



## Distribution of epi-endogeic and endogeic earthworm species (*Oligochaeta: Lumbricidae*) in the forest belt of the Northwest Caucasus

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### Abstract

The distribution of the often dominant in density and biomass epi-endogeic and endogeic earthworm species in forests of the Northwest Caucasus was estimated based on a large array of field data and GIS modeling of modern potential areas. Quantitative accountings of earthworms were conducted annually from 2014 to 2019 in different types of forests: sticky alder forest, small-leaved forests, broadleaf forests (hornbeam and beech forests), coniferous-deciduous forests, dark coniferous forests, and pine forests (792 geographic locations). It is shown that the native species of the Caucasian fauna dominate in the number and biomass from piedmont to high mountain forests. The most widespread species that is found in all types of forests from low to high mountains and makes the main contribution to the biomass of earthworms is the Crimean-Caucasian subendemic *Dendrobaena schmidti*. Peregrine species of epi-endogeic and endogeic earthworms inhabit sticky alder forest, small-leaved, broadleaf and pine forests in which they inhabit together with native species, while not dominating either in numbers or in biomass among other species. Dark coniferous forests are inhabited mainly by the native endogeic species *D. schmidti* and *A. jassyensis*. Maxent modeling shows that the species of the endogeic earthworm group have wider potential areas than epi-endogeic species. The most significant bioclimatic factors that make the greatest contribution to the distribution: amount of precipitation in the driest month, altitude above the sea level, isothermality.

**Key words:** soil, spatial modeling, maxent, potential area, climatic parameters, mountain forests, peregrine species, endemic, native species

### Introduction

The forest ecosystems of the Northwest Caucasus are unique in their floral and faunal composition. Forests are inhabited by endemics of Caucasian and Mediterranean flora and fauna. The fauna earthworm is represented by Crimean-Caucasian subendemics, Mediterranean and East Asian species, and peregrine species—originate from Europe (Rapoport 2014; Rapoport & Tsepikova 2015; Geraskina 2016; Geraskina 2018; Geraskina & Shevchenko, 2019a). Currently, it is suggested that peregrine earthworm species have a competitive advantage over native species, actively penetrate land ecosystems almost around the globe, and suppress endemic fauna (Callaham *et al.* 2016; McCay & Scull 2019). However, research in the forests of the Northwest Caucasus shows that despite the large representation of peregrine earthworms, mountain forests are dominated by species of Caucasian origin. In some forest communities, species with different areas dwell together, occupying common habitats (Geraskina & Shevchenko 2019b). In this regard, the distribution of “Caucasian” and peregrine earthworm species in the mountain forest belt is of great interest. Assessment of potential areas of species in GIS programs allows for a spatial assessment of territories where these endemic species can still be found and where they could have disappeared as a result of any reason, that is, to assess the scale of the reduction of the modern areas, as well as to identify areas on which species can be restored in the future.

In connection with the problem of invasive species, using the analysis of maps of potential areas, it is possible to predict further changes in the ranges of native and peregrine species.

Among the functional groups of earthworms in the forests of the Northwest Caucasus, epi-endogeic and endogeic

worms make the largest contribution to biomass (Geraskina 2016; Rapoport & Tsepkova 2019). The ecological role of these groups is to process litter (epi-endogeic worms), humify, and mellow the upper soil levels (both groups). The faunal composition of these groups is represented by species with different areas.

The work objective of this study is to estimate the distribution and confinement of epi-endogeic and endogeic earthworm species to different types of forests based on field data and GIS modeling. The main task of this study is to assess the influence of climatic and altitude factors on the potential range of species, the contribution of each factor to the areal.

## Materials and methods

### Study area

The material was collected during expeditions in the spring and summer seasons from 2014 to 2019 in the territory of the Northwest Caucasus (Krasnodar Territory, the Republic of Adygea and the Karachayevo-Circassian Republic). The research was carried out in the forest belt at altitudes from 42 to 1965 meters above sea level. The climate of the district is moderate and humid: the average annual temperature is 7.7–11.1 °C above zero, the average temperature in January is 4–5 °C below zero, and in July and August—about 15 °C above zero; the annual precipitation varies from 500 to 3.000 mm.

