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## Spatial distribution of the epigeic species of earthworms *Dendrobaena octaedra* and *D. attemsi* (Oligochaeta: Lumbricidae) in the forest belt of the northwestern Caucasus

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**Abstract:** Evaluation of the spatial distribution of 2 ecologically similar, but different, in terms of their spatial ranges, earthworm species, *D. octaedra* and *D. attemsi*, in the belt forests of northwestern Caucasus were based on our own natural data and using geographic information system (GIS) modeling of modern potential distributions. The quantitative records of earthworms were collected in beech, deciduous, dark coniferous, coniferous-deciduous, and pine forests (1028 geographic locations). Of the most important microsites inhabited by the epigeic earthworms, 2 (plant litter and deadwood) were examined. It was demonstrated that there was high correlation of the 2 species with the humidity of the habitat and the presence of deadwood at different stages of decomposition, especially for *D. attemsi*, which lives mainly in deadwood in all of the forest types. The high correlation of these species to coniferous-deciduous forests and dark coniferous forests was demonstrated on both the basis of the field data analysis and the GIS modeling results.

**Key words:** Soil fauna, plant litter, microsite, deadwood, spatial modeling, potential distribution, climatic parameters

### 1. Introduction

Potential species distribution modeling methods and identification of the most significant factors for the soil invertebrate spreading limitation (Crawford and Hoagland, 2010; Marek et al., 2012) have been increasingly used in modern soil zoology studies. Despite reasonable approaches to the geographic information system (GIS) modeling method application for species distribution evaluation (including Maxent software), the number of similar studies for soil invertebrates is currently small, since the labor-intensive soil- and zoology-related methods of material collection limit the number of places for finding species (Smith et al., 2008). Application of the GIS modeling method with Maxent software for earthworm potential distribution has been demonstrated in a small number of studies (Marchan et al., 2015, 2016; Latif, 2017; Hughes et al., 2018). Nowadays, earthworms are increasingly attracting the attention of researchers, not only as key species of soil invertebrates that regulate soil fertility, but also as a group capable of rapid invasion in different geographic areas. As a rule, the first effects of earthworm invasion lead to a decrease in plant litter stocks in forests, which, on the one hand, locally reduces biomass and changes the spatial distribution of other epigeic invertebrates (Eisenhauer et al., 2007; Ferlian et al., 2018), while on the other hand, contributes to the development

of a number of groups of soil microorganisms and soil microfauna (McLean et al., 2006; Eisenhauer et al., 2007). Epigeic, endogeic, and anecic morphoecological groups differ in their habitats, different soil horizons, and their functional role in the mineralization of organic residues (Bouche, 1977; Eisenhauer, 2010; McLean et al., 2006). Epigeic and anecic worms play the most significant part in plant litter decomposition. As a rule, the epigeic species group is more abundant in immature soils than endogeic worms, which are more often confined to well-developed rich soils (Perel, 1979; Lavelle, 1988).

The mountainous regions of the Caucasus are known to be one of the earthworm species formation centers (Kvavadze, 1985); 22 species of the family Lumbricidae inhabit northwestern Caucasus and the endemic species dominate very often in the forest communities in terms of biomass and abundance (Rapoport and Tsepikova, 2015; Geraskina, 2016a).

*D. octaedra* and *D. attemsi* (small pigmented worms of not more than 70 mm in length, up to 4 mm in width, living in the plant litter horizon) are among the epigeic species of earthworms most often found in northwestern Caucasus (Perel, 1979). The functional role of the epigeic earthworm group is in their primary destruction of the litter (following the leaching or destruction of polyphenolic and other chemically resistant compounds).

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The specific surface of the substrate increases hundreds of times during the grinding of plant material with its increasing availability for microorganisms (Tiunov et al., 1997; Tiunov and Kuznetsova, 2000; Cunha et al., 2016; Zheng et al., 2018). Being confined to the top horizon, epigeic earthworms are the most sensitive to the thickness, humidity, and temperature of the plant litter.

*D. octaedra*, a cosmopolitan species, is able to spread very quickly and, at present, new points of invasions of this species have been noticed (Henshue et al., 2018; Wackett et al., 2018). This earthworm is widely known to be one of the few species (as well as *Dendrodriulus rubidus tenuis*) living in the forest plant litter in northern dark coniferous forests. The natural area of *D. attemsi* includes northern Turkey and Caucasus, southern and central Europe, Ireland, England, and Sweden (the northernmost point of natural distribution), and the Slovakian, Ukrainian, and Rumanian Carpathians (Kvavadze, 1985; Omodeo and Rota, 1989; Rota and Erseus, 1997; Castin-Buchet and Andre, 1998). Finds of this species beyond the boundaries of these territories are currently in the western United States (Fender, 1982, 1985), Kamchatka (Shekhovtsov et al., 2014), Canada (Marshall and Fender, 2007), and Australia (Martinsson et al., 2015). These findings are most likely related to human influence (Rota and Erseus, 1997; Martinsson et al., 2015).

