acidity conditions for various earthworm groups. Broad-leaved and mixed forests feature the most favorable trophic and topical conditions. In all types of forests, small-grass, buckler-fern–small-grass, forb, and hazel–forb communities are most densely populated by earthworms, while in dead-cover, green-moss, and rhododendron communities, earthworms are less abundant.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest

The authors declare that they have no conflict of interest.

Statement on the Welfare of Animals

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

Ashwood, F., Vanguelova, E.I., Benham, S., and Butt, K.R., Developing a systematic sampling method for earthworms in and around deadwood, *For. Ecosyst.*, 2019, vol. 6, no. 1, pp. 1–12.

Babel, U., Ehrmann, O., and Krebs, M., Relationships between earthworms and some plant species in a meadow, *Soil Biol. Biochem.*, 1992, vol. 24, no. 12, pp. 1477–1481.

Backes, K. and Leuschner, C., Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought, *Can. J. For. Res.*, vol. 30, pp. 335–346.

Binkley, D.A.N. and Giardina, C., Why do tree species affect soils? The warp and woof of tree-soil interactions, in *Plant-Induced Soil Changes: Processes and Feedbacks*, Dordrecht: Springer, 1998, pp. 89–106.

Bouche, M.B., Lombriciens de France, in *Ecologie et Systematique*, Paris: INRA, 1972.

Bouche, M.B., Strategies lombriciennes, *Ecol. Bull.*, 1977, no. 25, pp. 122–132.

Campana, C., Gauvin, S., and Ponge, J.F., Influence of ground cover on earthworm communities in an unmanaged beech forest: linear gradient studies, *Eur. J. Soil Biol.*, 2002, vol. 38, no. 2, pp. 213–224.

Cesarz, S., Fahrenholz, N., Migge-Kleian, S., Platner, C., and Schaefer, M., earthworm communities in relation to tree diversity in a deciduous forest, *Eur. J. Soil Biol.*, 2007, vol. 43, pp. 61–67.

Cortez, J., Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity, *Soil Biol. Biochem.*, 1998, vol. 30, no. 6, pp. 783–793.

Curry, J.P. and Schmidt, O., The feeding ecology of earthworms—a review, *Pedobiologia*, 2007, vol. 50, no. 6, pp. 463–477.

Gebauer, T., Water turnover in species-rich and species-poor deciduous forests: xylem sap flow and canopy transpiration, *PhD Thesis*, Göttingen: University of Göttingen, 2010.

Geraskina, A.P., Problems of quantifying and accounting for the faunistic diversity of earthworms in forest communities, *Russ. J. Ecosystem Ecol.*, 2016, vol. 1, no. 2, pp. 1–9.

Geraskina, A.P., The population of earthworms (Lumbricidae) in the main types of dark coniferous forests in Pechora-Ilych Nature Reserve, *Biol. Bull. (Moscow)*, 2016a, vol. 43, no. 8, pp. 819–830.

Geraskina, A.P., Earthworms (Oligochaeta, Lumbricidae) in the vicinity of the village Dombay of the Teberda Nature Reserve (North-West Caucasus, Karachay-Cherkessia), *Tr. Zool. Inst. Ross. Akad. Nauk*, 2016b, no. 4, pp. 450–466.

Geraskina A.P., Dynamics of the complex of earthworms during post-cutting successions in the forests of the North-West Caucasus, *Vopr. Lesn. Nauki*, 2018, vol. 1, no. 1, pp. 1–14.

Geraskina, A.P. and Shevchenko, N.E., Biotopic occurrence of earthworms in intact forests of the Teberda Biosphere Reserve, *Lesovedenie*, 2018, no. 6, pp. 464–478.

Gvozdetskii N.A., *Kavkaz. Ocherk prirody* (Caucasus. Essay on Nature), Moscow: Geografgiz, 1963.

Hättenschwiler, S., Effects of tree species diversity on litter quality and decomposition, in *Forest Diversity and Function: Temperate and Boreal Systems*, Scherer-Lorenzen, M., Köhler, C., and Schulze, E.-D., Eds., Ecological Studies, Heidelberg: Springer, 2005, vol. 176, pp. 149–164.

Hättenschwiler, S. and Gasser, P., Soil animals alter plant litter diversity effects on decomposition, *Proc. Natl. Acad. Sci. U. S. A.*, 2005, vol. 102, no. 5, pp. 1519–1524.