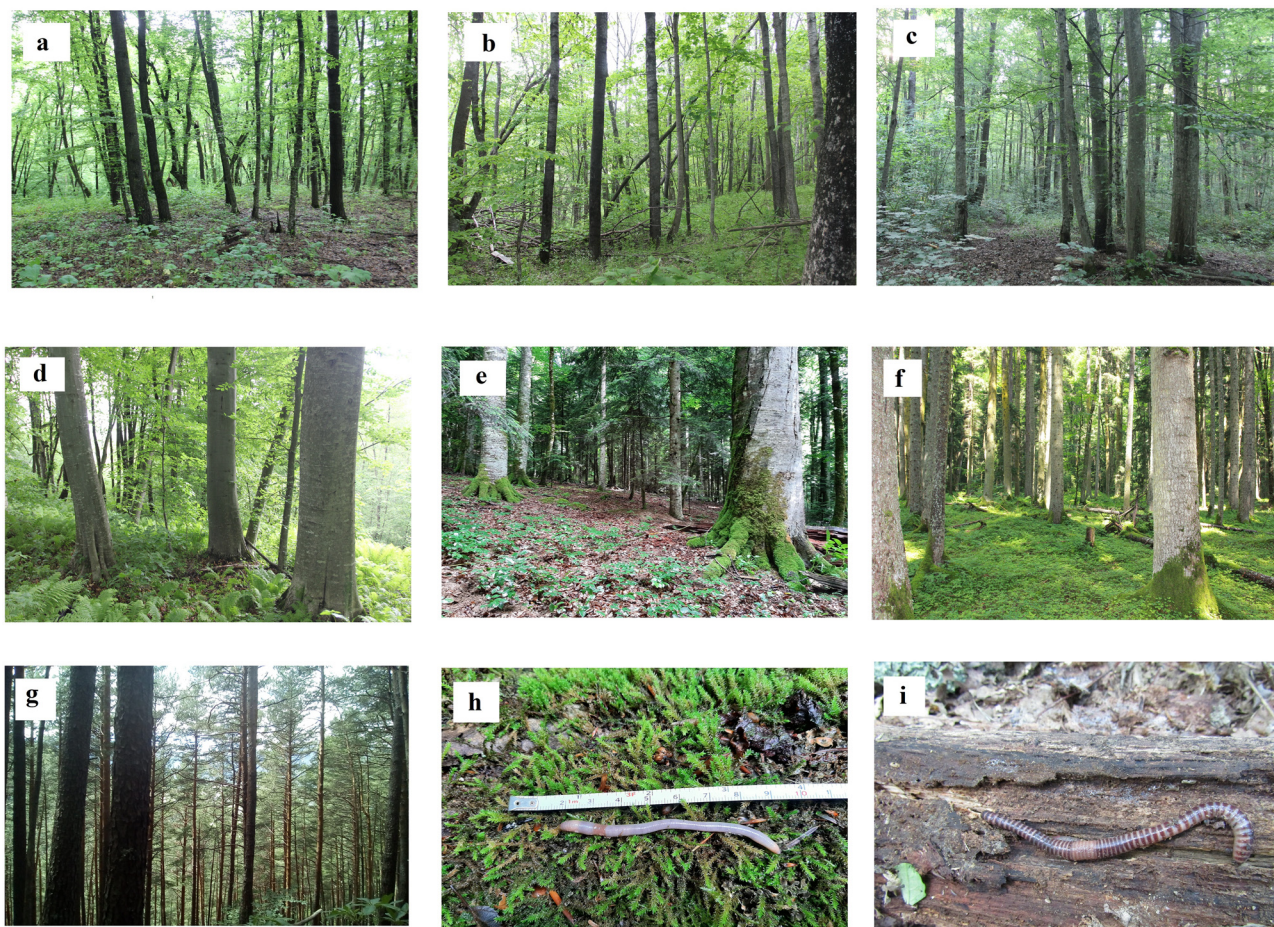
On the routes from the lower border of forests to the upper were investigated: sticky alder forest (forests dominated by *Alnus glutinosa*), small-leaved forests (forests dominated by *Betula pendula* and *Populus tremula*), beech forests (forests with a predominance of *Fagus orientalis*, the forest crop may also include *Carpinus betulus*, *Acer platanoides*, *P. tremula*), hornbeam forests (forests with a predominance of *C. betulus*, the forest crop may also include single *Betula pendula*, *Quercus* sp., *P. tremula*), dark coniferous forests (dominants: *Picea orientalis*, *Abies nordmanniana*), coniferous-deciduous forests (the forest crop most often includes *F. orientalis*, *Carpinus betulus*, *Quercus* sp., *Acer* sp., ash, *Picea orientalis*, *Abies nordmanniana*, less often *Cerasus avium*, *Tilia begoniifolia*, This indicates that earthworms, as typical representatives of the soil habitat, have little effect on air *baccata*) and pine forests (forests dominated by *Pinus sylvestris*) (Fig. 1; Tab. 1). A total of 792 geographical locations were surveyed (the distance between the locations was at least 200 m). The soils are mostly brown or gray forest, with medium- and light-loam in particle-size distribution (in sticky alder forest, heavy-loam with signs of gleyzation) (World Reference Base... 2015).

**TABLE 1.** Main characteristics of the Northwest Caucasus forests

Forest type	Number of geographical locations (n1)	Number of soil samples (n2)	Number of deadwood samples (n3)	litter deepness, cm	soil moisture, %	soil pH
Sticky alder forests (large fern and tall herb cover)	19	76	8	2-8	45±3	6.0±0.5
Small-leaved forests (nemoral small herb cover)	42	168	20	1-4	35±5	5.9±0.3
Hornbeam forests (small herb cover, motley grass)	156	608	102	1-3	35±2	5.8±0.6
Beech forests (dead-cover, small herb and large fern cover)	310	680	185	2-8	30±5	5.6±0.2
Coniferous-broadleaf forests (nemoral and boreal small herb cover, dead-cover)	147	588	90	2-4	25±5	5.5±0.1
Dark coniferous forests (boreal small herb cover and green moss cover)	88	352	36	2-6	20±6	5.5±0.4
Pine forests (small herb and rhododendron)	30	120	12	1-5	15±4	5.7±0.3



Most of the surveyed forests belong to forests of high naturalness. There are no traces of felling and fires in them (Shevchenko & Geraskina 2019). Often closer to human habitation, there were sticky alder forest and small-leaved forests. Sometimes there was grazing near the forests.



**FIGURE 1.** Forest types and earthworm habitats of the North-Western Caucasus.

**Note:** a—sticky alder forest; b—small-leaved forest; c—hornbeam forest; d—beech forest; e—coniferous-broadleaf forest; f—dark coniferous forest; g—pine forest; h—*D. schmidtii* (endogeic form); i—*D. veneta* in deadwood.

### 1.1. Species and biogeographical date

For earthworm accountings, 2–4 soil samples were taken at each location (the size of one sample: 25×25 cm<sup>2</sup>, depth 30 cm. A total of 2.592 soil samples were surveyed. Humidity and acidity were measured for each soil sample using a portable pH 300 field indicator (Tab. 1). In addition, earthworm accountings in deadwood were conducted. The earthworms were counted separately in the trunks of the fallen trees with the deadwood fragments at decomposition stages 2, 3, and 4 (Spirin & Shirokov, 2002). Analysis of the deadwood at decomposition stage 2 was conducted in nonhumified trunks that retained mechanical strength; the complete analysis was made for decomposition stages 3 and 4. Fallen trunks were dismantled at each location where there was deadwood (on the site 20 x 20 m where the geobotanical description was carried out). Several pieces of deadwood were randomly selected in these locations. The diameter and length of the trunk fragment were measured; to compare deadwood earthworm data to those from standard earthworm soil sampling, the results were calculated per surface area (Ashwood *et al.* 2019). The calculation used the area of the lateral surface of the cylinder:  $S = 2 \pi R h$  (Geraskina & Shevchenko 2019b). A total of 453 deadwood samples were surveyed in 360 location (Tab. 1).