Study objective: evaluation of the spatial distribution of 2 earthworm species, *D. octaedra* and *D. attemsi*, which are

ecologically similar, but different in terms of their ranges in the belt forests of northwestern Caucasus.

Research tasks:

1. Evaluation of the confinement of the 2 epigeic species to different forest types in northwestern Caucasus.
2. Search for the most favorable habitats of *D. octaedra* and *D. attemsi* in the northwestern Caucasus forests.
3. Evaluation of distribution of the 2 epigeic earthworm species in northwestern Caucasus based on the analysis of the climatic parameters and height above sea level using the GIS modeling.

## 2. Materials and methods

### 2.1. Study area

The material was collected during expeditions in the spring-summer seasons, from 2014 to 2018, on the territory of northwestern Caucasus (Krasnodar Krai, the Republic of Adygea and the Karachay-Cherkess Republic) (Figure 1). The studies were conducted in the forest belt at altitudes of 42 to 1965 m above the sea level. Beech, deciduous, dark coniferous, coniferous-deciduous, and pine forests were predominantly surveyed. The earthworm counts were conducted at 1028 points on the northwestern Caucasus forest belt.

### 2.2. Species and biogeographical date

At each geographical location, 4 soil samples (sample size: 25 × 25 cm<sup>2</sup>, depth, up to 30 cm) were taken. The earthworms were counted separately in the trunks of the fallen trees,

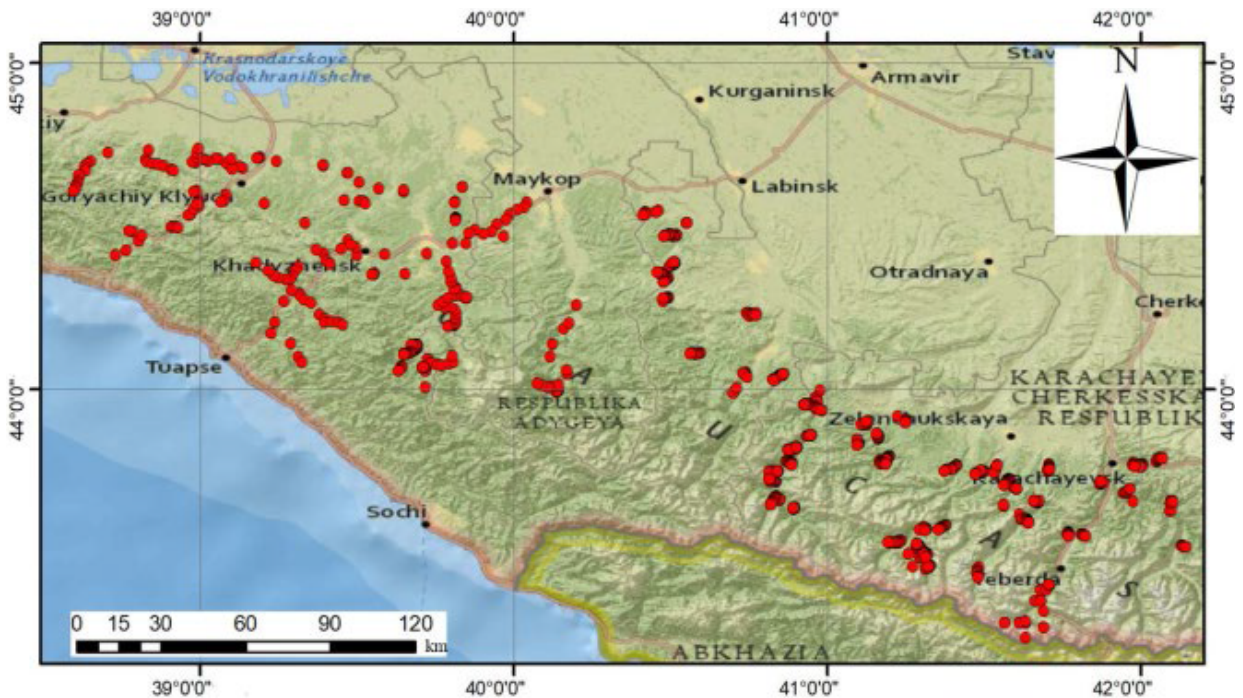


Figure 1. Locations of the earthworms of northwestern Caucasus.

with the deadwood fragments at decomposition stages 2, 3, and 4 (Shirokov et al., 2001; Spirin and 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. Since epigeic earthworms live in plant litter and deadwood, the plant litter depth was measured for the microsite volume calculation, while the stem length and diameter were measured for the microsite volume calculation in the deadwood (Geraskina, 2016b). The calculations were given in  $\text{dm}^3$  for comparison of the epigeic species amount in the litter and deadwood samples.