Hendriksen, N.B., Leaf litter selection by detritivore and geophagous earthworms, *Biol. Fertil. Soils*, 1990, vol. 10, no. 1, pp. 17–21.

Hendrix, P.F., Earthworms, biodiversity, and coarse woody debris in forest ecosystems of the southeastern USA, in *Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity*, General Technical Report no. SE-94, USDA Forest Service, Athens, GA, 1996, pp. 2122–2130.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., and Thomas, F.M., Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity, *Soil Biol. Biochem.*, 2009, vol. 41, no. 10, pp. 2122–2130.

Kecher, P., Gebauer, T., Horna, V., and Leuschner, C., Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies, *Ann. For. Sci.*, 2009, vol. 66, pp. 101–115.

Kvavadze, E.Sh., *Dozhdevye chervi (Lumbricidae) Kavkaza* (Earthworms (Lumbricidae) of the Caucasus), Tbilisi: Metsniereba, 1985.

Lavelle, P., Earthworm activities and the soil system, *Biol. Fertil. Soils*, 1988, vol. 6, no. 3, pp. 237–251.

Lavelle, P., Blanchart, E., Martin, A., Martin, S., and Spain, A., A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics, *Biotropica*, 1993, vol. 25, no. 2, pp. 130–150.

Lee, K.E., *Earthworms. Their Ecology and Relationships with Soils and Land Use*, New York: Academic, 1985, pp. 211–221.

Liebeke, M., Strittmatter, N., Fearn, S., Morgan, A.J., Kille, P., et al., Unique metabolites protect earthworms against plant polyphenols, *Nat. Commun.*, 2015, vol. 6, p. 7869.

Mamaev, B.M., Zoological assessment of the stages of natural destruction of wood, *Izv. Akad. Nauk SSSR, Ser. Biol.*, 1960, no. 4, pp. 610–617.

Milcu, A., Partsch, S., Scherber, C., Weisser, W.W., and Scheu, S., Earthworms and legumes control litter decomposition in a plant diversity gradient, *Ecology*, 2008, vol. 89, no. 7, pp. 1872–1882.

Muys, B., Lust, N., and Granval, P.H., Effects of grassland afforestration with different tree species on earthworm communities, litter decomposition and nutrient status, *Soil Biol. Biochem.*, 1992, vol. 24, no. 12, pp. 1459–1466.

Needham, A.E., Components of nitrogenous excreta in the earthworms *Llumbricus terrestris*, L. and *Eisenia foetida* (Savigny), *J. Exp. Biol.*, 1957, vol. 34, no. 4, pp. 425–446.

Noirfalise, A. and Vanesse, R., *Consequenses de la monoculture des conifères pour la conservation des sols et pour le bilan hydrologique*, Bruxelles: Association des Espaces Verts, 1975.

Orlova, M.A., Lukina, N.V., Kamaev, I.O., Smirnov, V.E., and Kravchenko, T.V., Mosaicism of forest biogeocenoses and soil fertility, *Lesovedenie*, 2011, no. 6, pp. 39–48.

Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F., and Cohen, Y., Moose browsing and soil fertility in the boreal forests of Isle Royale National Park, *Ecology*, 1993, vol. 74, no. 2, pp. 467–480.

Perel', T.S., *Rasprostranenie i zakonomernosti raspredeleniya dozhdevykh chervei fauny SSSR* (Distribution and Distribution Patterns of Earthworms of the Fauna of the USSR), Moscow: Nauka, 1979.

Qulehle, F., Hofmeister, J., Cudlin, P., and Hruska, J., The effect of reduced atmospheric deposition on soil solution chemistry at a site subjected to long-term acidification, Nacetin, Czech Republic, *Sci. Total Environ.*, 2006, vol. 370, nos. 2–3, pp. 532–544.

Rapoport, I.B., Seasonal activity of earthworms (Oligochaeta, Lumbricidae) of the subalpine belt of the Central Caucasus, *Izv. Samarsk. Nauchn. Tsentra Ross. Akad. Nauk*, 2011, vol. 13, no. 5, pp. 148–151.

Rapoport I.B., Altitude distribution of earthworms (Oligochaeta, Lumbricidae) in the central part of the North Caucasus, *Zool. Zh.*, 2013, no. 1, pp. 3–10.