Earthworms were preserved in 96% ethanol. The species composition was defined using by key of earthworm Russian fauna (Vsevolodova-Perel 1997) and addition to the fauna of earthworms of the Caucasus (Vsevolodova-Perel 2003); diagnoses were clarified following the keys of earthworms of Turkey (Omodeo & Rota 1989, 1991). More information on the areas is given following the checklist of the earthworm fauna of Turkey (Csuzdi *et al.* 2006)

and the combined checklist of earthworms of the Northeastern Mediterranean region (Szederjesi 2017). Ecological groups of earthworms are given according to the classification M. Bouche (1977) with additions for earthworms of Russia according to T.S. Perel (1979), due to the fact that some species cannot be strictly assigned to one category Marcel Bouché's triangle. This applies to species *Lumbricus rubellus* Hoffmeister 1843 and *Eisenia fetida* (Savigny 1826), which, according to the Russian classification, belong to the epi-endogeic group of earthworms (according to the classification M. Bouché they are belong to the epigeic group). The species *Allolobophora chlorotica* (Savigny 1826) in this research, as in most reports, is assigned to the endogeic group (according to the classification M. Bouché this species was given an intermediate position).

This paper presents materials only two groups of earthworms: epi-endogeic and endogeic. The study of forests also found epigeic group of earthworms, a report on their distribution was provided earlier (Geraskina & Shevchenko 2019a) and anecic worms (only one species *Dendrobaena mariupoliensis* (Wyssozky, 1898) unpublished data).

The maps of the potential habitats of earthworms were created with the Maxent 3.3.3k software (<http://www.cs.princeton.edu/~schapire/maxent/>). With the help of the color gradations, the obtained maps indicate the level of probability of finding a species at a particular point and determine the degree of influence of the environmental parameters (in %) on the boundaries of their distribution, that is, the contribution of each factor to the model construction. The resulting color image shows the assumed probability that the search conditions are suitable: red and orange indicate a high probability of suitable conditions for the species; green - conditions similar to those in which the species is located. The maximum entropy method was used to determine the potential area of the model tree species. The quality of the models has been estimated by the AUC (area under the curve) values—the area under the ROC curve representing the proportion of true and false positively classified cases (Fawcett 2006) and the omission rate characterizing false-negative cases (error of the second kind). The model quality is rated as excellent with the AUC values of 0.9–1.0; good with the 0.8–0.9 values (we only used this level); very bad—if less than 0.6; the model accuracy corresponds to a random choice at 0.5 (Phillips *et al.* 2008). The visualization of the obtained GIS maps was conducted with the DIVA-GIS 7.5.0 software ([www.diva-gis.org](http://www.diva-gis.org)) (Scheldeman & Zonnevels 2010).

8 most significant layers for this territory from the WorldClim climate base ([www.worldclim.org](http://www.worldclim.org)) were used in the modeling (minimum resolution—5 arc-minutes or ~9 km per pixel) which allow for the interpolation of the observed data from the years of 1950 to 2000. This method was used earlier to create maps of potential habitats of epigeic earthworms in the Northwest Caucasus (Geraskina & Shevchenko 2019b). Maps of potential habitats have been created only for species that were found in more than 30 different geographical locations. No algorithm predicted consistently well with small sample size ( $n < 30$ ) and this should encourage highly conservative use of predictions based on small sample size and restrict their use to exploratory modeling (Wisz *et al.* 2008).

## 1.2 Statistical methods

Statistical data processing was carried out using MS Excel 2019 and Statistica 6.0 software packages. Parameters found during calculations: mean ( $\bar{X}$ ), standard error of mean (SE), median (M), quartiles (Q1, Q3). The Spearman's rank correlation coefficient ( $r_s$ ) was used to calculate the relationship between the number of earthworms and soil moisture.

## Results

### Distribution of earthworms in different types of forests (field data results)

#### Epi-endogeic earthworm group

From the group of epi-endogeic species, the forests of the Northwest Caucasus are inhabited by four species: the Crimean-Caucasian subendemic *Dendrobaena schmidtii* (Michaelsen 1907); the Mediterranean species *Dendrobaena veneta* (Rosa 1886), which has now spread more widely due to its active use in vermiculture, therefore, it is sometimes referred to as widely introduced peregrine species (Csuzdi & Zicsi 2003; Csuzdi *et al.* 2006) and peregrine *E. fetida* and *L. rubellus*.