More than 4000 soil samples were taken in total and 900 deadwood fragments were examined. Moisture and acidity for each soil sample and deadwood fragment were determined using a portable field pH 300 meter.

The earthworms were fixed in 96% ethanol. Species composition was determined using Russian Cadastre, the earthworm diagnoses were based on those of Vsevolodova-Perel (1997), and the morphological descriptions of the variations in *D. attemsi* were based on those presented in the monographic study of Rota and Erseus (1997). The present paper included the materials of only 2 epigeic species, i.e. *D. octaedra* (Sav., 1826) and *D. attemsi* (Mich., 1902).

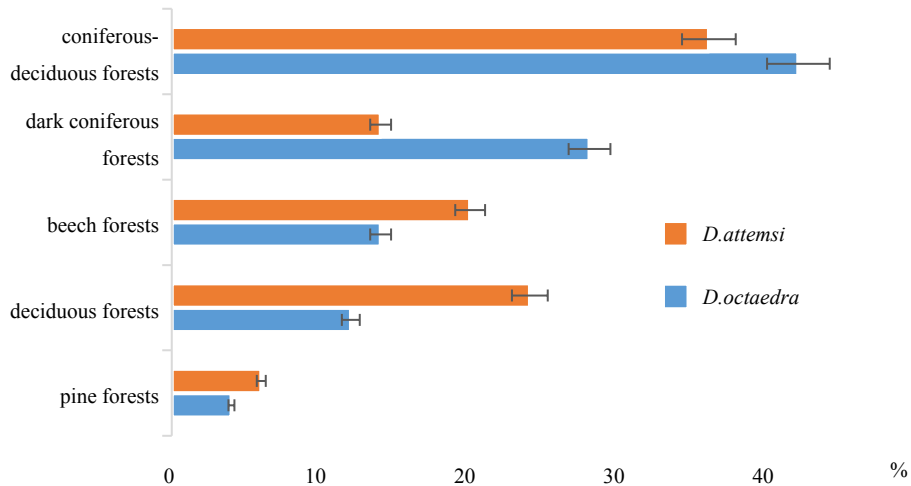
The maps of the potential habitats of the model tree species were created with Maxent 3.3.3k software (<http://www.cs.princeton.edu/~schapire/maxent/>). Using the color gradations, the obtained maps indicated the level of probability of finding a species at a particular point and determined the degree of influence of the environmental parameters (%) on the boundaries of their distribution, i.e. the contribution of each factor to the model construction. The maximum entropy method was used to determine the potential area of the model tree species. This method and its uses have been described in detail in a number of publications (Phillips et al., 2006; Phillips and Dudik, 2008; etc.). The essence of the method lies in using the points of the species finding for determination of the environment characteristics that turn out to be similar for all of the points of species detection. The use of additional (climatic) databases helped to isolate the specific environmental parameters, similar to the entire set of the analyzed points, and, on this basis, to identify a potential area suitable for the species distribution. Extrapolation of the probability of species finding in the analyzed area was conducted for this purpose. For the resulting model testing, 25% of the points were used. The sampling was carried out on the basis of the bootstrap approach. The number of repeated replications of the model was set to 20. The regularization multiplier was set to 2.0. The rest of the program settings were set to default. The cumulative format was chosen as the output format of the model values.

The quality of the models was estimated using the area under the curve (AUC) values, with the area under the ROC curve representing the proportion of true- and false-positively classified cases (receiver operating characteristics; Fawcett, 2006), and the omission rate characterizing false-negative cases (error of the second kind). The model quality was rated as excellent with AUC values of 0.9–1.0, good with values of 0.8–0.9, very bad with values of less than 0.6, and the model accuracy corresponded to a random choice at a value of 0.5 (Phillips et al., 2008). The visualization of the obtained GIS maps was conducted with DIVA-GIS 7.5.0 software ([www.diva-gis.org](http://www.diva-gis.org)) (Scheldeman and Zonnevels, 2010).