Rapoport, I.B., Biotopic distribution of earthworms (Oligochaeta, Lumbricidae) in the Teberda protected area with the highest degree of protection (Arkhyz area, Northwestern Caucasus), in *Sovremennye problemy OOPT i puti ikh resheniya. Materialy mezhreg. nauch.-prakt. konf.* (Current Problems of Protected Areas and Ways to Solve Them, Proc. Int. Sci.-Pract. Conf.), Voronezh: Voronezh. Gos. Univ., 2014, pp. 214–218.

Rapoport, I.B., Fauna and population structure of earthworms (Lumbricidae) in forest communities of the Teberda nature reserve and adjacent territories (North-West Caucasus), in *Problemy pochvennoi zoologii. Materialy XVII Vserossiiskogo soveshchaniya po pochvennoi zoologii, posvyashchennogo 75-letiyu so dnya rozhdeniya chlen-korrespondenta RAN D.A. Krivolutskogo* (Problems of Zoology, Proc. XVII All-Russian Conf. on Soil Zoology Dedicated to the 75th Anniversary of the Birth of the Corresponding Member of the Russian Academy of Sciences D.A. Krivolutskii), 2014a, pp. 176–178.

Rapoport I.B., Fauna, structure of communities, and altitudinal-zonal distribution of earthworms (Oligochaeta, Lumbricidae) in the central part of the Kuban variant of zonation (North-Western Caucasus, Republic of Adygea), *Vestn. Adygeisk. Gos. Univ., Ser. 4: Estestv.-Matem. Tekhn. Nauki*, 2014b, vol. 147, no. 4, pp. 77–84.

Rapoport I.B., Earthworms (Oligochaeta, Lumbricidae) of the buffer zone of the eastern section of the Caucasian reserve (North-Western Caucasus), in *Priroda, nauka, turizm v OOPT. Materialy mezhdunarodnoi yubileinoi nauchnoi konferentsii, posvyashchennoi 20-letiyu Ritsinskogo reliktovogo natsional'nogo parka* (Nature, Science, and Tourism in Protected Areas: Proceeding of the International Jubilee Scientific Conference Dedicated to the 20th Anniversary of the Ritsa Relict National Park), 2016, pp. 155–161.

Rapoport, I.B., Species composition and biotopic distribution of earthworms (Oligochaeta, Lumbricidae) in the middle reaches of the Bol'shaya Laba River (Northwestern Caucasus), in *Gornye ekosistemy i ikh komponenty. Materialy VI Vserossiiskoi konferentsii s mezhdunarodnym uchastiem, posvyashchennoi Godu ekologii v Rossii i 100-letiyu zapovednogo dela v Rossii* (Mountain Ecosystems and Their Components: Proceedings of the VI All-Russian Conference with International Participation Dedicated to the Year of Ecology in Russia and the 100th Anniversary of Nature Reserve Management in Russia), 2017, pp. 109–110.

Rapoport, I.B. and Tsepkova, N.L., Population structure and topical preferences of earthworms (Oligochaeta, Lumbricidae) in the soils of the standard forest formations of the Teberda and Bol'shoi Zelenchuk river basins (Teberda Nature Reserve, Northwestern Caucasus), *Izv. Samarsk.*

Nauchn. Tsentra Ross. Akad. Nauk, 2015, vol. 17, no. 6, pp. 33–39.

Rapoport, I.B. and Tsepkova, N.L., Earthworm populations (Oligochaeta, Lumbricidae) in the basin of the middle reaches of the Bol'shaya Laba River (Northwestern Caucasus, Buffer Zone of Caucasian Nature Reserve), *Biol. Bull. (Moscow)*, 2019, vol. 46, no. 9, pp. 1012–1029.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., et al., Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species, *Ecol. Lett.*, 2005, vol. 8, no. 8, pp. 811–818.

Van Rhee, J.A., Earthworm activities in the breakdown of organic matter in agricultural soils, in *Soil Organisms: Proceedings of the Colloquium on Soil Fauna, Soil Microflora and Their Relationships*, Doeksen, J. and Van Der Drift, J., Eds., Amsterdam: North-Holland Publishing Company, 1963, pp. 55–59.

Römbke, J., Blick, T., and Dorow, W.H.O., *Allolobophoridella eiseni* (Lumbricidae), a truly arboreal earthworm in the temperate region of Central Europe, *Soil Organisms*, 2017, vol. 89, pp. 75–84.