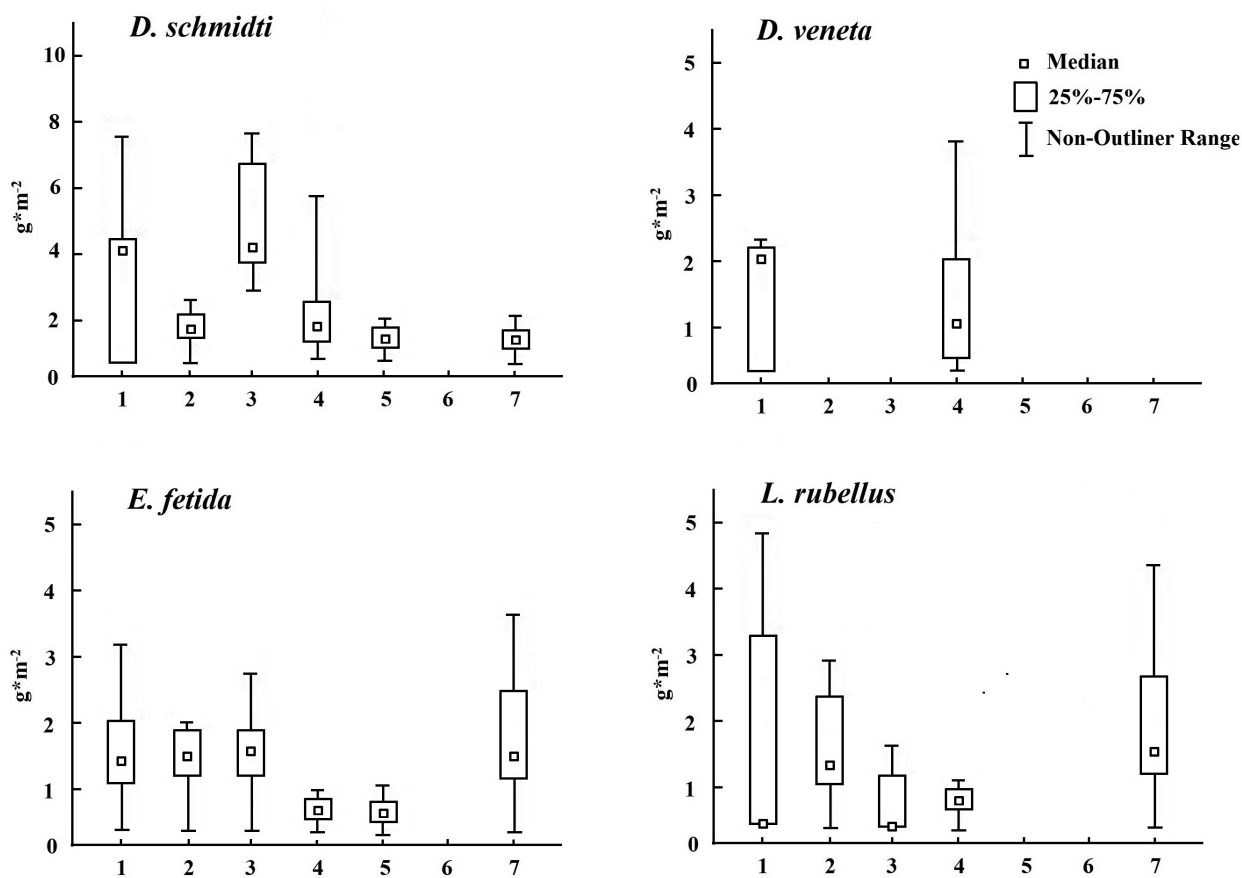


**TABLE 2.** Percentage contribution of bioclimatic indicators to the potential area of earthworm species.

Climatic layers: 1—altitude above the sea level; 2—isothermality (average annual temperature / average daily temperature range for each month) \* 100; 3—standard deviation of temperatures; 4—annual amplitude temperature (maximum temperature of the warmest month - minimum temperature of the coldest month of the year); 5—average temperature in the wettest quarter; 6—average temperature in the driest quarter; 7—amount of precipitation per year; 8—amount of precipitation in the driest month.

Species of earthworms	Functional group	Number of locations	Climatic layers							
			1	2	3	4	5	6	7	8
<i>Dendrobaena schmidti</i>	epi-endogeic	105	19.9	14.5	9.8	2.6	0	7.8	0.8	44.6
<i>Dendrobaena tellermanica</i>	epi-endogeic	59	19.4	11	7.5	3.0	1.8	11.9	1.1	44.3
<i>Aporrectodea jassensis</i>	endogeic	349	12.7	18.2	9.4	7.5	0.4	6.9	3.3	41.6
<i>Dendrobaena schmidti</i>	endogeic	575	10.5	15.6	8.3	12.5	1.8	2.8	6.8	41.7

*D. schmidti* is a polymorphic species, represented in the Caucasus by three forms: small pigmented—epigeic form; medium-sized earthworms with a pigmented cephalic—epi-endogeic form; medium-sized, non-pigmented earthworms—endogeic form (Rapoport 2009; Shekhovtsov *et al.* 2020). In this research, among the group of epi-endogeic species, *D. schmidti* is the most widespread representative of this group (found in 105 geographical locations (hereinafter referred to as g.l.). It is found in all types of forests except dark coniferous forests. The largest number and biomass of the *D. schmidti* epi-endogeic form were observed in forests with moderate soil moisture: small-leaved, hornbeam, and beech forests. Species also inhabit waterlogged sticky alder forest and dry pine forests (Fig. 2; Tab. 3). The correlation rate with humidity ( $r_s$ ) of this form is 0.65.



**FIGURE 2.** Biomass of epi-endogeic earthworm in different forest types.

**Note:** 1—sticky alder forests; 2—small-leaved forests; 3—hornbeam forests; 4—beech forests; 5—coniferous-broadleaf forests; 6—dark coniferous forests; 7—pine forests.

**TABLE 3.** Density (ind./m<sup>2</sup>±SE) epi-endogeic and endogeic earthworm in soil of different forest types of the Northwest Caucasus.