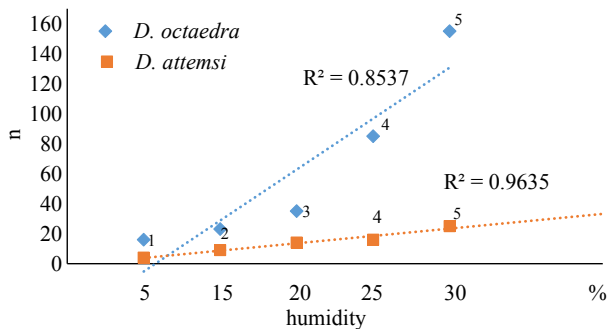
The following layers from the WorldClim climate base ([www.worldclim.org](http://www.worldclim.org)) were used in the modeling (minimum resolution: 5 arc/min or ~9 km per pixel), which allowed for interpolation of the observed data from 1950 to 2000. The climatic layers were: BIO1: average annual temperature; BIO2: average monthly temperature; BIO3: isothermality ( $\text{BIO2/BIO7} \times 100$ ); BIO4: temperature seasonality (standard deviation  $\times 100$ ); BIO5: maximal temperature in a warm month; BIO6: minimal temperature in a cold month; BIO7: annual amplitude temperature (b5-b6); BIO8: average temperature in the wettest quarter; BIO9: average temperature in the driest quarter; BIO10: average temperature in the warmest quarter; BIO11: average temperature in the coldest quarter; BIO12: amount of precipitation per year; BIO13: amount of precipitation in the wettest month; BIO14: amount of precipitation in the driest month; BIO15: precipitation seasonality (coefficient of variation); BIO16: amount of precipitation in the most humid quarter; BIO17: amount of precipitation in the driest quarter; BIO18: amount of precipitation in the warmest quarter; BIO19: amount of precipitation in the coldest quarter; and ALT: altitude above sea level.

### 3. Results

*D. octaedra* and *D. attemsi* inhabited all of the examined forest types: coniferous-deciduous, dark coniferous, beech, deciduous, and pine (Figure 2), and were found in both the litter and deadwood (Figure 3). The results of the occurrence of these species in the different forest types showed that both species most often inhabited coniferous-deciduous forests (Figure 2). The *D. octaedra* population density, taking into account both the plant litter and deadwood in the coniferous-deciduous forests, was 12.5 ind./ $\text{dm}^3$ , while for *D. attemsi* it was 10.1 ind./ $\text{dm}^3$ . The lowest density of these species was revealed in pine forests (0.2 ind./ $\text{dm}^3$  for *D. octaedra* and 0.1 ind./ $\text{dm}^3$  for *D. attemsi*). In the other forest types, these species had various distribution: *D. octaedra* was twice as abundant as *D. attemsi* in dark coniferous forests (8.2 ind./ $\text{dm}^3$ : for



**Figure 2.** Occurrence of earthworms in the samples (plant litter + deadwood) in the main forest types of northwestern Caucasus (n; coniferous-deciduous forests: 824, dark coniferous forests: 492, beech forests: 980, deciduous forests: 2275, and pine forests: 220).



**Figure 3.** Sampling frequency *D. attemsi* in the plant litter and deadwood in the main forest types of northwestern Caucasus.

*D. octaedra* and 4.0 ind./dm<sup>3</sup> for *D. attemsi*). *D. attemsi* inhabited both deciduous (6.0 ind./dm<sup>3</sup> for *D. attemsi* and 3.2 ind./dm<sup>3</sup> for *D. octaedra*) and beech forests more densely than *D. octaedra* (*D. octaedra*: 4.1 ind./dm<sup>3</sup>, *D. attemsi*: 5.4 ind./dm<sup>3</sup>).