Sariyildiz, T. and Küçük, M., Litter mass loss rates in deciduous and coniferous trees in Artvin, northeast Turkey: relationships with litter quality, microclimate, and soil characteristics, *Turk. J. Agricult. For.*, 2008, vol. 32, no. 6, pp. 547–559.

Satchell, J.E., Lumbricidae, in *Soil Biology*, A. Burges, F. Raw. London: Academic, 1967, pp. 259–322.

Sayad, E., Hosseini, S.M., Hosseini, V., and Salehe-Shooshtari, M.H., Soil macrofauna in relation to soil and leaf litter properties in tree plantations, *J. For. Sci.*, 2012, vol. 58, no. 4, pp. 170–180.

Schelfhout, S., Mertens, J., Verheyen, K., Vesterdal, L., Baeten, L., et al., Tree species identity shapes earthworm communities, *Forests*, 2017, vol. 8, no. 3, pp. 85–105.

Scheu, S., Linkages between tree diversity, in *Soil Fauna and Ecosystem Processes. Forest Diversity and Function: Temperate and Boreal Systems*, Ed. M. Scherer-Lorenzen, C. Köhler, E.-D. Schulze, Ecological Studies, Heidelberg: Springer, 2005, vol. 176. pp. 211–233.

Schmidt, O., Shutenko, G.S., and Keith, A.M., Multiple records confirm presence of *Dendrobaena attemsi* (Oligochaeta: Lumbricidae) in Ireland, *Irish Nat. J.*, 2015, vol. 34, pp. 110–112.

Schonholzer, F., Hahn, D., and Zeyer, J., Origins and fate of fungi and bacteria in the gut of *Lumbricus terrestris* L. studied by image analysis, *FEMS Microbiol. Ecol.*, vol. 28, pp. 235–248.

Schultz, J.C., Hunter, M.D., and Appel, H.M., Antimicrobial activity of polyphenols mediates plant–herbivore interactions, in *Plant Polyphenols*, Boston: Springer, 1992, pp. 621–637.

Shleynis, R.I., Difference in soil formation beneath spruce and oak forests in northwestern USSR, *Soviet Soil Science-USSR*, 19656 no. 3, p. 226.

Spirin, V.A. and Shirokov, A.I., Features of humification of dead wood in undisturbed fir–spruce forests of the Nizhny Novgorod region, *Mikol. Fitopatol.*, 2002, vol. 36, no. 3, pp. 25–31.

Suarez, E.R., Fahey, T.J., Yavitt, J.B., Groffman, P.M., and Bohlen, P.J., Patterns of litter disappearance in a northern hardwood forest invaded by exotic earthworms, *Ecol. Appl.*, 2006, vol. 16, no. 1, pp. 154–165.

Szlavecz, K., Chang, C.H., Bernard, M.J., Pitz, S.L., Xia, L., et al., Litter quality, dispersal and invasion drive earthworm community dynamics and forest soil development, *Oecologia*, 2018, vol. 188, no. 1, pp. 237–250.

Vorobeichik, E.L., Ermakov, A.I., Nesterkova, D.V., Grebennikov, M.E., and Nesterkov, A.V., Restoration of communities of soil mesofauna after the cessation of industrial emissions, in *Materialy XVIII Vserossiiskogo soveshchaniya po pochvennoi zoologii. Problemy pochvennoi zoologii 22–26 oktyabrya 2018* (Proc. XVIII All-Russia Conf. on Soil Zoology: Problems of Soil Zoology, October 22–26, 2018), Moscow: IPEE im. A.N. Severtsova Ross. Akad. Nauk, 2018, p. 54.

Vsevolodova-Perel', T.S., *Dozhdevye chervi fauny Rossii. Kadastr i opredelitel'* (Earthworms of the Russian Fauna. Cadastre and Identification Guide), Moscow: Nauka, 1997.

Wedin, D.A. and Tilman, D., Species effects on nitrogen cycling: a test with perennial grasses, *Oecologia*, 1990, vol. 84, no. 4, pp. 433–441.

World Reference Base for Soil Resources 2014, International Soil Classification System for Naming Soils and Creating Legends for Soil Maps. World Soil Resources Reports/IUSS Working Group, Rome: FAO, 2015, no. 106.

Zaugol'nova L.B., Braslavskaya T.Yu., *Metodicheskie podkhody k ekologicheskoi otsenke lesnogo pokrova v basseine maloi reki* (Methodological Approaches to Environmental Assessment of Forest Cover in the Small River Basin), Moscow: KMK, 2010.

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