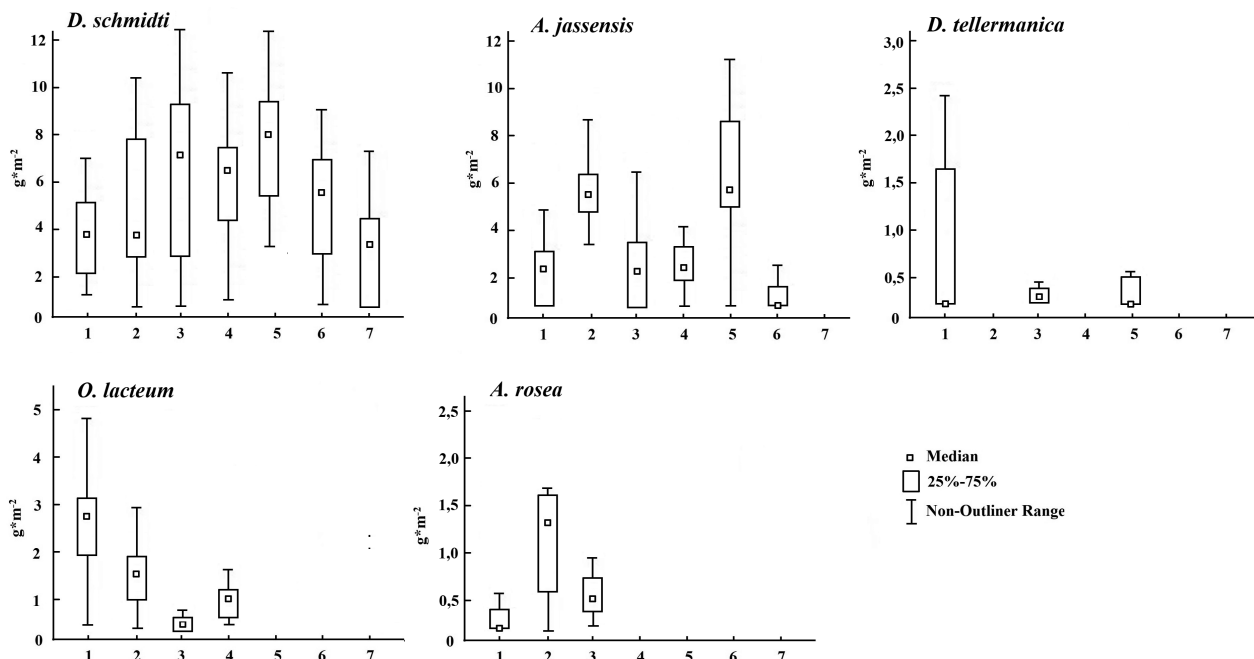
		Forest type	1	2	3	4	5	6	7
Epi-endogeic group	<i>D. schmidti</i>		2.9±1.7	9.8±6.3	7.0±6.8	1.9±1.8	1.1±3.7	0	1.9±1.7
	<i>D. veneta</i>		1.7±0.8	0	0	0.6±0.5	0	0	0
	<i>E. fetida</i>		2.1±0.8	1.0±0.5	0.63±0.7	0.2±0.1	0.2±0.9	0	1.7±2.5
	<i>L. rubellus</i>		1.1±0.9	0.6±0.4	0.9±0.6	0.1±0.05	0	0	0.5±0.1
Endogeic group	<i>D. schmidti</i>		14.5±6.4	27.3±12.4	24.4±9.8	10.9±6.8	22.7±9.3	18.6±8.7	11.3±5.7
	<i>A. jassyensis</i>		3.6±2.5	7.7±5.8	11.4±6.7	5.2±4.8	11.7±9.6	2.6±1.3	0
	<i>D. tellermanica</i>		0.2±0.5	0	0.5±0.3	0	1.8±0.7	0	0
	<i>O. lacteum</i>		5.7±4.8	1.9±0.8	0.2±1.5	0.3±0.5	0	0	0
	<i>A. rosea</i>		0.6±0.4	0.8±0.6	0.2±0.2	0	0	0	0
	<i>A. caliginosa</i>		0.5±0.2	1.5±0.7	0	0	0	0	0
	<i>A. chlorotica</i>		0	0	0.2±2.5	0	0	0	0

**Note:** Legend 1–7 as at Figure 2. Legend 1–7 as at Figure 2.

*D. veneta* (g.l. = 13) is found in sticky alder forest and broadleaf forests. The number and biomass of this species are low (Fig. 2; Tab. 3). In addition to soil samples, this species was found when examining deadwood under the bark of deciduous trees (alder, hornbeam, beech). The correlation rate with humidity ( $r_s$ ) of this species is 0.71.

*E. fetida* (g.l. = 29) is found in small-leaved, hornbeam, beech, broadleaf, coniferous-broadleaf forests, and pine forests. The number and biomass of this species are low (Fig. 2; Tab. 3). The correlation rate with humidity ( $r_s$ ) in *E. fetida* is 0.61. As *D. veneta*, this species is often found in deadwood of deciduous trees.

*L. rubellus* (g.l. = 15) lives in areas from piedmont to high mountain forests; the largest biomass of this species is observed in sticky alder forest, broadleaf, and beech forests. The species is also found in pine forests. The species is not found in coniferous-broadleaf and dark coniferous forests (Fig. 2; Tab. 3). The correlation rate with humidity ( $r_s$ ) is 0.82.



**FIGURE 3.** Biomass of endogeic earthworms in different forest types.

**Note:** Legend 1–7 as at Figure 2.

## Endogeic earthworm group

Seven species were found from the endogeic species group in the Northwest Caucasus forests. Among them are three species of Caucasian origin (Omodeo 1952): *D. schmidtii* endogeic form, *Aporrectodea jassyensis* (Michaelsen 1891) East-Mediterranean species, *Dendrobaena tellermanica* Perel 1966 Caucasian-Anatolian species, which is also found in the Crimea, Kazakhstan, Central Russian Upland, South Urals, and Altai (Vsevolodova-Perel, 2003) and four peregrine species: *Octolasion lacteum* (Örley 1885), *Aporrectodea rosea* (Savigny 1826), *Aporrectodea caliginosa* (Savigny 1826), *A. chlorotica*.

The endogeic form of *D. schmidtii* (g.l. = 575) inhabits all types of forests (Fig. 3; Tab. 3), dominates in the number and biomass by at least 2 times over other earthworm species. The high number and biomass of the endogeic form of *D. schmidtii* are also observed in dark coniferous forests, where other species are often absent (Fig. 2, 3). The correlation rate with humidity ( $r_s$ ) is 0.59.

*A. jassyensis* (g.l. = 349) is found in all types of forests except pine forests (Fig. 3; Tab. 3). The low number and biomass of this species in sticky alder forest and dark coniferous forests are observed. The correlation rate with humidity ( $r_s$ ) is 0.66.

*D. tellermanica* (g.l. = 59) is found in three types of forests: sticky alder, hornbeam, and beech forests. Its number and biomass in these forests are low (Fig. 3; Tab. 3). The correlation rate with humidity ( $r_s$ ) is 0.88.