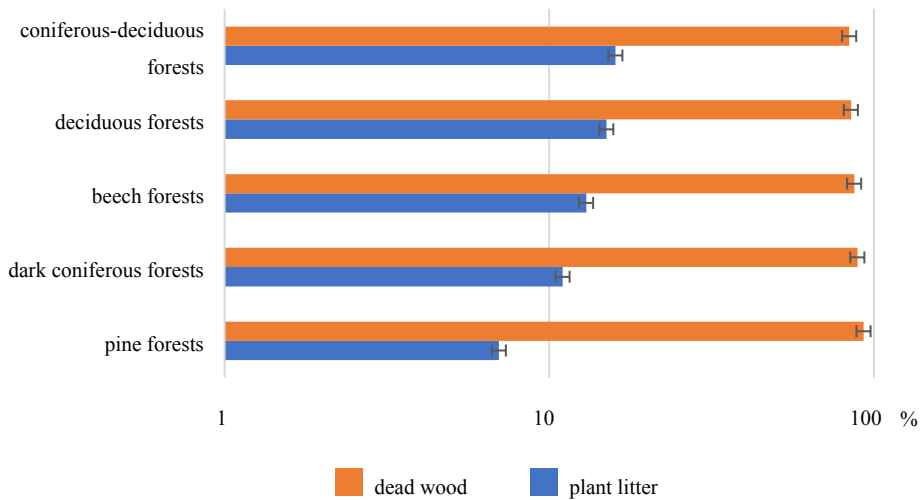
The distribution of these species according to humidity demonstrated that correlation with the moisture gradient was high for the 2 epigeic species and was statistically more significant for *D. attemsi* (Figure 4). No correlation was found in terms of litter acidity (the litter pH ranged from 5.5 in dark coniferous, pine, and coniferous-deciduous forests to 6.5 in beech and deciduous forests).

The distribution of the 2 epigeic species by microsites (plant litter and deadwood) demonstrated that *D. attemsi* predominantly inhabited the deadwood in all of the forest types (Figure 3). The highest abundance of *D. attemsi* in coniferous-deciduous forests was found in the deadwood of *Carpinus betulus* (10–15 ind./dm<sup>3</sup>); in deciduous forests, in the deadwood at decomposition stages 3 and 4 in *Acer*

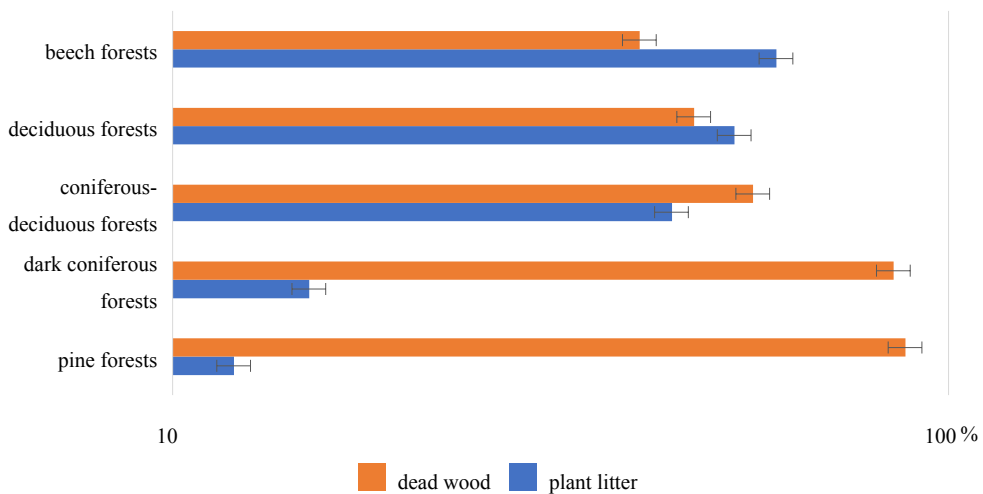
(8–11 ind./dm<sup>3</sup>); and in dark coniferous forests at stage 3 in the deadwood of *Abies nordmanniana* and stage 4 in the deadwood of *Picea orientalis* (10–12 ind./dm<sup>3</sup>). The abundance of *D. attemsi* in beech forests in the deadwood of *Fagus orientalis* was low (2–4 ind./dm<sup>3</sup>), but in the presence of *Quercus*, deadwood even at decomposition stage 2 was observed, where the amount of *D. attemsi* worms reached 20–30 ind./dm<sup>3</sup>. The amount of *D. attemsi* in the plant litter was minimally 0.05 ind./dm<sup>3</sup> in pine forests, it reached 0.5 ind./dm<sup>3</sup> in dark coniferous forests, and was the highest in coniferous-deciduous, beech, and deciduous forests, at 2–6 ind./dm<sup>3</sup>.

*D. octaedra*, in forests with well-moistened plant litter (coniferous-deciduous, beech, and deciduous forests), was found almost equally in both the plant litter and deadwood (Figure 5) at amounts of 4–12 ind./dm<sup>3</sup>. In drier forests (pine and dark coniferous forests) *D. octaedra* mainly inhabited the deadwood of *Pinus*, with density in the deadwood of 2–4 ind./dm<sup>3</sup> and 0.5–1.0 ind./dm<sup>3</sup> in the plant litter. The correlation between the occurrence of *D. octaedra* and the plant litter humidity was higher ( $R^2 = 0.89$ ) than that between the occurrence of *D. octaedra* and the deadwood humidity ( $R^2 = 0.76$ ).

The largest density of *D. octaedra* in dark coniferous forests was revealed at decomposition stage 3 in the deadwood of *Abies nordmanniana* and *Picea orientalis* (5–10 ind./dm<sup>3</sup>). In beech forests with *Quercus*, the abundance of *D. octaedra* in the deadwood was at decomposition stages 2 and 3, and reached 20 ind./dm<sup>3</sup>. *D. octaedra* often inhabited the deadwood of *Carpinus betulus* at decomposition stage 3 in coniferous-deciduous forests (8–10 ind./dm<sup>3</sup>), and the deadwood of *Acer* at decomposition stage 3 in deciduous forests (6–10 ind./dm<sup>3</sup>).



**Figure 4.** Correlation of the sampling frequency of earthworms *D. octaedra* and *D. attemsi* in the main forest types, depending on humidity (n: amount of samples). 1: pine forests, 2: dark coniferous forests, 3: coniferous-deciduous forests, 4: beech forests, and 5: deciduous forests. sss



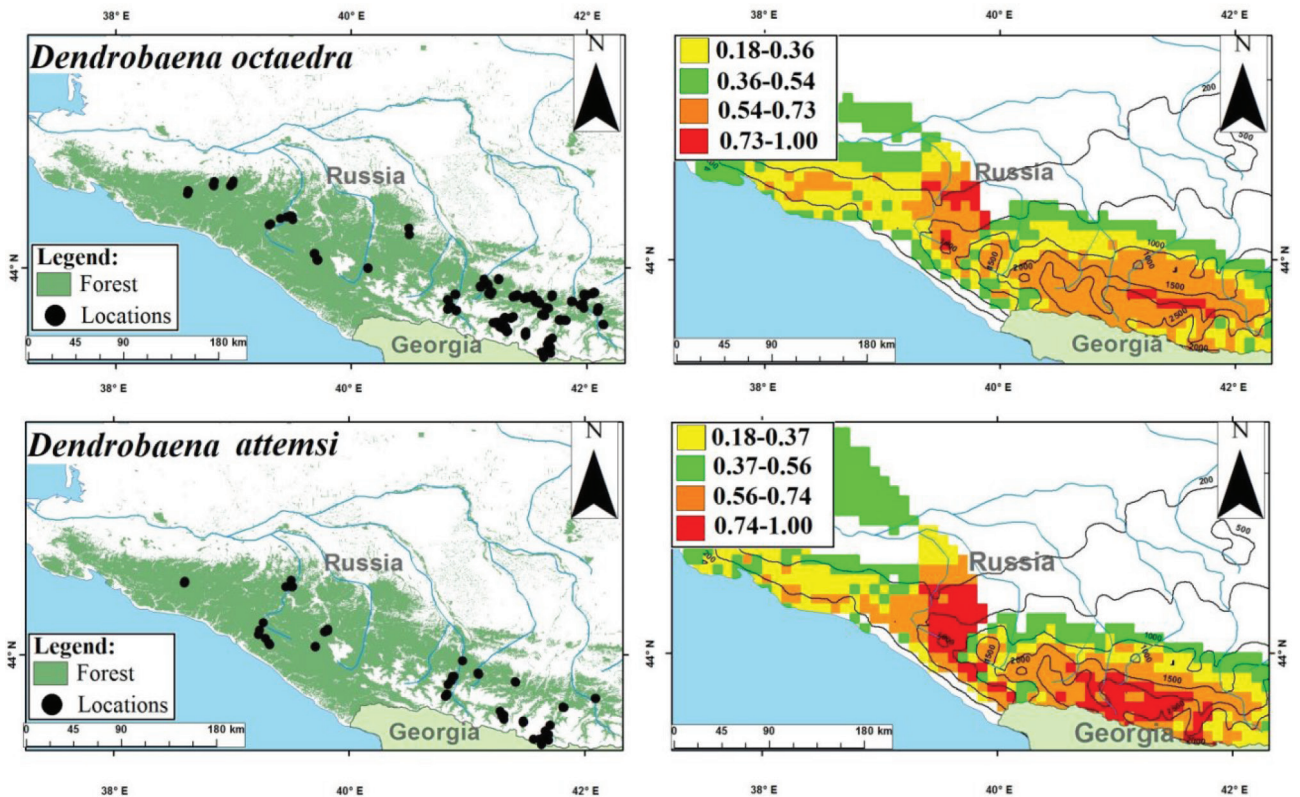
**Figure 5.** Sampling frequency *D. octaedra* in the plant litter and deadwood in the main forest types of northwestern Caucasus.