*O. lacteum* (g.l. = 29) lives from piedmont to mid-mountain forests; the largest number and biomass of this species were found in waterlogged sticky alder forest; the species is found singly in small-leaved, hornbeam, and beech forests. It was not found in pine forests and dark coniferous forests (Fig. 3; Tab. 3). The correlation rate with humidity ( $r_s$ ) is 0.92.

*A. rosea* (g.l. = 15) is confined to sticky alder forest, small-leaved, and hornbeam forests but was not found in other types of forests (Fig. 3; Tab. 3). It most often inhabits forests near villages where livestock grazing takes place.

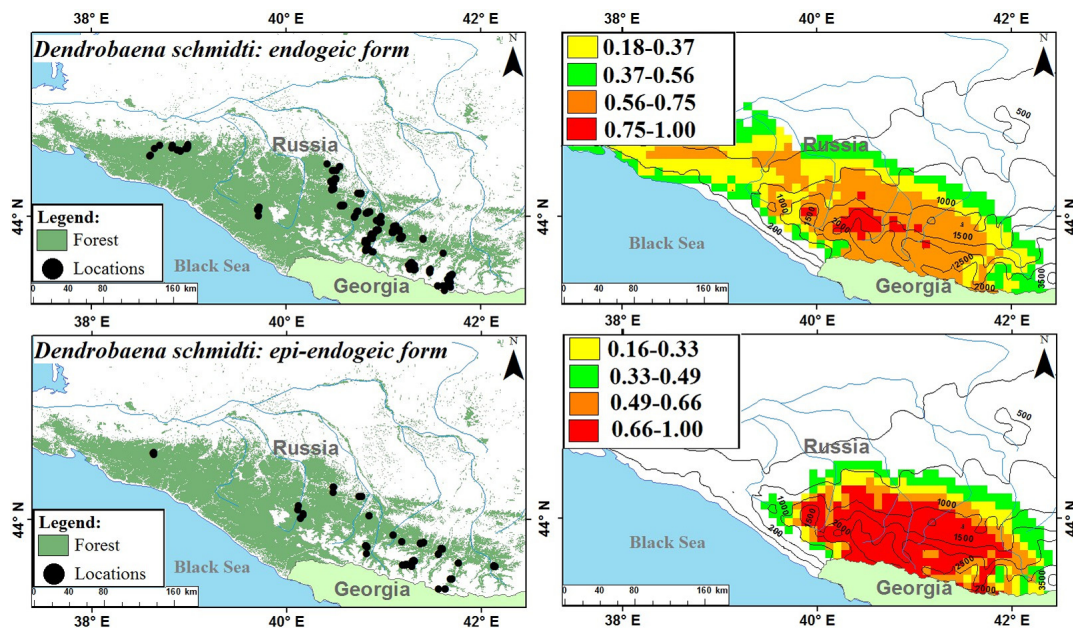
*A. caliginosa* (g.l. = 11) is found mainly in small-leaved forests in the Karachayevo-Circassian Republic in the Teberda Nature Reserve in the valleys of the Bolshaya Khatipara and Khadjibey Rivers, near cattle pastures, as well as in the Bolshoy Zelenchuk River valley, where bison grazing is observed.

*A. chlorotica* (g.l. = 3) is found in the Krasnodar Territory (the valley of the Khodz River) and the Karachayevo-Circassian Republic (the valley of the Bolshaya Laba River) in broadleaf forests with a predominance of beech (beech-oak-hazel-herb) and (hornbeam-beech with small herb cover). A total of 6 individuals of this species were found.

## Modeling of potential modern areas of earthworms

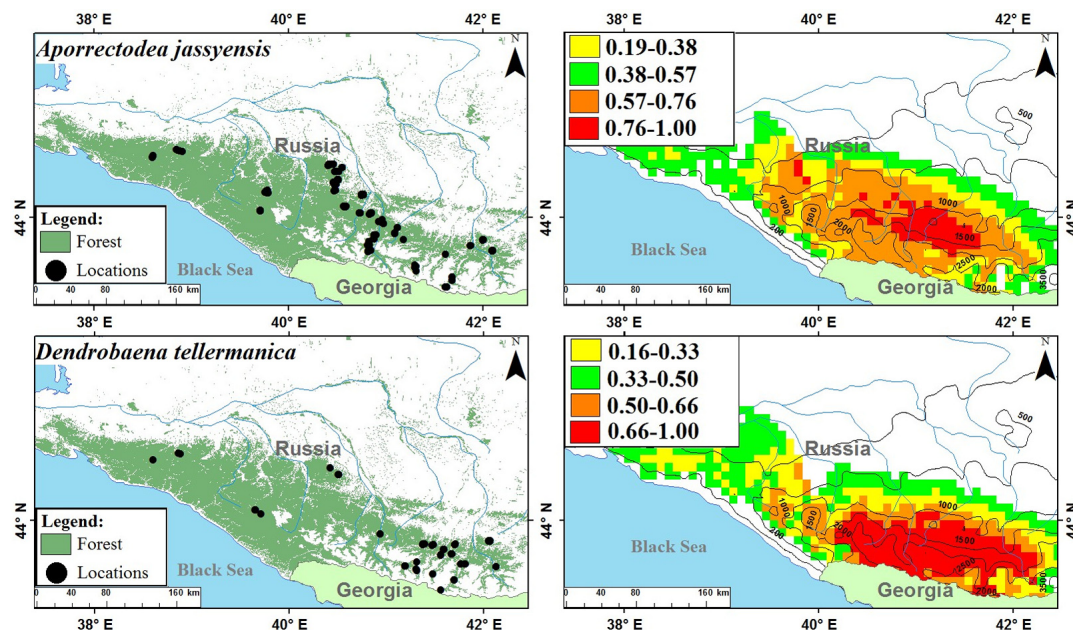
The results of spatial modeling of the potential areas of two most common forms of *D. schmidtii* show that the endogeic form in comparison with the epi-endogeic one is characterized by a much wider potential area, which includes in addition to mid-mountain and high mountain forests (probability level > 75%), also low mountain and lowland piedmont territories (probability level—37–75%). The potential area of the epi-endogeic form covers mainly mid-mountain and high mountain forests (probability level > 49%) (Fig. 4). The analysis of the contribution of bioclimatic indicators shows that for the epi-endogeic form of *D. schmidtii*, the value of the altitude above sea level is a more significant indicator (19.9%) than for the endogeic form (10.5%). However, the amount of precipitation in the driest month of the year (41.7–44.6%) was the most significant indicator for two forms of *D. schmidtii*. The indicator isothermality makes approximately the same contribution to the potential areas of the two forms of *D. schmidtii*. The indicator of the annual temperature amplitude is more significant for the endogeic form of *D. schmidtii*, the indicator of the average temperature of the driest quarter of the year—for the epi-endogeic form. Other bioclimatic indicators make approximately the same and not so significant contribution to the modeling of the areas of these two forms (Tab. 2).