Maps of the potential distribution of the epigeic species of *D. octaedra* and *D. attemsi* were made based on the data of the climatic bases and height above sea level (Figure 6).

The spatial modeling results demonstrated that the current potential distributions of the 2 epigeic species generally coincided with each other (probability level of 56%–74%), but were much wider than the current real habitats, covering coniferous-deciduous and dark coniferous forests from the flat foothill landscapes to the highlands. The 2 species differed in their confinement to different altitudes. For *D. attemsi*, there was a high probability of habitat (over 74%) in the highlands of the central part of northwestern Caucasus, at an altitude range of 1500–2500 m above sea level, corresponding to the

modern distribution of dark coniferous forests (upstream of the Teberda, Aksaut, Bolshoi Zelenchuk, Urup, and Bolshaya Laba rivers). A high probability for the presence of *D. attemsi* occurred, also in the foothill areas of the Bolshaya Laba River valley, at an altitude of 200–500 m above sea level, where large massive coniferous-deciduous and dark coniferous forests are preserved. The most probable potential distribution in most mountainous territories of northwestern Caucasus for *D. octaedra* was demonstrated at an altitude range of 1000–1500 m above sea level (probability level of 56%–74%).

The analysis of the contribution of the climatic parameters and height above sea level to the construction of the GIS models of the modern distribution of *D. octaedra*



**Figure 6.** Real and potential distributions of *D. octaedra* and *D. attemsi* in northwestern 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 the model species and the contour isolines. The level of probability of finding a species at a specific point is indicated by the gradation of the colors and shades.

and *D. attemsi* (Table) demonstrated that the amount of precipitation in the driest month of the year (34.4%–36.3%) was the most important factor. A high contribution was made by such parameters as the height above sea level (10.1%–17.7%), isothermality (7.6%–11.7%), which is considered as the ratio of the average temperature to the annual amplitude of temperatures, and standard deviation of the temperatures (9.7%–12.1%).

#### 4. Discussion

Previous research on the lumbricofauna of northwestern Caucasus showed that epigeic species *D. octaedra* and *D. attemsi* inhabited practically all of the forest types (Rapoport, 2014; Rapoport and Tsepikova, 2015; Geraskina, Shevchenko, 2018). According to our data, these species were more numerous in coniferous-deciduous forests when compared not only to drier pine and dark coniferous forests, but even to well-hydrated deciduous forest communities. A number of studies have reported the advantage of mixed litter for different groups of saprophages, including earthworms (Sariyildiz et al., 2008; Sariyildiz and Küçük, 2008), as the slowly decomposable bedding of coniferous species, because it serves as a

favorable microsite for epigeic species of earthworms and the rapidly decomposable deciduous plants are an available source of nutrients (Sayad et al., 2012). Central Germany forest studies have demonstrated that the more diverse the forest stand is, the greater the biomass and the higher the functional diversity of the earthworms (Cesarz et al., 2007).

In the forests of the Bolshoy Zelenchuk River basin of northwestern Caucasus, Rapoport and Tsepikova (2015) demonstrated the replacement of *D. octaedra* to *D. attemsi* in pine, spruce, and small-leaved forests. According to those results, *D. octaedra* lives in spruce and beech forests, but *D. attemsi* was not found. Herein, throughout the entire northwestern Caucasus, it was shown that both species were found in different forest types, while in coniferous-deciduous forests, the number of *D. octaedra* and *D. attemsi* was approximately the same, *D. octaedra* was noticed more often in dark coniferous forests, *D. attemsi* likewise in deciduous and beech forests, and both species inhabited pine forests, but their numbers were very low. Moreover, cohabitation of the 2 species was observed in most types of forests in the territory of the Republic of Adygea (Rapoport, 2014).