The potential area of *A. jassyensis* covers low and mid-mountain forests (probability level > 57%); the species can also live in piedmont areas (probability level—38–57%). Among the bioclimatic indicators, the largest contribution to the modeling of the potential area of this species is made by the amount of precipitation in the driest month of the year (41.6%), much lower—by the isothermality indicator (18.2%) and the altitude above sea level (12.7%). The contribution of other indicators is less than 10% (Tab. 2).



**FIGURE 4.** Known locations of presence and potential distributions of endogeic and epi-endogeic form *D. schmidti* in North-Western Caucasus.

**Note:** The left column shows the maps of the location points (Locations) of the model species in the current forest borders (Forest), on the right—the potential area of model species and the contour isolines. The level of probability of finding a species at a specific point is indicated by the gradation of colors and shades.



**FIGURE 5.** Known locations of presence and potential distributions of *A. jassyensis*, *D. tellermanica*, in North-Western Caucasus.

**Note:** Legend as at Figure 4.

The potential area of *D. tellermanica* covers medium and high mountain forests (probability level > 66%) and low mountain forests (probability level—50–66%) (Fig. 5). Among the bioclimatic indicators, the largest contribution to the modeling of the potential area of this species is made by the amount of precipitation in the driest month of the year (44.3%), the altitude above sea level (19.4%), and the average temperature of the coldest quarter of the year (11.9%) (Tab. 2).



## Discussion

### Distribution of epi-endogeic and endogeic groups of earthworms in different types of forests

The distribution of epi-endogeic and endogeic earthworm species across different types of forests shows that the number and biomass of endogeic species in the group are significantly higher in all studied types of forests compared to epi-endogeic species. Epi-endogeic earthworms were not found in dark coniferous forests, but these forests are inhabited by particular representatives of the endogeic group (*D. schmidti* and *A. jassyensis*); at the same time, the *D. schmidti* biomass can be high (Fig. 3). The differences in the confinedness of two groups under discussion to different types of forests are primarily due to the quality of plant litter and soil properties. The very properties of leaf litter and soil are currently considered as the main drivers of the spread of earthworms in forests (De Wandeler *et al.* 2016). Soil acidity in all types of forests is within the limits favorable for earthworms and does not limit their habitation in the studied types of forests (Tab. 1). The optimal acidity for the active life of most earthworm species ranges from pH 5.5 to the values close to neutral (Perel 1979; Hirth *et al.* 2009; Moore *et al.* 2013). Endogeic groups of earthworms are represented in all types of forests since they are less dependent on the quality of leaf litter because they decompose the already well-processed plant residues along with the soil during their vital activity. At the same time, earthworms of epi-endogeic groups are active in the litter layer and process poorly decomposed plant litter (Bouche 1977; Perel 1979). In dark coniferous forests, spruce and fir dead-cover with a high content of polyphenols, lignin, and tannins is difficult to access for most soil saprophages (Lavelle *et al.* 1993; Schwarz *et al.* 2015). Both groups of earthworms are well represented in the sticky alder forest, small-leaved, and hornbeam forests. These forests are characterized by good soil moisture (sticky alder forest is sometimes waterlogged, but since earthworms are generally moisture-loving, this does not limit their vital activity) and, in addition, the dead-cover of deciduous tree species serves as a favorable trophic resource. The species diversity of earthworms in beech forests is lower than in other leaf forests, but the hard-to-decompose beech dead-cover creates a deep litter that persists during the summer season and serves as a favorable habitat for epi-endogeic species to a greater extent, the biomass of which in these forests is higher than that of endogeic species. It is known that even in dead-cover of beech forests, the number and biomass of earthworms can be high (Geraskina 2016; Rapoport *et al.* 2017).

The endogeic species dominate in coniferous-broadleaf forests numerically, but epi-endogeic species, which in addition to the soil also inhabit deadwood of deciduous species of trees (oak, maple, hornbeam, linden) of late decomposition stages, are also widely represented. In general, the presence of mixed plant litter in forests is more favorable trophically and topically for earthworms than the leaf litter of a single tree species (Sariyildiz 2008; Sariyildiz & Küçük 2008). Coniferous-broadleaf forests proved to be more favorable than other types of forest also to epigeic species—*D. octaedra* and *D. attemsi* (Geraskina & Shevchenko, 2019b) and anecic species—*D. mariupoliensis* (unpublished data).

Pine forests are characterized by dry soils and a large fraction of hard-to-decompose pine litter. In these forests, epi-endogeic earthworms (epi-endogeic forms of *D. schmidti*, *L. rubellus*, *E. fetida*) are singly represented, the endogeic form is represented with *D. schmidti* only (endogeic form). Their biomass is low, which is generally typical for pine forests (Taylor *et al.* 2019; Geraskina 2020).