**Table.** Percentage contribution of the climatic parameters to the potential distribution of earthworm species.

Species	ALT	BIO 3	BIO 4	BIO 5	BIO 7	BIO 8	BIO12	BIO 14	Other
<i>D. attemsi</i>	10.1	11.7	9.7	3.3	5.1	8.8	9.1	34.4	7.6
<i>D. octaedra</i>	17.7	7.6	12.1	5	6.7	2.4	6.8	36.3	5.5

**Note:** The parameter designation is listed in the Materials and methods section.

It is well-known that humidity is an important limiting factor for earthworms (Bouche, 1977; Lavelle, 1983; Lee, 1985), while humidity fluctuations on the forest floor can be a very strong factor during dry months of the year. Therefore, populations of epigeic species under such conditions are characterized by high mortality, which is partly offset by their high reproductive potential (Lavelle, 1988). It is also known that in old growth forests with a well-developed microhabitat structure, there are more possible microsites to avoid unfavorable conditions, and most of all, the presence of deadwood in the later stages of decomposition contributes to the survival of the epigeic earthworms on litter that is drying out (Perel, 1977; Goncharov et al., 2015; Geraskina, 2016b).

A detailed analysis of the deadwood and comparison of the amount of earthworms in the samples of deadwood and plant litter samples revealed a large number of *D. attemsi* finds in various types of forests. Generally, only plant litter and soil are examined in detail during soil-zoological studies, and especially for the study of the earthworms, the microsites of deadwood are not studied carefully. The study herein clearly demonstrates the role of deadwood in the forests of various types for epigeic species, especially for *D. attemsi*, which was mainly found in the deadwood of the forests; particularly where the plant litter was dried out during the summer (pine forests and dark coniferous forests). A high correlation with deadwood was also demonstrated for *D. octaedra*, but this species was equally likely to occur in both plant litter and deadwood with litter that was not drying out, whereas *D. attemsi* was more confined to deadwood, even in forests with litter that was not drying out (Figure 4). Therefore, it can be said that despite the fact that these 2 species had similar ecological preferences, they occupied different ecological niches in the forests and avoid competition, which was confirmed by our detailed study of various microsites in the forests of northwestern Caucasus.

The constructed maps of the current potential distribution of *D. attemsi* and *D. octaedra* also demonstrated a high probability of coexistence between the 2 species in the forest belt of northwestern Caucasus and their association with both the most common coniferous-deciduous forests and the less preserved dark coniferous forests. Both species showed a high connection with the

preserved bulk of dark coniferous forests in the Bolshaya Laba valley. The biotopic association of these species with the dark coniferous forests of northwestern Caucasus has been noted in other studies (Rapoport, 2014; Rapoport and Tsepikova, 2015; Geraskina, 2016a; Geraskina, 2018). *D. octaedra* was often the only species that would persist in a number of communities and northern dark coniferous forests, thanks to good resistance to extreme temperatures (Berman et al., 2001; Rasmussen, Holmstrup, 2002), high migration, and reproductive abilities (Zhukov, 2004), which also explained its widespread invasion into new areas of boreal forests (Addison, 2009). The modern potential distribution of *D. attemsi* interestingly demonstrated a high probability of survival at high altitudes in the highland part of northwestern Caucasus, which also corresponded to the distribution of dark coniferous forests (Gulisashvili et al., 1975). This was probably due to the fact that, according to the analysis of climatic parameters, the amount of precipitation in the driest month of the year makes the most significant contribution, which indirectly characterizes the likelihood of drying of the litter horizon and other microsites during the summer, being the most significant factor for epigeic earthworms, which are not capable of deep vertical migration or summer diapause under adverse conditions, like other groups of earth worms. This parameter limits the survival rate of epigeic earth worms in the summer. Other climatic parameters make far less contribution to the modeling of the ranges of the studied species of earthworms, including temperature, to which earthworms are also sensitive: isothermal and standard deviation of temperatures. As is known, the temperature factor is of great importance for earthworm distribution (Meshcheryakova and Berman, 2014).

Therefore, the analysis of the field distribution of *D. attemsi* and *D. octaedra* in different forest types in northwestern Caucasus revealed that there were more optimal conditions for the habitat of the 2 species in coniferous-deciduous forests. The least favorable conditions were revealed in pine forests, where the smallest amounts and occurrences of epigeic species were observed. These 2 species were distributed differently in the other forest types; the abundance and occurrence of *D. octaedra* were higher in dark coniferous forests, while



with *D. attemsi*, they were in deciduous and beech forests. Deadwood at decomposition stages 2 to 4 played an important role in the conservation of the populations of the 2 epigeic species, especially for *D. attemsi*, which dwelt mainly in decaying wood in all of the forest types. The modern potential distribution modeling demonstrated that the distributions of the 2 species were coincidental and confined to the spatial distribution of coniferous-deciduous and dark coniferous forests. The amount of precipitation in the driest month of the year largely reflected the ability of the worm to protect its population in extreme

conditions like the low humidity of the habitat and made the greatest contribution to distribution construction.

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