### Distribution peregrine and native of earthworm species

The distribution of earthworm species with different areas within the mountain forest belt shows that both peregrine and native species live together in some forests. Native species predominate in all types of forests in terms of number and biomass. Peregrine earthworm species of the epi-endogeic group—*E. fetida* and *L. rubellus* are found from piedmont sticky alder forest to high mountain pine forests but their biomass is 3–5 times lower than that of the most widespread Crimean-Caucasian subendemic *D. schmidti*. Peregrine species of the endogeic group—*O. lacteum*, *A. rosea*, and *A. caliginosa* mainly inhabit piedmont and low-mountain forests and are also often confined to cattle grazing places. *A. caliginosa* is massively encountered in the Karachayevo-Circassian Republic in the Teberda Nature Reserve in the valleys of the Bolshaya Khatipara and Khadjibey Rivers in small-leaved forests near livestock pastures (Geraskina 2016) and in the forests of the Bolshoy Zelenchuk River valley where free-living bisons were observed (Geraskina & Shevchenko 2019a). In addition, these species widely inhabit high mountain pastures (Geraskina 2016) and meadows of the Caucasus (Rapoport *et al.* 2017).

Many papers claiming that the worldwide distribution of peregrine earthworm species often reduces native species densities due to their competitive advantage (Winsome *et al.* 2006; Didham *et al.* 2007; Callaham *et al.* 2016; McCay & Scull 2019). At the same time, there is evidence that peregrine species do not affect native earthworm species (Gonzalez *et al.* 2006; Golovanova *et al.* 2018) and contribute to the sustainable functioning of local species by enhancing digging activities and improving habitat (Baker *et al.* 2002). Often, competitive relationships between peregrine and native earthworm species are currently observed in pastures and meadows where livestock is grazing (Winsome *et al.* 2006); there are many examples of the competitive relationship between peregrine and native earthworm species and in the forests, especially in North America (Hendrix & Bohlen 2002; Migge-Kleian *et al.* 2006; Hendrix *et al.* 2008; Ferlian *et al.* 2018). At the same time, there is an assumption that peregrine earthworm species can occupy free ecological niches in forests (Hale *et al.* 2005, 2006). In some cases where invasions have occurred, native species have remained dominant over exotic species (Hendrix & Bohlen 2002;). For example, in deciduous forests in Kentucky, only native earthworms occur in undisturbed or slightly disturbed sites, whereas exotic species occur only in severely disturbed sites (Kalisz & Dotson 1989). We find a similar distribution in forests of the Northwest Caucasus. In the best-preserved forest (broadleaf forests, coniferous-deciduous forests, dark coniferous forests) peregrine species are few in number, or completely absent; these species are massively found only near anthropogenic territories, and in forests where livestock grazing occurs nearby. We believe that absence disturbance in forest (without felling and fires), good quality of litter, variety of ecological niches in forest ecosystems (including the presence of additional favorable habitats, especially dead wood) combined with a favorable set of climatic factors are of great importance for the stability of populations native earthworm species.

## Modeling of potential modern areas of earthworms

The results of spatial modeling show that the potential areas of some earthworm species, as a rule, are wider than the current real ranges and cover large territories not only in the mountain forest belt. The excess of the potential range of earthworms of the boundaries of modern forests is associated with the history of nature management and the reduction in the area of modern forests in the Northwest Caucasus as a result of anthropogenic impact, which is confirmed by historical and geographical data. Over the past 200 years, the forest area of the Northwest Caucasus has decreased by about 1/3 as a result of anthropogenic impact (Shevchenko & Geraskina, 2019).

The largest contribution to modeling potential areas for most earthworm species is made by the amount of precipitation in the driest month. Since humidity is the main limiting factor for earthworms, a significant decrease in the number of earthworms occurs during the summer season when soil moisture decreases (Singh *et al.* 2020). In forest ecosystems, part of the population survives, which is preserved in wet habitats—deadwood, depressions, and hollows (Ashwood *et al.* 2019). Another indicator that contributes to the distribution of earthworms is the altitude above the sea level (alt). This indicator was much more significant for representatives of the epi-endogeic group than for the endogeic group. Since altitude is related to the amount of precipitation and determines the types of forests, epi-endogeic species (as more moisture-loving and directly dependent on the litter quality) are more dependent on this indicator than endogeic.

The indicator standard deviation of temperatures and the average temperature in the wettest quarter (for this region this is the summer season) were not significant for earthworms. This indicates that air temperature fluctuations in forest communities during the season have little effect on earthworms, as typical representatives of the soil habitat. At the same time, the isothermality indicator was significant for the majority of the studied species, since it reflects the average annual temperature amplitude, and in the season of negative temperatures, earthworms as poikilothermic organisms are not active and in a state of winter diapause.

Based on the contribution of bioclimatic indicators, the created maps of potential areas show that most of the discussed species can inhabit a vast territory from lowland to high mountain areas. Most species are confined to the coniferous-broadleaf forests belt. A narrower area is shown for the epi-endogeic form of the Crimean-Caucasian subendemic *D. schmidtii*, an area that includes only mountain forests and does not cover lowland territories, in contrast to the endogeic form of *D. schmidtii*, which is more widely found in field studies and an area of which covers larger territories than the mountain forest belt.

Thus, it is shown that in the mountain forest belt of the Northwest Caucasus, peregrine and native species inhabitant together, with the latter dominating in biomass and number in different types of forests from piedmont

to high mountain areas. Peregrine fauna of earthworms is more confined to deciduous forests on hydromorphic soils, as well as to soils associated with cattle grazing. Maxent modeling shows that most endogeic species of earthworms have wider potential areas than epi-endogeic species, and their areas include not only the territories of the mountain forest belt but also piedmont and lowland areas. The excess of the potential range of native species of earthworms in the modern forests of the Northwest Caucasus confirms that the area of modern forests in this region was be larger if it were not for anthropogenic impact. The most significant bioclimatic factors that make the greatest contribution to the distribution of earthworms: amount of precipitation in the driest month, altitude above the sea level, isothermality.

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